

RESEARCH ARTICLE SUMMARY

WILDLIFE DISEASE

Wildlife trade drives animal-to-human pathogen transmission over 40 years

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INTRODUCTION: The wildlife trade is an important form of human-animal interaction that affects around a quarter of all mammal species. Multiple trade-related activities, including harvesting, breeding, warehousing, transport, market placement, and end use, create opportunities for cross-species pathogen transmission. As such, the human-animal interactions occurring throughout wildlife trade networks can lead to infectious disease outbreaks in humans, including epidemics and pandemics with major socioeconomic impacts. Although several high-profile outbreaks, including the emergence of HIV, the 2014 West African Ebola epidemic, the 2003 mpox outbreak in North America, and the COVID-19 pandemic, have been linked to traded wildlife, the long-term impact of the wildlife trade in shaping pathogen exchange between humans and wild animals remains unclear.

RATIONALE: Research on the determinants of host-pathogen interactions has mostly focused on ecological and evolutionary drivers in the absence of human influence, and disease dynamics in the wildlife trade remain poorly studied. In theory, traded wildlife should be more likely to share pathogens with humans because frequent and close contact increases opportunities for cross-species transmission. Therefore, the longer and more intensely species are traded, the more pathogens they should share with humans. We empirically tested whether traded species are more likely to share pathogens with humans than nontraded species, how live-animal markets and illegal trade modify this risk, and whether time spent in trade predicts the number of zoonotic pathogens hosted by wild animal species.

RESULTS: Focusing on mammals, we showed that, among 2079 traded species, 41% share at least one pathogen with humans,

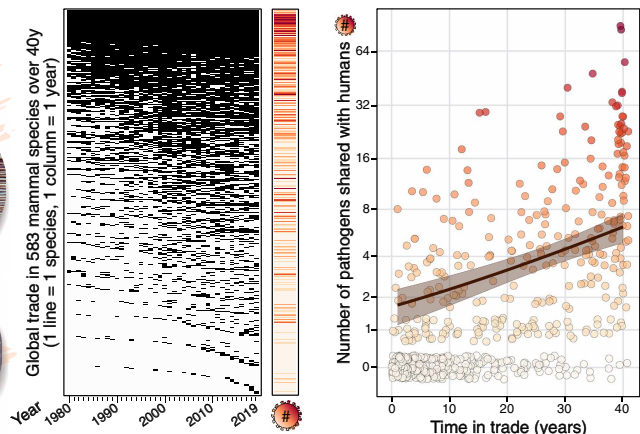
compared with 6.4% of nontraded species. Traded mammals are about 1.5-fold as likely to be zoonotic hosts, even after controlling for phylogeny, geography, research effort, synanthropy, and consumption by humans. Synanthropic species and those consumed as food are also more likely to share pathogens with humans, but these effects are weaker and partly mediated by trade and research effort. In addition, species traded live are more likely to share pathogens with humans, and illegally traded species share more pathogens with humans than those traded only legally. Finally, a temporal analysis of 583 mammal species listed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) over 40 years (1980–2019) shows that time in trade is a key predictor of zoonotic pathogen richness. On average, a wild mammal species shares one additional pathogen with humans for every 10 years it is present in the global wildlife trade.

CONCLUSION: Wildlife trade is a major driver of animal-to-human pathogen transmission. Trade status strongly increases the probability that a mammal is a zoonotic host, and cumulative time in trade predicts how many pathogens it shares with humans. Live-animal markets and illegal trade further amplify these risks. These findings highlight that cross-species pathogen transmission is an inherent consequence of diverse uses of wildlife by humans and underscore the need to strengthen biosurveillance and integrate zoonotic risk considerations into wildlife trade regulations to help prevent future pandemics. □

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Wildlife trade drives zoonotic pathogen transmission over 40 years.

By analyzing 40 years of international trade in wild mammal species, we show that the number of zoonotic pathogens hosted by a wildlife species increases with the number of years it has been present in trade: On average, a species shares an additional pathogen with humans for every decade it has been present in trade.



WILDLIFE DISEASE

Wildlife trade drives animal-to-human pathogen transmission over 40 years

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The wildlife trade affects a quarter of terrestrial vertebrates and creates opportunities for cross-species pathogen transmission, but its precise role in shaping animal-human pathogen exchange remains unclear. In our analysis of 40 years of global wildlife trade data, we show that traded mammals are 1.5-fold as likely to share pathogens with humans as nontraded mammals, and that illegal and live-animal trade further exacerbate pathogen sharing. Time spent in trade predicts the number of zoonotic pathogens that a wildlife species hosts. On average, a species shares an additional pathogen with humans for every 10 years it is traded.

Interactions between humans and wild animals promote the transmission of parasites and pathogens (1, 2) and can lead to infectious disease outbreaks (3, 4), including epidemics and pandemics that cause large numbers of fatalities and long-lasting socioeconomic harm (1, 5, 6). Understanding what shapes the spread of zoonotic (i.e., transmissible to humans) pathogens (including parasites) across species is a public health priority and is important for understanding disease ecology (1, 7).

The wildlife trade is one form of human-animal interaction that creates opportunities for animal-to-human pathogen spillover. This can happen across all stages of trade, including harvesting, breeding, transport, stockpiling, warehousing, retail, consumption, and companionship (1, 8–12). For instance, a person buying three Finlayson's (variable) squirrels (*Callosciurus finlaysonii*) in a Laotian wildlife market has been estimated to have an 83% chance of getting at least one leptospirosis-infected individual (11). The wildlife trade is also a common source of disease outbreaks in humans (8, 13), including the COVID-19 pandemic (14, 15). Although the hunting and consumption of wild meat has been linked to major epidemics such as the HIV pandemic (16) and some Ebola outbreaks (17), various types of wildlife use and trade can also cause human infectious disease outbreaks (8, 13). For example, anthrax infections have been linked to hides sourced from wildlife used for drums traded among musicians (18), and the trade in exotic pets has been implicated in multiple outbreak events, including the 2003 mpox outbreak in North America linked to prairie dogs (*Cynomys ludovicianus*) (19) and recent *Salmonella* hospitalizations traced back to bearded dragons (*Pogona vitticeps*) (20).

Recent research on the determinants of host-pathogen interactions has mostly focused on environmental, life history, ecological, and evolutionary drivers (4, 9, 21–28). However, disease dynamics in the wildlife trade, including transmission to and from humans, remain poorly studied (1, 29, 30), and previous empirical work has only focused on quantifying the number of zoonotic pathogens occurring in traded

animals (31–34). In theory, traded wildlife should be more likely to share pathogens with humans because frequent and close contact with humans increases opportunities for pathogen transmission (1, 2). This can occur either through zoonotic spillover, where pathogens from wildlife infect humans (35), or through reverse zoonosis (or anthroponosis), where pathogens are transmitted from humans back to wildlife [e.g., white-tailed deer contracting severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2)] (2, 36). Moreover, the more frequently species are traded, the more pathogens they should share with humans.

Here, we investigated links between the global wildlife trade and pathogen sharing between humans and wildlife while accounting for potential biases and the influence of other anthropogenic factors. We focused our analysis on mammals because many human emerging infectious diseases originate in them (26, 37) and because their pathogens have been studied in substantially more detail than any other vertebrate clade (29, 38, 39). Moreover, a quarter of all mammal species are involved in the global wildlife trade, either as living animals (e.g., biomedical research and exotic pets) or as products (e.g., the fur industry and traditional medicine) (40, 41). As a foundation for our analyses, we used three extensive wildlife trade datasets to assess the occurrence of mammal species in the legal and illegal global wildlife trade: the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (42), the Law Enforcement Management Information System (LEMIS) (43, 44), and the Dataset of Seized Wildlife and their intended uses (DSW) (45). The CITES trade database documents the legal international wildlife trade in live animals and animal products. It is global in scale and spans five decades (1975 to present), although it only contains records for CITES-listed species (~13% of all mammal species) (42, 46). The LEMIS trade database compiles records of live animals and animal products imported into the US between 2000 and 2022 (43, 44, 47). Although LEMIS is limited to US importations and covers a shorter timespan than the CITES trade database, it includes all mammal species and thus provides valuable information on the trade in species not recorded by CITES. Therefore, we used both CITES and LEMIS to assess the taxonomic extent of the legal global wildlife trade (i.e., all illegal trade records reported in these databases were excluded). The DSW (45) is the most comprehensive compilation of seizures of illegally traded wildlife currently available. It collates illegal trade records between 2010 and 2019 from three databases: CITES, LEMIS, and Trade Records Analysis of Flora and Fauna in Commerce (TRAFFIC) (48). Using the CITES, LEMIS, and DSW data, we built a comprehensive picture of wild mammal species occurring in the legal and illegal global wildlife trade, including exchanges of both live animals and animal products (fig. S1). Next, we assessed which wild mammal species are known to share pathogens with humans using the CLOVER database, the largest hand-curated resource of mammal-pathogen associations to date (49). CLOVER documents >190,000 associations between mammals and viral, bacterial, fungal, helminth, and protozoan pathogens and parasites [see (50) and table S1 for a more detailed description].

Combining the mammal trade and mammal-pathogen association datasets, we tested (i) whether traded mammal species are more likely to share pathogens with humans compared with nontraded mammals, (ii) whether illegal trade and live-animal markets increase transmission risk, and (iii) whether the number of years that a mammal species has spent in the global wildlife trade predicts the number of pathogens that it shares with humans. All analyses accounted for potential biases, including phylogenetic nonindependence, geographic variation, and uneven research effort, as well as other anthropogenic factors that could mediate the link between the wildlife trade and human-wildlife pathogen sharing. Because evolutionary relatedness can influence pathogen sharing (4, 26, 51), we controlled for phylogenetic nonindependence among mammal species using 10 phylogenetic eigenvectors as covariates in all of our models [(50) and fig. S2]. We included the species' biogeographic realm of origin as a random intercept to

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account for spatial variation in zoonotic pathogen distribution (7, 52, 53). Because pathogens are more likely to be detected in well-studied species (24, 54), we incorporated an index of research effort as a covariate [(50) and Fig. 1A]. We also accounted for wild mammals consumed as food (i.e., wild meat) because they are more likely to be traded and to transmit pathogens to humans (55, 56). Finally, we accounted for the potential influence of synanthropy (tending to live in or near human-modified environments) on the link between zoonotic pathogens and the wildlife trade. This effect could exist because synanthropic species are more likely to share pathogens with humans because of their frequent contact with humans or domesticated species (9, 24, 25, 57) and to occur in the wildlife trade because they are easier to harvest than species found only in remote areas (13, 58, 59). We tested the robustness of our findings by running sensitivity analyses on the wildlife trade and host-pathogen association datasets (figs. S3 to S5).

Results

Traded mammals are more likely to share pathogens with humans

Among 2079 traded mammal species, 41% shared at least one pathogen with humans compared with only 6.4% of nontraded mammals (Fig. 1, A to C). Using a binomial model, we showed that traded mammals are 1.5-fold as likely to share pathogens with humans ($P < 0.0001$; Fig. 1D; see table S4 for detailed statistics and table S5 and fig. S3 for sensitivity analyses). The model indicates that synanthropic species are 1.2-fold as likely to share pathogens with humans ($P < 0.0001$; Fig. 1D), whereas species used as wild meat show a weaker, marginal association (1.1-fold, $P = 0.052$; Fig. 1D). To disentangle direct and indirect relationships between trade and zoonotic host status, we used a piecewise structural equation model linking trade, synanthropy, wild meat use, research effort, and zoonotic status (Fig. 1E). The structural equation model confirms a strong, direct positive effect of trade on zoonotic host status [standardized effect (Std. Eff.) = 0.15, $P < 0.0001$] and smaller direct

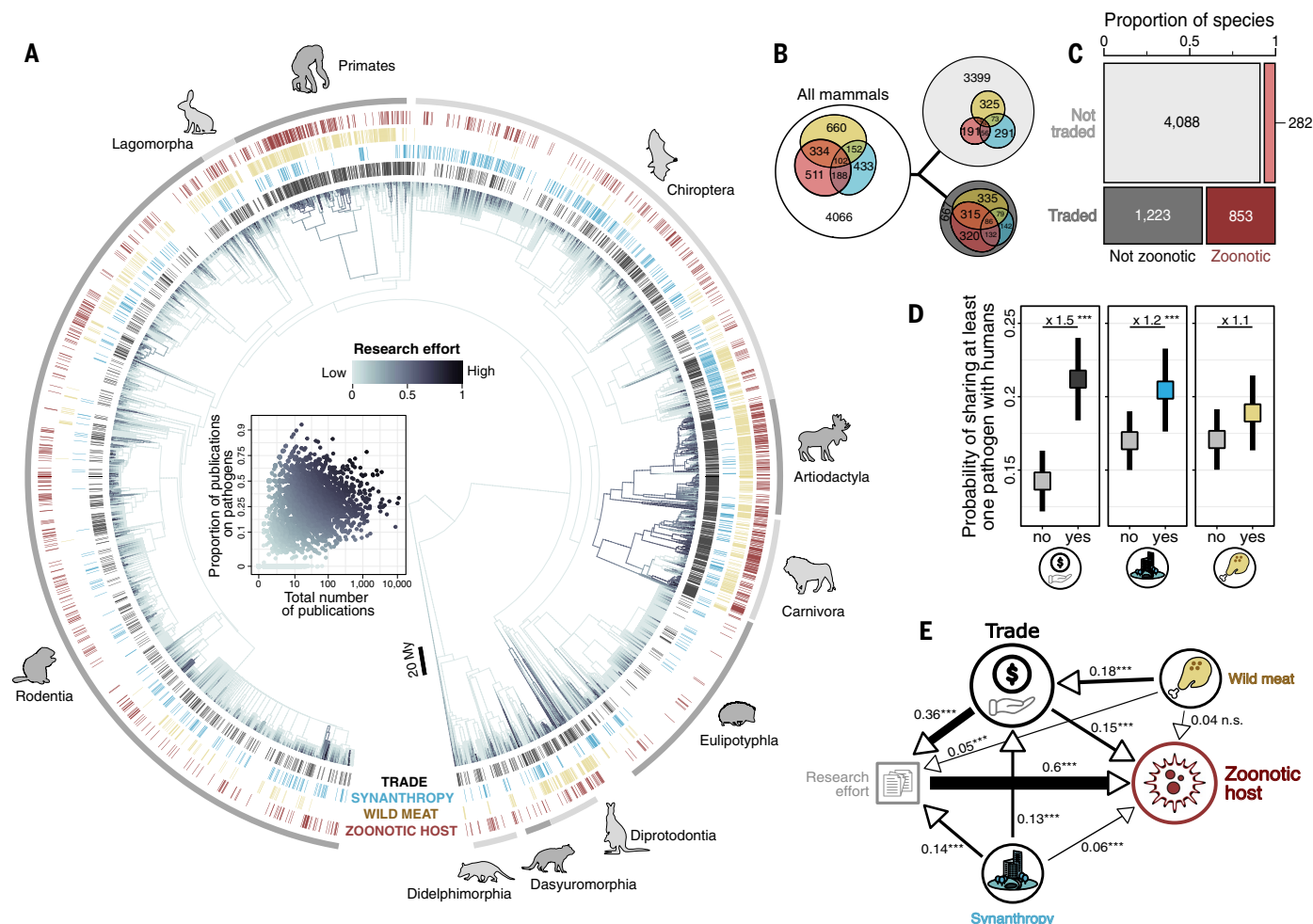


Fig. 1. The probability of sharing pathogens with humans is higher in traded species. (A) Distribution of traded, synanthropic, consumed (wild meat), and zoonotic host (i.e., those known to share at least one pathogen with humans) species among extant wild mammals (6446 of the 6456 species shown in the phylogram). The color of the branches represents the research effort index used to account for knowledge bias in statistical analyses (see inserted plot). The 10 mammalian orders with the greatest species richness are indicated. (B) Overlap among synanthropic (blue), wild meat (yellow), and zoonotic host (red) species for all mammals (left Euler plot) and species traded or not (right Euler plots). (C) Proportions of zoonotic host species (red) among traded (dark colors) and nontraded (light colors) mammals. The number of species in each group is indicated. (D) Average effects (estimate \pm 95% CI) of trade, synanthropy, and wild meat usage on the probability of sharing pathogens with humans with their respective marginal risk ratio and effect significance level (binomial generalized linear mixed model; *** $P < 0.001$). (E) Structural equation model showing the strength and significance of hypothesized causal relationships among trade, synanthropy, meat usage, research effort, and zoonotic host status in wild mammals. Black arrows indicate positive links between variables. Numbers along arrows are standardized structural equation model estimates (n.s., $P > 0.05$; *** $P < 0.001$). The width of each arrow is proportional to these estimates. Phylogenetic eigenvectors are not represented for readability.

effects of synanthropy (Std. Eff. = 0.06, $P < 0.0001$) and wild meat use (Std. Eff. = 0.04, $P = 0.05$). Beyond its direct influence, trade also affects zoonotic status indirectly through research effort (Std. Eff. = 0.22, for a total effect of 0.37; Fig. 1E). Synanthropy and wild meat use have smaller total effects on zoonotic host status (0.16 and 0.13, respectively) that is mainly mediated by trade and research effort (Fig. 1E and table S6). Overall, mammals present in the wildlife trade are substantially more likely to share at least one pathogen with humans, and this association is partially mediated by greater research attention and reinforced by synanthropy and use as wild meat. Even after accounting for research effort, synanthropy, and wild meat use, trade remains the dominant predictor of pathogen sharing with humans, consistent with increased opportunities for zoonotic transmission from traded species.

Role of live-animal markets and illegal trade

Although simple presence in trade emerges as a strong predictor of zoonotic host status, wildlife trade is a complex, multidimensional phenomenon encompassing both legal and illegal channels and different market types, particularly live-animal and animal product markets (46, 47, 60). These dimensions are likely to affect zoonotic transmission risk: Illegal trade may pose higher risks because hygiene protocols and veterinary inspections are often absent (31, 61), and the live-animal trade is plausibly riskier than the trade in products because live hosts are more likely to carry viable pathogens and remain infectious for longer periods (33, 62).

Expanding our previous model to account for whether mammal species are found in live-animal markets or illegal trade substantially improved model fit [change in Akaike information criterion (Δ AIC) = 26, likelihood ratio test $P < 0.0001$]. Even after controlling for the effect of the overall trade status (marginal effect = 1.36, $P < 0.0001$; Fig. 2), species traded alive were 1.34-fold as likely to share pathogens with humans ($P < 0.0001$; Fig. 2B), whereas species involved in illegal trade were not (marginal effect = 1.11, $P = 0.13$; Fig. 2C; see table S7 for detailed statistics and fig. S4 for sensitivity analyses). These results support the idea that live-animal markets represent a riskier interface (31), but this increased risk remains moderate and is not greater than the risk associated with being traded in general (table S7). We found no evidence for a strong effect of illegal trade on zoonotic transmission risk (but see Fig. 3). These findings suggest that cross-species

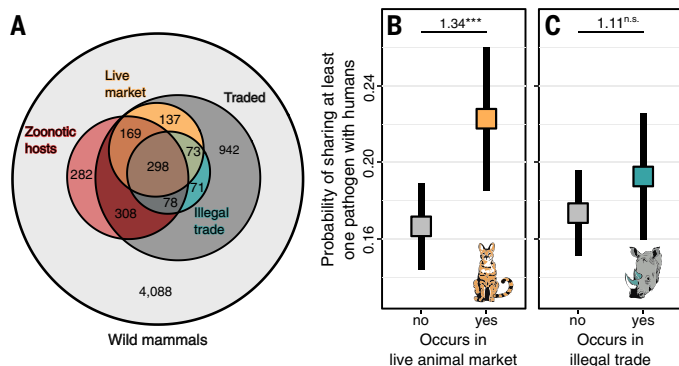


Fig. 2. Mammal species found in live-animal markets are more likely to share at least one pathogen with humans. (A) Overlap between species that are found in live-animal markets or illegal trade channels and zoonotic host species. Note that 95% of species found in live-animal markets and in illegal trade are also traded as products and legally (respectively). (B and C) Average effects (estimate \pm 95% CI) of species presence in live-animal markets and in illegal trade on the probability of sharing at least one pathogen with humans, with their respective marginal risk ratio and effect significance levels (binomial generalized linear mixed models; n.s., $P > 0.05$, *** $P < 0.0001$). [Illustrations of serval and rhinoceros head by P. Gippet-Vinard]

pathogen transmission is an inherent risk of wildlife trade and that focusing solely on one aspect of trade is unlikely to efficiently prevent outbreaks (63).

Time in trade predicts the number of pathogens shared with humans

Other underexplored attributes of trade likely contribute to cross-species pathogen transmission. In particular, the history of trade dynamics, which can vary greatly among species (64, 65), represents the cumulative set of opportunities for cross-species transmission. Therefore, species that have been traded for longer should host a greater number of zoonotic pathogens. To test this hypothesis, we performed a temporal analysis of the global trade in wild mammals over the past 40 years (1980 to 2019) using the CITES trade database, the only long-term longitudinal dataset of the global wildlife trade (42). We analyzed >236,000 trade records for 583 mammal species that have been traded at least once between 1980 and 2019 [among species listed in CITES Appendices I or II (50)] and calculated the number of years with recorded trade per species (hereafter, “time in trade”; Fig. 3A). Using a negative-binomial model, we then tested whether this variable predicted the number of pathogens that wild mammals share with humans while accounting for, as in previous analyses, phylogeny, geography, uneven research effort, synanthropic status, wild meat use, and species presence in live-animal markets and illegal trade (Fig. 3A).

As expected, we found that time in trade increased the number of pathogens shared with humans [Std. Eff. = 1.55, 95% confidence interval (95% CI) = 1.34 to 1.80; $P < 0.0001$; Fig. 3, B and C; see (50), table S8, and fig. S5 for sensitivity analysis]. Using this statistical relationship, we estimated that, on average over the period considered, a wild mammal species shared one additional pathogen with humans for every 10 years of presence in trade [mean = 9.9, 95% CI = 9.3 to 10.9; see equation 4 in (50) for calculation details]. This finding implies that pathogens hosted by traded species that currently do not infect humans are more likely to do so in the near future compared with those hosted by nontraded species. Furthermore, because new species are expected to enter the global wildlife trade (40), additional wildlife pathogens will gain opportunities to infect humans, thereby increasing the risk of future zoonotic disease outbreaks, potentially including epidemics and pandemics of new pathogens. These results exemplify the dynamic nature of human-wildlife pathogen interaction networks and parallel the positive correlation observed between time since domestication and the number of pathogens shared with humans in domesticated mammals (66). These analogous trends underscore the importance of sustained, close physical contact between animals and humans in promoting cross-species pathogen transmission and in shaping contemporary host-pathogen associations.

Consistent with our previous findings, our model also showed that among traded mammals, species found in live-animal markets share on average 1.5-fold more pathogens with humans than those traded solely as products ($P = 0.013$; Fig. 3E and table S8). In addition, and in slight contrast to our previous general analysis focusing on zoonotic host status, we found that species present in illegal trade shared 1.4-fold more pathogens with humans than those traded exclusively through legal channels ($P = 0.01$; Fig. 3D and table S8). These patterns align with the hypothesis that illegal trade and live-animal markets facilitate cross-species pathogen transmission, although their effects are weaker and less robust than the effects of time spent in trade (Fig. 3, B to E; see fig. S5 for sensitivity analyses). Overall, these results support the view that illegal trade and live-animal markets constitute higher-risk interfaces for pathogen spillover (31, 61, 62) but also highlight that trade frequency is a stronger predictor of zoonotic pathogen richness.

Discussion

Although correlational approaches such as ours cannot fully disentangle the precise mechanisms and directionality of pathogen transmission in the wildlife trade, animal-to-human transmission is the

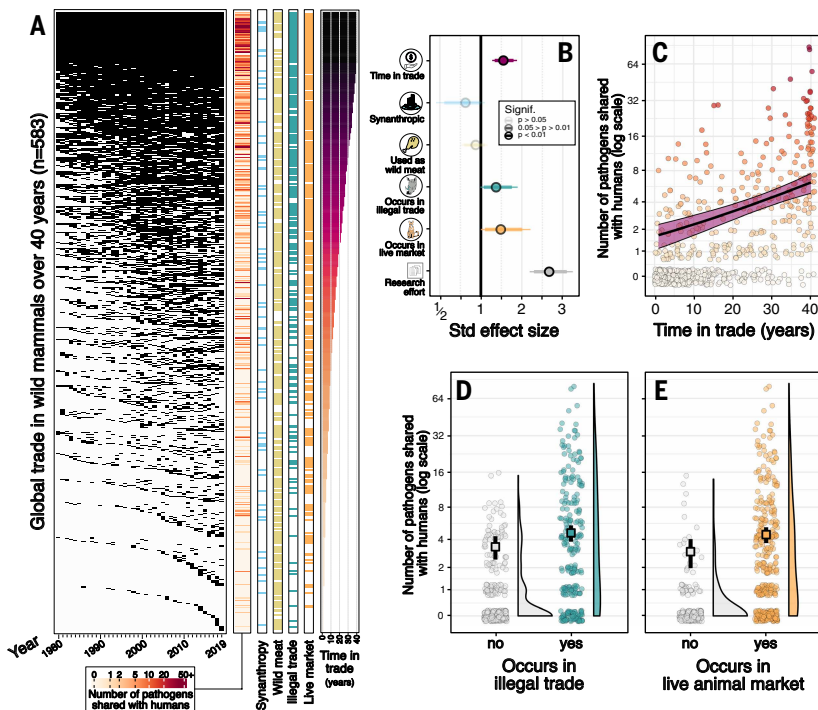


Fig. 3. Frequently traded species share more pathogens with humans. (A) Left, barcode plot representing mammal species occurrence in trade in the past 40 years. Each line is a mammal species that has been traded at least once between 1980 and 2019 ($n = 583$). Each column is a year (black cells indicate trade). Lines (i.e., species) are ordered by zoonotic host status and time in trade (and time since first trade event). (B) Standardized effect sizes (estimate \pm 95% CI and 99% CI) of main predictors (phylogenetic eigen vectors are not displayed) estimated using a negative-binomial mixed model. The x axis has been modified to allow an intuitive and undistorted comparison of positive and negative effects. Phylogenetic eigenvectors are not represented for readability. (C) Effect of time in trade on the number of pathogens that traded mammals share with humans. Each dot is a traded mammal species; dot color reflects the number of pathogens shared with humans. Dots are jittered to improve readability. The line and ribbon represent the average effect (slope \pm 95% CI) estimated by the model. (D and E) Effect of species presence in the illegal wildlife trade (D) and in live-animal markets (E) on the number of pathogens shared with humans (negative-binomial generalized linear mixed model). Squares are average model predictions (estimate \pm 95% CI). Circles are mammal species, and the accompanying density plots represent their distribution along the y axis.

most likely driver of trade-related pathogen exchange given the asymmetry of human-animal interactions (e.g., humans regularly consume wildlife, but the opposite is extremely rare) (2) and because wildlife frequently act as a source of pathogens for humans, whereas the opposite is less common (67). However, more granular aspects of trade most likely play a complex role in cross-species pathogen transmission. For example, keeping multiple species in the same locations (e.g., breeding facilities or wildlife markets) may promote interspecific pathogen transmission (15, 68), whereas adequate sanitary practices (e.g., masking) might limit it (69, 70). Building a more detailed understanding of cross-species pathogen transmission dynamics will require more precise data on the temporal dynamics of cross-species transmission (27), potentially through the use of genomic tools capable of tracing pathogen flow between species (16, 71–74) and across ecological interfaces [e.g., *Mycobacterium bovis* transmission between wildlife and livestock in South Africa (75)]. Expanding genomic surveillance in wild, captive, and domesticated animal populations (74, 76–78), together with museomics [the study of genomic data from historical museum specimens (79, 80)], could further reveal when and how pathogens infected wild and captive animals in recent decades and centuries (81–83). Such data will be essential for evaluating whether traded species act as reservoirs with a high risk of pathogen transmission,

common but dead-end hosts with low transmission risk, or anecdotal hosts (84). This knowledge can help to identify high-risk species and will be key to refining trade regulations because blanket bans may dilute control efforts or even backfire if trade is diverted to illegal channels (85).

Our study focused on species traded at a global scale and does not capture local but widespread wildlife markets, such as regional exotic pet markets (86, 87). These types of wildlife trade likely influence cross-species pathogen transmission differently from international trade because they often follow distinct spatial patterns, have longer histories, and involve different handling practices (87–89). Moreover, wildlife trade practices vary across social and cultural contexts, reflecting differences among societies, socioeconomic groups, or genders (69, 90–93). Integrating these local and social dimensions will require stronger national and international capacity to survey, compile, and share information at all stages of the wildlife trade supply chain, including traded species, trade purposes, and pathogen prevalence—data that currently remain fragmented and geographically uneven (11, 94–97). Strengthening this capacity is essential to understanding how human behavior shapes pathogen transmission through trade and to identify the human populations most at risk.

Conclusions

Overall, our findings underscore the urgent need to improve biosurveillance of traded animals and animal products for pathogens and to assess their potential for transmission to humans (10, 11, 98, 99). The COVID-19 pandemic sparked a thorough reevaluation of current wildlife trade regulations among policy-makers, exposing critical gaps in our ability to monitor and limit disease outbreaks linked to exploited and traded species (100). Currently, the primary multilateral agreement regulating the international wildlife trade, CITES, focuses exclusively on preventing species extinction caused by overexploitation of natural populations (101). Our findings offer specific and new implications for ensuring the effectiveness of upcoming regulations aimed at pandemic prevention, including potential reforms to CITES (102), the World Organization for Animal Health (WOAH)–CITES collaborative agreement (103), and obligations created under Articles 4 and 5 of the recently adopted World Health Organization (WHO) Pandemic Agreement (104). Our finding that wild animals share, on average, one additional pathogen with humans for every decade of presence in the global wildlife trade emphasizes that mitigation of future zoonotic pathogen emergence will require reducing the volume of animals in the wildlife trade. This includes species that currently pose a risk to human health and those that might soon and will involve taking actions to reduce high-risk trade, which will have long-term benefits over the coming century.

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Figs. S1 to S5; Tables S1 to S8; References (105–136); MDAR Reproducibility Checklist

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Wildlife trade drives animal-to-human pathogen transmission over 40 years

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Editor's summary

The closer and longer the contact between species, the higher the chances of transmission of pathogens. This rule of thumb applies to human-to-human contacts as well as contacts with other species. Gippet *et al.* examined trade data for wildlife species from the past 40 years and showed that the longer a species had been legally traded, the greater the likelihood that humans and the trade species will share some sort of pathogen (virus, bacterium, fungus, or parasite). The authors estimate that traded wildlife species share one additional pathogen with humans for every decade in the global wildlife market. —Caroline Ash

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