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Poison Frogs Traded and Maintained by U.S. Private Breeders

Wildlife trade and the collection of wild animals for pets are contributing to the global loss of biodiversity (Bush et al. 2014; Scheffers et al. 2019; Morton et al. 2021). Most studies on the impacts of the pet trade focus on birds, reptiles, and fish, but there is also a sizeable market for amphibians (Carpenter et al. 2014). Amphibian trade has been linked to overexploitation of wild populations, invasive species introductions, and the spread of infectious diseases (Rowley et al. 2016; Wombwell et al. 2016; Lockwood et al. 2019), but there could also be conservation benefits. For example, consumer demand for threatened species can generate funds for their conservation through biocommerce programs (Yeager et al. 2020) and harvesting wild amphibians for the pet trade could contribute to sustainable local livelihood strategies in biodiverse developing countries (Robinson et al. 2018). Considering amphibians are one of the most threatened vertebrate groups, with nearly 20% of all species on the brink of extinction (Ceballos et al. 2020), understanding trade dynamics of widely kept species is necessary for identifying threats and informing policy, especially when weighing the costs and benefits of the pet trade to both people and the environment.

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Of all amphibians, poison frogs (superfamily Dendrobatoidea) are some of the most popular to keep in captivity because of their attractive aposematic coloration and diurnal behavior (Mohanty and Measey 2019). Aquarium enthusiasts in Germany and the Netherlands pioneered the poison frog hobby during the early 1970s (e.g., Polder 1973; Broodman 1974; Zimmermann 1974), with the first frogs commercially available alongside exports of tropical fish from South America. English language literature describing poison frog captive care began appearing in the mid-1980s with the rise of the pet reptile industry (e.g., Ensman 1985; Zimmermann 1986). In 1987, growing demand and concern that overcollection could deplete wild populations led the family Dendrobatidae to be added to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Gorzula 1996), though barely 100 people in the U.S. were recorded keeping poison frogs at that time (Bertram 1988). Today, an estimated 50,000–100,000 people in the U.S. keep poison frogs (Z. Brinks, pers. comm), with large numbers bred domestically to meet demand. At the same time, private collectors in the U.S. and Europe widely acknowledge the founding stock of many commonly kept poison frogs originated through illicit means (Pepper et al. 2007). By some estimates the illegal trade makes up 10% of poison frog trade volume in Europe (Auliya et al. 2016). In the case of the Critically Endangered Lehmann's Poison Frog (*Oophaga lehmanni*), overexploitation has been linked to reduced genetic diversity in wild populations, with ca. 81,000 individuals extracted over the last four decades, leading to population declines and extirpation of the population at the type locality (Betancourth-Cundar et al. 2020).

Increasing awareness about the negative impacts of harvesting wildlife for the pet trade has led to a growing push to supply consumers with animals from sustainable sources (Pasmans et al. 2017; Yeager et al. 2020). Poison frog breeding ventures have been developed in Colombia, Ecuador, and Peru, which aim to curb illegal trade and, in some cases, fund habitat protection with their profits (Tapley et al. 2011; Sinovas and Price 2015). However, illicit trade could undermine such sustainable breeding operations. Indeed, the criteria needed for wildlife farming to have conservation benefits often are not met owing to ongoing illegal trade and wildlife poaching (Tensen 2016). Ranching and breeding programs supplying the international pet trade also sometimes are used to launder wild-caught animals as captive-bred (Bulte and Damania 2005; Lyons and Natusch 2011; Robinson et al. 2015). Additionally, high-value species of poison frog have been documented entering the trade illegally ahead of legal imports (Pepper et al. 2007), filling consumer demand with smuggled frogs and jeopardizing the viability of breeding operations in range countries. Considered altogether, the negative effects of the trade could outweigh possible conservation benefits depending on the scale and scope of illicit activity.

Despite the size of the poison-frog hobby today, there are few records of the frogs maintained in private collections and their origins. Discrepancies in CITES records related to the illegal trade obscure frog sources further, with wild animals laundered through Europe or Asia and then imported to the U.S. as captive-bred (Nijman and Shepherd 2010). Furthermore, some species are polymorphic, with private collectors managing breeding groups to represent distinct naturally occurring geographic color morphs. In some cases, color variants appearing in U.S. collections are known to occur only in countries that have not allowed their export. Thus, species exported from a native country but with a phenotype matching those known from a different country make it challenging to identify the true level of illicit activity when wildlife trade is monitored mainly at the species or genus level. The purpose of this article is to document the poison frogs maintained and bred in U.S. collections, determine the ways they initially entered the trade, and examine how the origins and sources of new poison frogs have changed over the last thirty years.

Materials and Methods

The data used to summarize poison frog trade included: 1) primary sources such as social media group posts, internet forums, printed literature, and unstructured interviews with private breeders/dealers, 2) the CITES trade database, 3) the IUCN Red List, and 4) the U.S. Fish and Wildlife Service (USFWS) Law Enforcement Management Information System (LEMIS). To compile a list of the different poison frogs in captivity, I relied first on personal knowledge and recorded familiar species and color morphs. I then added to the list by searching internet forums and social media groups, noting the species and color morphs traded as well as when they first began appearing online. The Way Back Machine (Internet Archive 2021) was used to document poison

Table 1. All poison frogs (superfamily Dendrobatoidea) maintained and bred by U.S. private breeders during 1990–2020 and their current IUCN Red List category. "Morphs" is the number of discrete captive populations collectors were intentionally breeding separate from others, usually corresponding to a wild phenotype and/or a particular import from a known source. "Currently kept?" indicates if there was evidence a species was in a U.S. collection in 2015–2020.

Taxon	Morphs	Red List category	Currently kept?
Adelphobates castaneoticus	1	Least Concern	Yes
Adelphobates galactonotus	10	Least Concern	Yes
Adelphobates quinquevittatus	1	Least Concern	Yes
Allobates femoralis	2	Least Concern	Yes
Allobates zaparo	2	Least Concern	Yes
Ameerega altamazonica	2	N/A	Yes
Ameerega bassleri	5	Vulnerable	Yes
Ameerega bilinguis	2	Least Concern	Yes
Ameerega cainarachi	1	Endangered	Yes
Ameerega hahneli	2	Least Concern	Yes
Ameerega pepperi	4	Vulnerable	Yes
Ameerega picta	1	Least Concern	No
Ameerega pongoensis	1	Vulnerable	Yes
Ameerega silverstonei	2	Endangered	Yes
Ameerega trivittata	5	Least Concern	Yes
Andinobates bombetes	1	Vulnerable	No
Andinobates fulguritus	1	Least Concern	No
Andinobates minutus	1	Least Concern	No
Dendrobates auratus	33	Least Concern	Yes
Dendrobates leucomelas	6	Least Concern	Yes
Dendrobates tinctorius	42	Least Concern	Yes
Dendrobates truncatus	3	Least Concern	Yes
Epipedobates anthonyi	12	Near Threatened	Yes
Epipedobates boulengeri	2	Least Concern	Yes
Epipedobates darwinwallacei	2	N/A	Yes
Epipedobates tricolor	5	Vulnerable	Yes
Excidobates mysteriosus	1	Endangered	Yes
Hyloxalus azureiventris	2	Endangered	Yes
Oophaga arborea	1	Critically Endangered	Maybe
Oophaga granulifera	7	Vulnerable	Yes
Oophaga histrionica	23	Critically Endangered	Yes
Oophaga lehmanni	6	Critically Endangered	Yes
Oophaga pumilio	85	Least Concern	Yes
Oophaga speciosa	1	Extinct	No
Oophaga sylvatica	15	Near Threatened	Yes
Oophaga vicentei	2	Endangered	Yes
Phyllobates aurotaenia	5	Least Concern	Yes
Phyllobates bicolor	5	Endangered	Yes
Phyllobates lugubris	2	Least Concern	Yes
Phyllobates terribilis	5	Endangered	Yes
Phyllobates vittatus	2	Vulnerable	Yes
Ranitomeya amazonica	7	Data Deficient	Yes
Ranitomeya benedicta	3	Vulnerable	Yes
Ranitomeya fantastica	10	Vulnerable	Yes
Ranitomeya flavovittata	2	Least Concern	Yes
Ranitomeya imitator	15	Least Concern	Yes
Ranitomeya reticulata	6	Least Concern	Yes
Ranitomeya sirensis	8	Least Concern	Yes
Ranitomeya summersi	2	Endangered	Yes
Ranitomeya uakarii	3	Least Concern	Yes
Ranitomeya vanzolinii	2	Least Concern	Yes
Ranitomeya variabilis	8	Data Deficient	Yes
Ranitomeya ventrimaculata	1	Least Concern	Yes

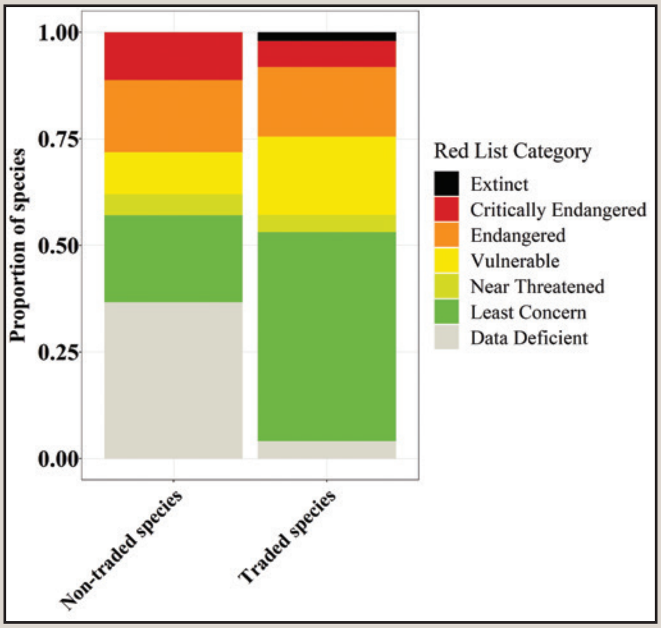

Fig. 1. The IUCN Red List status of 49 poison frog species in the family Dendrobatidae that were traded 1990–2020 (right) compared to the IUCN Red List status for the remaining 142 non-traded species (left). Four traded species (*Allobates femoralis, A. zaparo, Ameerega altamazonica*, and *Epipedobates darwinwallacei*) were excluded from the comparison because they are not recorded in Dendrobatidae by the IUCN Red List.

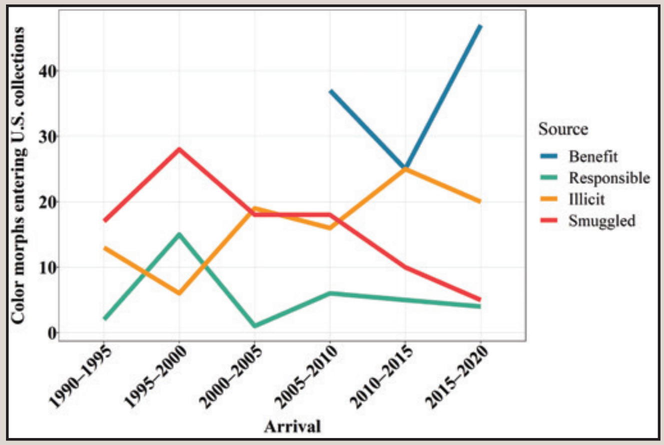

Fig. 2. The origin of all color morphs of poison frogs (Dendrobatoidea) maintained in U.S. private collections 1990–2020. The sources correspond to the four categories A–D in Table 2.

frogs kept on now-defunct websites dating back to 1998, with a focus on U.S. trade because of its accessibility and presence as one of the largest markets for pet amphibians (Schlaepfer et al. 2005; Herrel and Van Der Meijden 2014). To examine the types of frogs kept prior to widespread internet use, I reviewed animal dealer price lists, pet trade books and magazines (e.g., *Tropical Fish Hobbyist*, *Reptiles*), the American Dendrobatid Group newsletter (running 1992–2000; available at: archive.org/details/americandendrobatidgroup), and the International Society for the Study of Dendrobatids newsletter (running 1988–1992; available at: archive.org/details/issd_bulletin). For each species, I recorded the trade names of color morphs, information about their origin in the U.S. (how they were imported, year of import, etc.), and when the color morph was most recently maintained in collections. A color morph was defined as a distinct captive population that collectors were intentionally breeding separate from others, regardless of appearance. Synonyms of trade names were noted and combined, and I updated the taxonomy of old records to agree with Frost (2021). I then circulated the spreadsheet and made inquiries to 29 current or former private breeders and/or dealers in the U.S., as well as one breeder in Canada and one in the Netherlands. Specific color morphs were considered currently in U.S. collections if there was evidence (e.g., a social media post, classifieds ad, confirmation from a private breeder, etc.) they had been kept during 2015–2020.

After compiling the dataset from primary sources, I compared the time of arrival to records of U.S. imports in the CITES Trade Database (CITES 2020). Recommendations by Robinson and Sinovas (2018) were followed about interpreting CITES data. In some cases, it was not possible to confirm the year when a color morph was first imported because CITES only records data to the species- or genus-level and has no way of recording successfully smuggled animals. However, by working with the network of private breeders, I was able to infer the year of first arrival in the U.S. to a five-year range or less for all color morphs and species. The earliest year in the five-year range was used to summarize how trade has changed through time. For example, if a frog first became established at some point during 1992–1996, the year 1992 was used as the year of arrival for analyses. Additionally, many species and color morphs were imported or entered U.S. collections through a variety of different pathways. For example, new color morphs of a species were sometimes smuggled to the U.S. years before legal commercial imports arrived, with frogs from both sources subsequently bred together. Therefore, for color morphs that arrived from multiple sources and had since been bred together, I grouped their origin into a single source corresponding to the earliest way they arrived and became established.

To examine whether threatened species were more likely to be kept in private collections, I compared the IUCN Red List (2020) status of traded dendrobatids with the IUCN Red List status of non-traded species. I excluded *Ameerega altamazonica* and *Epipedobates darwinwallacei* from the comparison because the two species are not recorded in the IUCN Red List. *Allobates femoralis* and *A. zaparo* were also excluded because they are in the poison frog family Aromobatidae rather than Dendrobatidae.

Lastly, the LEMIS database was used to examine U.S. import volume. For the years 2000–2014, I accessed the LEMIS database made available by the EcoHealth Alliance (see Smith et al. 2017) and combined those data with data from the years 2015–2019 received from a Freedom of Information Act request with USFWS. Data from LEMIS for 2020 were unavailable at the time of the request. Data was compiled and summarized using Google Sheets, Microsoft Excel, and R version 3.6.2 (R Core Team 2019).

Results

From 1990–2020, 378 color morphs of 53 poison frog species were maintained in U.S. private collections (Table 1). The species maintained in collections increased 108% (23 pre-1990; 48 in 2020), and the number of different color morphs by 766% (41 pre-1990; 355 in 2020). Five species and 23 color morphs were in U.S. collections but are no longer kept, including one recently extinct species (*Oophaga speciosa*; IUCN 2020). For 47 color morphs of 19 species, I was unable to confirm if they currently are

Table 2. Ten pathways poison frogs enter U.S. private collections, categorized by the potential benefit or detriment to natural resource management and conservation.

Category	Pathway
A. Responsible trade with an intended conservation benefit	1. Imported or descended from an established breeding or ranching program in the native range of the species that funds conservation efforts.
B. Responsible trade in agreement with regulations and quota systems	2. Imported as wild-caught frogs for commercial purposes from a country in the species native range and in agreement with trade regulations.
	3. Imported from a European country but descended from animals most likely originally collected in a legal manner (e.g., regulated commercial harvest as above).
	4. Collected for a zoological institution or university and intentionally distributed to private breeders.
C. Illicit trade detrimental to good governance and responsible natural resource management	5. Misidentified wild-caught frogs imported for commercial purposes from a native range country.
	6. Imported from a country in the native range of the species but for which the color morph is only known to occur outside the exporting country.
	7. Imported from a breeding or ranching program in the native range of the species, yet the quantity, condition, and age of animals imported suggested they were likely collected from wild populations.
	8. Collected for a zoological institution or university and distributed to the trade in violation with agreements from the country of origin or the institution.
D. Illicit trade as above but also involving explicit wildlife poaching	9. Imported from Europe or Asia but descended from smuggled animals, or smuggled animals themselves, including those confiscated by, surrendered to, or gifted from a zoological institution and released to European private breeders (i.e., laundered frogs).
	10. Wild frogs smuggled directly to the U.S.

in collections. Four species made up more than half of all types of poison frogs kept: *Oophaga pumilio* (85 morphs), *Dendrobates tinctorius* (42 morphs), *D. auratus* (33 morphs), and *O. histrionica* (23 morphs). The full dataset of traded poison frog species, color morphs, and notes justifying origins in collections is available at: doi.org/10.13012/B2IDB-4717502_V1.

The proportion of threatened species (Critically Endangered, Endangered, and Vulnerable Red List categories) was similar between traded and non-traded species (Fig. 1). The IUCN Red List assessed 39% of traded species as threatened versus 38% of non-traded species. However, non-traded species were composed of a greater proportion of Data Deficient species; 4% of traded species were Data Deficient compared to 37% of non-traded species (Fig. 1).

Poison frogs have entered U.S. amphibian collections ten different ways (Table 2). New types of frogs originating from both legal wild commercial collection and smuggling decreased after 2000, coinciding with the development of breeding and ranching operations (Figs. 2, 3). There were 37 species represented by 109 color morphs that originated from breeding and ranching programs in native range countries. The first frogs from such breeding programs were imported to the U.S. in 2006. An additional 24 new color morphs originated after 1990 solely as wild frogs exported for commercial purposes, most of which (20 of 24) were color morphs of *Dendrobates tinctorius*. Six color morphs of four species were imported from Europe but appeared to have been offspring from legal wild commercial collection. Two color morphs of *D. auratus* originated in private collections after being released from a zoological institution to private breeders in the early 1990s. For 24 color morphs of 11 species entering collections post-1990, there were multiple origins and private breeders did not or no longer distinguished between frogs from the various sources.

Six illicit pathways were used to source poison frogs for U.S. collectors (Table 2). The two most common illicit trades routes were wild-caught frogs misleadingly imported as bred in captivity or ranched from native range countries (85 color morphs of 8 species), and smuggled frogs or their descendants imported from Europe (74 morphs of 31 species). I also traced the first availability of 22 color morphs for 8 species to instances of direct smuggling to the U.S., all but one of which occurred before 2005. Of the 96 color morphs originating from smuggling, more than half were native to three countries: Peru (23 morphs), Panama (17 morphs), and Ecuador (14 morphs; Fig. 4).

Data from the U.S. Fish and Wildlife Service showed that 142,211 individual poison frogs were imported during 2000–2019 (Figs. 5, 6). Annual import quantity peaked in 2006–2008, driven by two species: *D. auratus* and *O. pumilio*. Together, imports of *D. auratus* and *O. pumilio* from a single exporter in Panama accounted for more than half (85,348 individuals) of all poison frogs imported to the U.S. during 2000–2019. Of the Panamanian frogs, 94.5% of *D. auratus* and 98.6% of *O. pumilio* were recorded as captive-bred; however, private breeders widely believed most were wild-caught due to the age, condition, and quantity of frogs arriving.

Discussion

The poison frogs traded among U.S. collectors originated from diverse sources. Species and color morphs new to the trade that were descended from smuggled animals decreased over the last three decades, coinciding with businesses in Colombia, Ecuador,

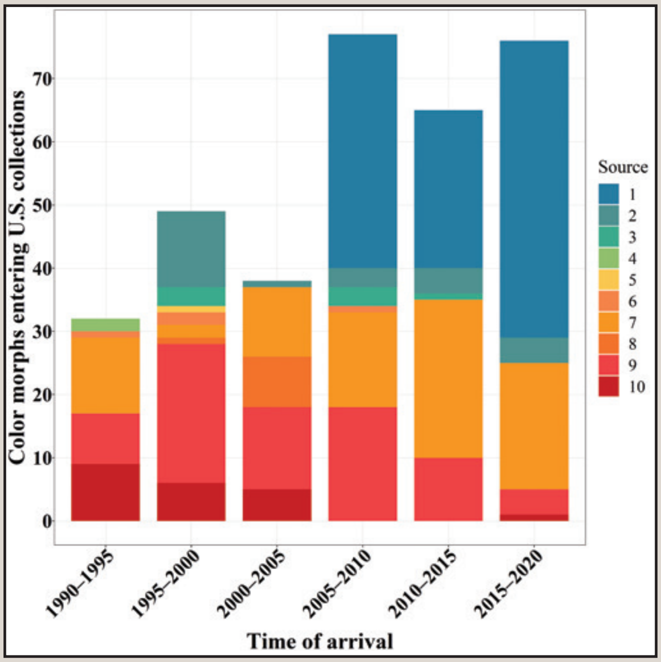

Fig. 3. The origin of all color morphs of poison frogs (Dendrobatoidea) maintained in U.S. private collections 1990–2020. The sources correspond to the categories in Table 2: 1) captive breeding and ranching programs with an intended conservation benefit; 2) wild-caught commercial imports; 3) non-smuggled European imports; 4) transparent release from a zoo or research program; 5) misidentified wild-caught commercial imports; 6) wild-caught commercial imports of a color morph only known to occur outside the exporting country; 7) wild-caught frogs imported from a native country as captive-bred or ranched; 8) descended from a research program which was not supposed to release frogs to the public; 9) European imports of smuggled or laundered frogs; 10) frogs directly smuggled to the U.S.

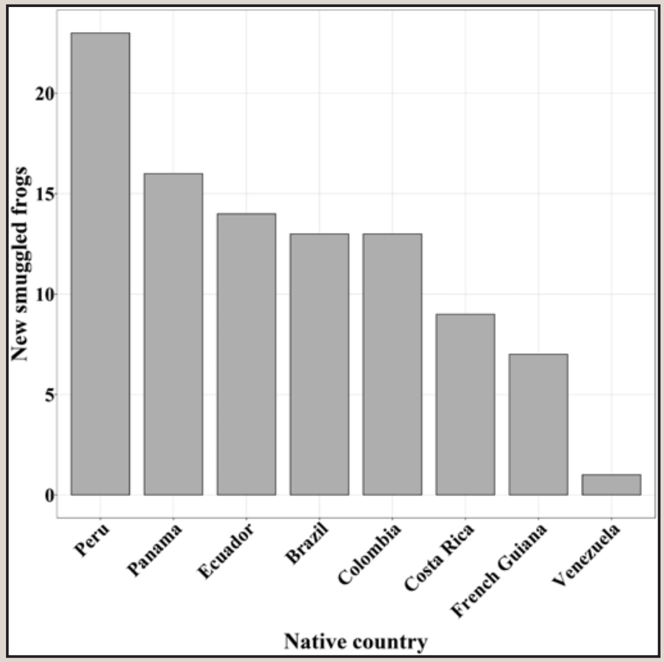

Fig. 4. The number of new types (color morphs and species) of poison frogs (Dendrobatoidea) descending from smuggled animals which entered U.S. collections 1990–2020 by their native country. The figure shows only frogs from sources 9 and 10 in Table 2, corresponding either to frogs that were directly smuggled to the U.S. or were laundered first through a European or Asian country.

and Peru developing captive breeding and ranching programs (Sinovas et al. 2017; Steffens 2018; Yeager et al. 2020). While breeding programs in native range countries increased, species and color morphs new to the trade that originated from legal wild-caught imports decreased. Such trends mirror patterns in the global trade of live reptiles; between 2001 and 2012 there was a 70% decrease in wild-caught reptiles and 50-fold increase in ranched reptiles (Robinson et al. 2015). The trend in new poison frogs entering collections from responsible sources is encouraging, but illegal collection also continues (Fig. 2). In some cases, smugglers have targeted recently described species and color morphs in the scientific literature (Auliya et al. 2016). Smuggling has not only impacted newly discovered populations but also damaged habitat, with trees selectively cutdown to access the phytotelmata of bromeliads where high value poison frogs are most easily captured (Brown et al. 2011). Peru was the native range country for the greatest number of poison frogs in U.S. collections descending from smuggled animals, followed by Panama and Ecuador.

Regarding trade volume, most poison frogs in U.S. collections are almost certainly bred domestically (Carpenter et al. 2014). Still, a Panama business accounted for the largest quantity of poison frog imports since 2000. Private breeders widely believed the Panama exporter was laundering wild-caught *D. auratus* and *O. pumilio* as captive-bred, which is a common method for illegally exploiting wildlife populations (Lyons and Natusch 2011; Janssen and Chng 2018). As evident by the large volume of frogs imported, there is likely sufficient demand to develop legitimate captive breeding or ranching programs in Panama with a conservation benefit, similar to ventures in Colombia, Ecuador, and Peru. Yet, without enforcement of trade regulations or pressure from consumers, such a program is unlikely to develop. Alternatively, considering *D. auratus* and *O. pumilio* are assessed as Least Concern by the IUCN Red List (IUCN 2020) and often are abundant in secondary or degraded habitat (Cove and Spínola 2013; McKone et al. 2014), wild populations might easily support regulated harvests. However, if authorities wrongly believe exported frogs are captive-bred rather than wild-caught, unsustainably high export quotas could put wild populations at risk, especially color morphs or localities in great demand from collectors. Indeed, overexploitation of wild populations for the pet trade has caused declines in other amphibian species of commercial value (e.g., Andreone et al. 2006; Rowley et al. 2016). For people who keep poison frogs as a hobby, it is important to avoid purchasing frogs from questionable sources, not only because of the impact unregulated harvest could have on wild populations, but also because the illicit trade puts legal trade at risk of further regulation (Wyatt et al. 2018).

Emerging infectious diseases and invasive species also are threats linked to the amphibian pet trade, but poison frogs likely present less risk than other commonly kept species. Notably, the global spread of the chytrid fungus *Batrachochytrium dendrobatidis* is associated with the amphibian trade (Fisher and Garner 2007; Schloegel et al. 2009; Wombwell et al. 2016), and the chytrid fungus *B. salamandrivorans* in Europe emerged through the importation of pet amphibians from Asia (Martel et al. 2014; Sabino-Pinto et al. 2015). Still, compared to other traded species, the quantity of poison frogs imported to the U.S. is relatively small. For example, during 2001–2009 nearly 9 million Dwarf Water Frogs (*Hymenochirus curtipes*) were imported to the U.S. (Herrel

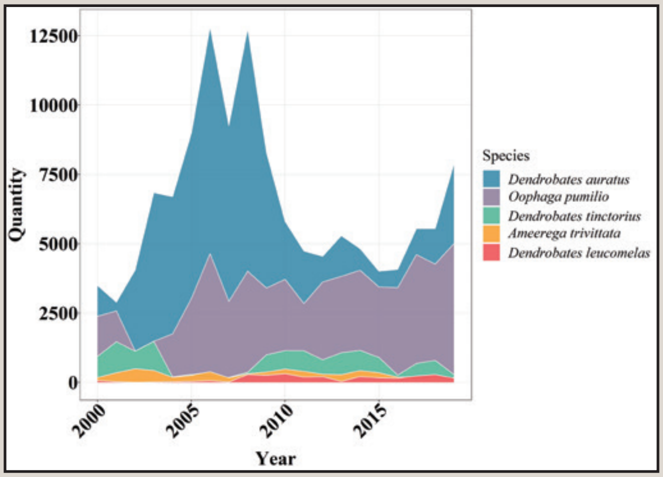

Fig. 5. Numbers of the top five species of poison frogs imported to the U.S. during 2000–2019 for trade and breeding purposes as recorded by the U.S. Fish and Wildlife Service. Two species, *Dendrobates auratus* and *Oophaga pumilio*, make up the bulk of poison frog imports.

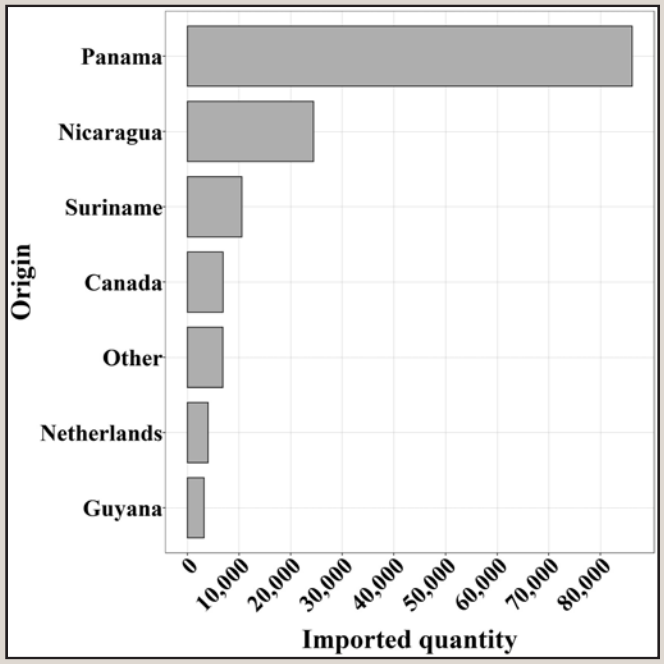

Fig. 6. U.S. imports of live poison frogs (Dendrobatoidea) for trade and breeding purposes by country of origin during the years 2000–2019. The category "Other" is the sum of the additional 12 source countries (quantity imported): Colombia (1,944), Peru (1,411), Germany (1,090), Ecuador (819), Czech Republic (593), Costa Rica (473), Norway (300), Indonesia (94), Denmark (89), China (49), France (20), and Belgium (11).

and Van Der Meijden 2014). During the same period, imports for the entire poison frog family Dendrobatidae numbered less than 80,000 individuals. Consequently, poison frogs likely warrant less concern than other heavily imported species with regard to spreading infectious diseases internationally. The amphibian pet trade also is responsible for introducing invasive species (Kopecký et al. 2016; Lockwood et al. 2019). Green and black poison frogs (*D. auratus*) have been established in Hawaii after an unsuccessful release for pest control in the early 20th century (Oliver and Shaw 1953). Nevertheless, poison frogs have a small body size and are relatively expensive, meaning they are less likely to be released by pet owners than are other commonly kept amphibian species, thus posing a lower risk of becoming established outside their native range through the pet trade (Stringham and Lockwood 2018).

Gorzula (1996) provided an overview of poison frogs traded during the first seven years after addition to CITES (1987–1993), concluding that the number of frogs traded "would not have filled a large trash can" and therefore was unlikely to be impacting wild populations. A similar outlook was common among the scientific community in the 1980s (e.g., Picket 1987; Mrosovsky 1988), with researchers only beginning to recognize that widespread amphibian extinctions and declines were a rising global phenomenon (Blaustein and Wake 1990; Wake 1991). Twenty-five years later, we better understand the severity of what has been dubbed the amphibian extinction crisis and have documented ways the live amphibian trade can exacerbate the problem (e.g., Fitzpatrick et al. 2018; Stringham and Lockwood 2018). Concurrently, many times more people now keep poison frogs, with demand for pet amphibians on the rise (Measey et al. 2019).

Considering responsible trade can have conservation benefits and blanket trade bans do not usually work (Garner et al. 2009; Pasmans et al. 2017), policies should aim to ensure amphibians in the pet trade originate from sustainably-managed sources rather than restrict trade overall. Further trade analyses are needed to inform policy and should focus on the scale of domestic production of pet amphibians, which is not captured in CITES or LEMIS data (Schlaepfer et al. 2005), as well as on the potential livelihood benefits to local people who catch and export wild amphibians for the pet trade (Robinson et al. 2018). Nicaragua, Panama, and Suriname supply the bulk of wild-caught poison frogs to the trade and should be the focus of future field studies examining trade impacts on wild populations.

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HERPETOCULTURE NOTES

TESTUDINES — TURTLES

***APALONE MUTICA* (Smooth Softshell). FORAGING TRACES.** Although sit-and-wait strategies may sometimes be used, *Apalone* are thought to primarily employ active foraging techniques as they seek to gain energy from their habitat (Webb 1962. University of Kansas Publications, Museum of Natural History 13:429–611; Ernst and Lovich 2009. Turtles of the United States and Canada. Second edition. Johns Hopkins University Press, Baltimore, Maryland. 827 pp.). Direct field observations of foraging softshells are difficult to make due to their extreme shyness and wariness; however, observations of captive softshells can provide some insight into their active foraging behavior.

I maintained several adult male and juvenile *A. mutica* over several years in a 7 × 15 m outdoor enclosure located within the species natural range in Searcy, Arkansas, USA. The enclosure contained a ca. 5 m^2 pool that varied in depth from 1–20 cm. The softshells successively overwintered in the pool substrate and fed and grew well on a diet of canned salmon and sardines. In addition, the turtles foraged on various naturally occurring invertebrates in the mixed sand and silt bottom substrate. The water was often slightly cloudy due to the stirring of bottom sediments by foraging activities of the softshells.

I occasionally observed a series of unusual whirl marks of unknown origin in the pool substrate and in September 2014, I discovered via a remote camera the source of the unusual marks. I observed an adult male *A. mutica* actively foraging in the pool, leaving behind the distinctive mosaic pattern of whirl marks in its meandering path (Fig. 1). The whirl marks were created by the turtle's forelimbs as they were repeatedly extended forward to a point directly anterior to the turtle's snout and then drawn back laterally in a breaststroke swimming motion, which drew the claws shallowly through the substrate. The turtle appeared to simultaneously probe the disturbed area with its snout and periodically eat whatever may have been uncovered by the limb movements. The turtle would then move forward a short distance and repeat the peculiar foraging behavior. The forward movement appeared to be made in a cohesive meandering path to thoroughly search a small patch (outlined in Fig. 1) before moving on to a new foraging patch.

I occasionally observed similar mosaic whirl traces in small shallow, still-water pools on the lee end of sandbars on the Kansas River near Lawrence, Kansas, but did not at the time recognize what the peculiar patterns represented (MVP, unpubl. data). Foraging traces likely may also be made in moving water, the preferred habitat of *A. mutica* (Webb 1962, *op. cit.*; Ernst and Lovich 2009, *op. cit.*), but probably are quickly obscured by the moving water.

Why *A. mutica* sometimes confine their foraging in patches is unknown. In the field, foraging *A. mutica* have been observed to root in the substrate (Webb 1962, *op. cit.*; Plummer and Farrar 1981. J. Herpetol. 15:175–179), but in no particular pattern. Confining foraging to patches could possibly be related to the distribution of prey in the substrate (Stephens and Krebs 1987. Foraging Theory.

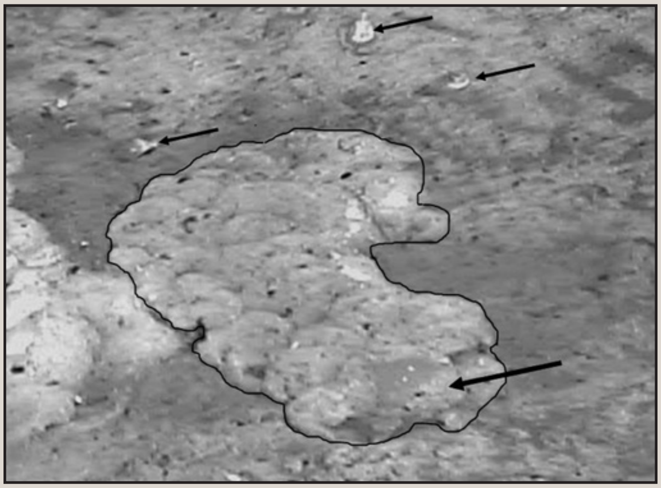

Fig. 1. A mosaic of whirling foraging traces (outlined) made by an adult male *Apalone mutica*. Large arrow indicates foraging softshell; small arrows indicate heads of three burrowed *Apalone*. Image taken through cloudy water on 12 September 2014.