When pets become pests: the role of the exotic pet trade in producing invasive vertebrate animals

Julie L Lockwood[1]*, Dustin J Welbourne[1], Christina M Romagosa[2], Phillip Cassey[3], Nicholas E Mandrak[4], Angela Strecker[5], Brian Leung[6], Oliver C Stringham[1,3], Bradley Udell[2], Diane J Episcopio-Sturgeon[2], Michael F Tlusty[7], James Sinclair[8], Michael R Springborn[9], Elizabeth F Pienaar[2,10], Andrew L Rhyne[11], and Reuben Keller[12]

The annual trade in exotic vertebrates as pets is a multi-billion-dollar global business. Thousands of species, and tens of millions of individual animals, are shipped both internationally and within countries to satisfy this demand. Most research on the exotic pet trade has focused on its contribution to native biodiversity loss and disease spread. Here, we synthesize information across taxa and research disciplines to document the exotic pet trade's contribution to vertebrate biological invasions. We show recent and substantial worldwide growth in the number of non-native animal populations introduced via this invasion pathway, which demonstrates a strong potential to increase the number of invasive animals in the future. Key to addressing the invasion threat of exotic pets is learning more about the socioeconomic forces that drive the massive growth in the exotic pet market and the socio-ecological factors that underlie pet release by owners. These factors likely vary according to cultural pet-keeping traditions across regions and whether purchases were legal or illegal. These gaps in our understanding of the exotic pet trade must be addressed in order to implement effective policy solutions.

Front Ecol Environ 2019; doi:10.1002/fee.2059

Non-native species are transported and introduced to new geographical regions via numerous pathways, with the influence of each pathway shifting with fluxes in global trade (Hulme 2009; Essl *et al.* 2011). Most non-native species introductions fall under one of two types of invasion pathways: accidental introductions – for example, species that are spread by "hitchhiking" in or on ships and airplanes transporting commodities and people – and pathways in which the species are themselves a commodity (Hulme 2009). The latter group, exemplified by the exotic pet trade (WebPanel 1; Figure 1), has received increasing attention over the past decade as global markets for live plants and animals have grown, resulting in a concomitant uptick in the number of invasive species arriving via this route (Padilla and Williams 2004; Keller and Lodge 2007). Despite the pet trade producing several high-profile invasive species, such as the red lionfish (*Pterois volitans*) in the Caribbean Sea and the Burmese python (*Python bivittatus*) in south Florida, most research has focused on how the pet trade affects wild populations (being collected in the source countries) and introduces disease (being spread in the destination countries) (Lyons and Natusch 2013; Tella and Hiraldo 2014). Yet for some vertebrate groups, such as reptiles and amphibians, the pet trade has contributed the largest number of established non-native species worldwide (Kraus 2009). Research examining the pet trade's role in producing invasive vertebrate species has remained diffuse and fragmented across disciplines and biological realms. We provide a comprehensive overview of the exotic pet trade as it pertains to vertebrate invasions, offering an understanding of the mechanistic processes while highlighting policy-relevant research gaps.

In a nutshell:

- The worldwide market for exotic pets is large and growing, with implications for both the conservation of native biodiversity and the emergence of invasive species
- The exotic pet trade pathway has already led to the establishment of several hundred non-native and invasive vertebrate animal species globally, and is poised to contribute to the establishment of even more in the future
- Characterizing and reducing the invasion risk posed by exotic pets requires integrated research on social, economic, and environmental factors

*[1]Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ *(julie.lockwood@rutgers.edu); [2]Wildlife Ecology and Conservation, University of Florida, Gainesville, FL; [3]Centre for Applied Conservation Science, and School of Biological Sciences, University of Adelaide, Adelaide, Australia; [4]Biological Sciences, University of Toronto, Scarborough, Canada; [5]Environmental Science and Management, Portland State University, Portland, OR; [6]Biology, McGill University, Montreal, Canada; [7]School for the Environment, University of Massachusetts Boston, Boston, MA; [8]School of Forest Resources and Conservation, University of Florida, Gainesville, FL; [9]Environmental Science and Policy, University of California Davis, Davis, CA; [10]Mammal Research Institute, University of Pretoria, Pretoria, South Africa; [11]Department of Biology, Marine Biology, and Environmental Science, Roger Williams University, Bristol, RI; [12]Institute of Environmental Sustainability, Loyola University Chicago, Chicago, IL*

A Toomes

Jim, the Photographer; CC BY 2.0

Figure 1. Exotic pets are those that are kept for non-utilitarian reasons and have a relatively short history of domestication; examples are as diverse as the (a) central bearded dragon (*Pogona vitticeps*) and (b) powder blue surgeonfish (*Acanthurus leucosternon*). Dragons are sourced from captive breeding facilities and surgeonfish from the wild, and although neither species is considered threatened with extinction, it is illegal to export dragons from their native Australian range.

Keeping vertebrate animals as household companions is extraordinarily widespread and growing in popularity globally (Ramsay *et al.* 2007; Carrete and Tella 2008; Bush *et al.* 2014). In the US, Australia, and the UK, over half of all households have at least one pet (Reaser and Meyers 2007). Although pet ownership per household is lower in China than in Western countries, China now ranks third among countries with the most pets, with a companion animal population of more than 100 million (Deng 2017). In the US, approximately 50% of pets can be considered "exotic" (APPA 2018): that is, pets without a long history of domestication, unlike dogs, cats, or horses (Figure 1; Bush *et al.* 2014). Exotic pet ownership has grown markedly in recent decades (Rhyne *et al.* 2012; Vall-llosera and Cassey 2017a). For instance, ownership of reptiles and amphibians in the US has more than doubled in less than two decades, from 2.4 million households in 1994 to 5.6 million in 2012 (APPA 2018). Keeping exotic pets is also geographically widespread. In Indonesia, Jepson and Ladle (2005) found that households were more likely to keep exotic pets, such as birds (22%) and fishes (9.5%), than they were to keep common domesticated pets, such as cats and dogs (3% or less). In some regions, such as Asia and South America, the exotic pet market is expanding rapidly as living standards improve (Ding *et al.* 2008; McNeely *et al.* 2009; Alves *et al.* 2010). Even if the per-capita demand for exotic pets worldwide remains stable, a growing human population and expanding middle class will lead to growing demand for vertebrates as exotic pets (Shepherd *et al.* 2007).

Keeping exotic pets often strains the common Western definition of household "pet". For example, Alves *et al.* (2010) reported that in Brazil "caged birds can be found on bar counters, in grocery stores, in shoe stores and in homes", and Su *et al.* (2015) documented the range of bird species kept captive just long enough to be released as part of traditional Asian religious services. A recent trend in Chinese markets is the selling of live-animal keychains, in which live reptiles, amphibians, or fishes are kept in small pouches as jewelry; these animals either die, are removed from the pouches and kept in captivity, or are released from the pouches into the wild (CNN 2011). For all of these examples, we categorize the animals as "exotic pets" because they are kept for non-utilitarian reasons (WebPanel 1) and pose an invasion risk when released into a new geographical locale.

A complex market

The trade in exotic pets can be legal, illegal, or both, as a species' status may change as it moves across political boundaries within the commodity chain, and this variation in legal status creates a confusing array of terminology that has inhibited comprehensive understanding of market dynamics (WebPanel 1). Published literature documenting the species composition of the pet trade, as well as the network of countries involved in that trade, often focuses exclusively on species listed under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; Bush *et al.* 2014). However, species traded under the guidance of CITES are a small fraction of all species sold as exotic pets (Bush *et al.* 2014). Moreover, most countries do not keep comprehensive records of the species imported as pets, and of those that do, large proportions of imports are often listed as "unidentified" (eg marine and freshwater fishes; Smith *et al.* 2008; Rhyne *et al.* 2012) or are misidentified and/or mislabeled (Gerson *et al.* 2008).

Despite these complications, a variety of sources indicate that the market for exotic pets is enormous. For example, Su *et al.* (2014) reported that 2–5 million individual birds were sold per year as pets worldwide during the 1990s, with one-quarter of all extant bird species being represented, while Robinson *et al.* (2015) found that, of CITES-listed reptile species, 18.8 million individuals were imported into the European Union (EU) between 1996 and 2012. The importation and keeping of fish species dwarf that of all other vertebrate groups traded as exotic pets. The US is the largest importer of marine aquarium fishes, with annual imports reaching more than 11 million individual fish, representing over 2300 species from 125 families (Rhyne *et al.* 2012, 2017). The number of freshwater fishes traded internationally is an order of magnitude greater than marine fishes (Livengood *et al.* 2014).

In most countries, the domestic exotic pet trade is potentially massive, but remains virtually undocumented. For any vertebrate group, intra-country trade can transport species outside of their native range and into novel regions within a country, potentially resulting in established non-native populations. Although specific statistics are unavailable, there are examples that hint at the potential magnitude of intra-country non-native pet introductions. Over 800 species and varieties of fishes are bred in Florida (FDACS 2018), the majority of which are not native. The red-eared slider (*Trachemys scripta elegans*), a turtle commonly kept as a pet in the US, is native to the south-central region of the US but has established non-native populations in numerous other parts of the country, including Hawaii (Kraus 2009). Similarly, Barroso de Magalhães and Jacobi (2013) identified 345 ornamental fish species for sale in stores in Minas Gerais, Brazil, 151 of which were not native to the region despite being native to other parts of Brazil.

A Toomes

Figure 2. Keeping vertebrate species as pets has increased greatly in popularity over the past several decades worldwide. Today's markets for exotic pets include direct sales through traditional outlets (eg pet stores) but also through sales of animals directly to consumers via online forums and pet fairs ("expos") as shown here. Some fraction of these purchased animals will escape confinement or be deliberately released and consequently have the opportunity to establish as non-native species.

Selling exotic pets can be a lucrative endeavor and, as with many other markets, there are financial opportunities in introducing new products. Annual revenues from the US reptile industry are estimated to be ~US$1.4 billion (Collis and Fenili 2011). Springborn *et al.* (2011) estimated that each additional species in the reptile and amphibian trade generated long-term profits to importers of approximately US$90,000, and Springborn *et al.* (2015) reported a similar value (US$79,300) for birds. These figures, while modest compared to other potential market investments, represent only the average value in a set that includes both highly lucrative species and those with relatively marginal profitability. For this reason, the global exotic pet market is taxonomically dynamic across time, with imports of some species ranging widely in magnitude per year and in the number of years that they persist in the trade (Romagosa 2014).

The rise of trade via non-traditional marketplaces (eg websites, fairs, social media) has vastly expanded direct-to-consumer sales (Figure 2), raising the importance of this pathway for analysis and enforcement. Although this pathway is more often associated with trade in non-living wildlife products (eg ivory, leather, feathers), trade in live species is substantial. Stringham and Lockwood (2018) documented 94,230 unique individual pet listings (representing 652 species) on three popular reptile and amphibian web vendors in the US between 2012 and 2016. Similarly, a survey of Facebook listings in the Philippines uncovered 1623 live birds and reptiles for sale over a 17-day period (Canlas *et al.* 2017). Grein and Chen (2018) reported that eBay recently removed 45,000 listings over a 12-month period that were not in compliance with their wildlife trade policies.

Exotic pets becoming exotic pests

Although most animals transported beyond their native range for sale as exotic pets remain in captivity for the duration of their lives and never establish a non-native population, many individuals are released or escape confinement while in the care of importers, wholesalers, retailers, or consumers (Duggan *et al.* 2006; Strecker *et al.* 2011; Vall-llosera and Cassey 2017a). Why owners release exotic pets is not widely documented, but reasons include difficulty in providing care for large, old, aggressive, or sick animals (Duggan *et al.* 2006; Holmberg *et al.* 2015; Stringham and Lockwood 2018). Surveys of aquarium owners indicated that 2–10% of consumers deliberately released unwanted fish (Duggan *et al.* 2006; Chang *et al.* 2009; Strecker *et al.* 2011). To the best of our knowledge, there are no published surveys demonstrating the propensity of consumers to release pet amphibians, reptiles, mammals, or birds, but Vall-llosera and Cassey (2017a) suggested that existing data on pet releases or escapes vastly underestimate the number of exotic pets that become free-living, especially highly mobile species like birds. In cases where an animal is purchased explicitly for release as part of a ceremony or competition, or the species is kept for only a brief period (eg as jewelry), the probability of release is quite high (Su *et al.* 2015).

Existing research indicates that past trade in exotic pets has resulted in the successful establishment of non-native species. Krysko *et al.* (2011) showed that, of the 140 non-native reptiles and amphibians that have been introduced into Florida, nearly 85% arrived via the pet trade. Rosa *et al.* (2017) determined that 70% of invasions by mammal species in Brazil over the past 30 years were also due to the pet trade. Hulme *et al.* (2008)

reported that exotic pet escapes were the primary source of new non-native species establishments of amphibians, reptiles, mammals, and birds in the EU; Rixon *et al.* (2005) identified at least 100 species of freshwater fishes in the aquarium trade that had been introduced into North American freshwater bodies, with 40 having established populations; and Rhyne *et al.* (2012) identified 33 marine fish species imported for the pet trade that had been introduced into US coastal waters. Furthermore, it is broadly suspected that the marked rise in the number of established non-native fishes in marine waters in the EU over the past decade is due to the recent rapid growth of the marine aquarium industry (Katsanevakis *et al.* 2013).

These reports clearly demonstrate that the exotic pet trade has contributed a wide variety of non-native species worldwide. However, evidence from invasion biology suggests that these tallies are only the tip of the iceberg. In a comprehensive evaluation of the link between trade volume and number of non-native species, Essl *et al.* (2011) showed a decade or more lag between the time when trade activity increases and when populations of non-native species were recorded as introduced. Most of the published statistics reviewed above stem from trade patterns that were manifest several decades ago and therefore do not reflect the current rise in exotic pet ownership worldwide. If current behaviors and policies continue unchanged, many countries will see the establishment of populations of exotic pet species at rates above historical trends over the next several decades.

Which exotic pets will establish non-native populations next?

A fundamental component of biosecurity policy is predicting which exotic pet species will establish new non-native populations – that is, which traded pet species will escape or be released, find suitable habitat, successfully reproduce, and persist to establish self-sustaining populations? This is a challenging question, given that a variety of factors – including the species characteristics, the nature of the pet market, and environmental conditions – will influence overall establishment success.

The ecological "fit" between a species' life-history requirements and the habitat into which it is introduced plays an important role in the successful establishment of exotic pets, as it does for most non-native species (Hayes and Barry 2008). At a basic level, an introduced exotic pet must be able to physiologically tolerate local environmental conditions; for example, marine fishes released into fresh water are unlikely to survive and establish non-native populations (Weigle *et al.* 2005), and freshwater fishes predominantly native to tropical or sub-tropical regions are unlikely to establish populations within temperate or boreal habitats (Bradie *et al.* 2013). Generally, established non-native vertebrate species are characterized by high fecundity and broad environmental tolerance (Springborn *et al.* 2011, 2015; Capellini *et al.* 2015; Howeth *et al.* 2016). Carrete and Tella (2008) also demonstrated that wild-caught bird species traded as exotic pets were more likely to establish non-native populations than captive-bred species.

Another key factor affecting establishment success is the number of individuals released and the number of release events, which together are known as "propagule pressure" (Cassey *et al.* 2018). For most exotic pet species, we simply do not know the magnitude or spatial extent of their introduction and therefore have no direct way of measuring propagule pressure. However, a consistent pattern in the literature is the relationship between the number of individuals imported into a country for sale as pets, how many years the species was for sale, and establishment success (van Wilgen *et al.* 2010; Kikillus *et al.* 2012; Vall-llosera and Cassey 2017a). All else being equal, the larger the number of individuals that are sold in a region, the larger the number that would be accidentally or deliberately introduced, thereby raising propagule pressure and elevating establishment success (eg Bradie *et al.* 2013). At local scales, most exotic pets are released within urban centers or in nearby aquatic ecosystems (van Ham *et al.* 2013), which is likely a function of the density of pet-owning households in cities and suburbs. As a result, cities tend to be hotspots for non-native animals that likely established after being kept as pets, especially if they are located in tropical and sub-tropical climates (eg Krysko *et al.* 2011).

Research into what makes some exotic pet species more popular than others is central to predicting the risk that trade contributes to biological invasions. The exotic pet trade exhibits similar supply-and-demand characteristics to those of other markets. For instance, Vall-llosera and Cassey (2017b) showed that the price of pet birds increased with reduced availability. The number of pet birds held by any one consumer therefore varies widely, from several individuals of very rare birds to several thousand in the case of very popular species (Vall-llosera and Cassey 2017b). However, exotic pet consumers also exhibit "bandwagon" and "snob" effects, so price is only one factor in the purchase decision (Chen 2016). For bandwagon consumers, the demand for a particular item increases as more people purchase it, whereas snob consumers demand a particular item precisely because few other consumers own it. Bandwagon species tend to be traded at higher volumes and lower prices and are consequently more likely to be released by owners or to escape confinement, especially if they become difficult to maintain in captivity (Rhyne *et al.* 2012; Holmberg *et al.* 2015; Stringham and Lockwood 2018).

Perhaps as a result of this dynamic, there is a consistent pattern in pet trade import data where a few species constitute the majority of individuals imported and sold, and these species are also the ones that are commonly introduced and regularly become established (Figure 3). For example, the green iguana (*Iguana iguana*) accounted for 46% of the total trade in reptiles in the US between 1996 and 2012 and non-native populations are now established across several US states (Figure 4; Robinson *et al.* 2015). Similarly, Rhyne *et al.* (2012) found that only 12%

of marine fish species were imported into the US at volumes greater than 1000 individuals, but these species make up a disproportionate number of those that have been recorded as introduced (Figure 3). Livengood *et al.* (2014) found that the top 23 of 255 ornamental freshwater fish species imported into the US in 2010 accounted for 87% of total fish imports and have consistently topped the list of imports over a 30-year time span, disproportionately contributing to the set of established non-native fishes in the US. Yet there are also a few species that have been introduced or have become established despite being imported in relatively small numbers (Figure 3), suggesting other factors contribute to release (eg difficulty in care) or establishment (eg environmental matching).

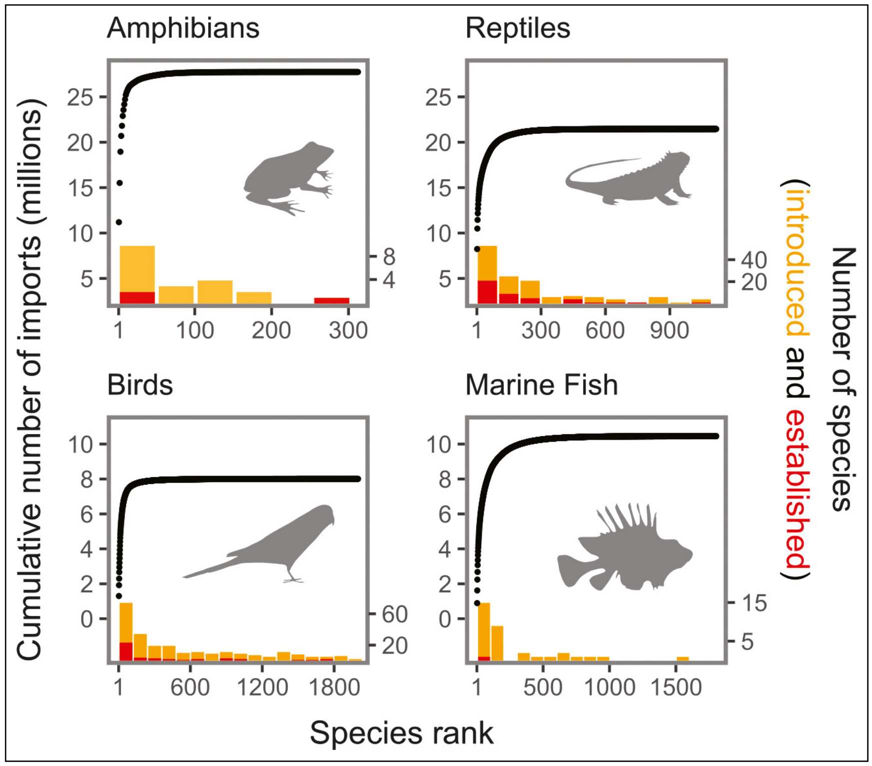

Figure 3. Cumulative (total) number of individuals across species imported as exotic pets for four taxonomic groups (amphibians, reptiles, birds, and marine fish). "Species rank" indicates the ranked number of imports for a species (ie a lower rank means more individuals were imported). Each black dot represents a single species, and signifies the total cumulative sum (primary y-axis) of the number of individuals for all species imported into the US up to that rank, as derived from US Fish and Wildlife Service records. For each taxonomic group, few species predominate in the number of individuals imported, causing the points on the cumulative import ranking curve to aggregate after the first few species (ie those with the highest number of imported individuals). The numbers of species recorded as introduced (orange bars) or established (red bars) within either 50-species (amphibians) or 100-species (reptiles, birds, marine fish) incremented import volume bins are depicted as overlapping histograms (secondary y-axis). As such, most exotic pets introduced or established were imported at very high volumes (left-hand side of each panel), but a few introduced species have established wild populations despite being imported in relatively small numbers (right-hand side of each panel); note: secondary y-axes differ in scale between taxa (number of species established: amphibians = 3, reptiles = 43, birds = 46, marine fish = 1). See Romagosa (2014; birds, amphibians, reptiles) and Rhyne *et al.* (2012; marine fishes) for details on time period of import records and data sources for species' non-native status.

Knowledge gaps

Existing research suggests that the exotic pet trade generates, and will continue to pose, a substantial invasion risk worldwide. The imperative to reduce this risk is growing as the impacts of several invasive species originating from the exotic pet trade become clear, and as this market experiences rapid future growth. We suggest four knowledge gaps that need to be addressed to reduce invasion risk.

First, existing knowledge about market dynamics, supply and demand, and consumer behavior largely originates from – and focuses on – the US, Australia, and the EU. As these regions are major components of the exotic pet trade, the attention is warranted, but this ignores the massive rise in pet-keeping in emerging economies such as Brazil, China, and Southeast Asian countries, where there is every reason to believe the invasion risk is considerable (Alves *et al.* 2010). Existing evidence suggests that the motivations and practices associated with pet-keeping in these cultures differ substantively from those observed in Western cultures (eg Alves *et al.* 2010; Su *et al.* 2015). Indeed, cultural "types" that relate to pet ownership (eg degree of agriculture or predominant religion; Knobel *et al.* 2008) may serve as useful predictors of invasion risk or management capacity, although this assertion remains unexplored in the context of invasive species policy.

Second, the interplay between market demand, consumer behavior, and species' traits is key to accurately characterizing invasion risk. If a species' establishment success is dictated by propagule pressure, which is driven by a high volume of sales to consumers, then a close look at life-history traits that support large numbers for sale is of considerable interest. There is also a need to explore the extent to which the life-history traits that increase establishment success are the same traits that make a species common in the exotic pet trade, and/or more likely to be deliberately released by pet owners and sellers. For example, wild-caught species that are common and widespread in their native range may be more profitable because they are easy to collect and their generalist habits require less specialized (ie cheaper) care. Behavioral and life-history traits associated with large native range sizes are known to correlate with establishment success in birds (Carrete and Tella 2008; Blackburn *et al.* 2009). Similarly, breeding centers tend to focus on housing highly fecund species that experience low mortality in captivity, either because of a wide environmental tolerance or low handling needs (eg behaviorally docile), both of which are correlated with establishment success. We also

M Sileo

Figure 4. Green iguanas (*Iguana iguana*) have long been imported into the US as exotic pets, with millions of individuals, largely derived from captive populations, having been sold to consumers since the 1970s. Non-native populations of this species have been established in Hawaii, Puerto Rico, Texas, and Florida.

Florida Fish and Wildlife Commission

Florida Fish and Wildlife Commission

Figure 5. Reducing the likelihood that exotic pets become invasive requires a combination of policy approaches that target pet owners and engage a wide variety of stakeholders in locating and controlling nascent populations. In Florida, state agencies and private companies have conducted removal and awareness events centered on (a) the lionfish (*Pterois* sp) invasion of nearby coral reefs, and (b) conducting educational outreach events to encourage owners of exotic pets, such as Nile monitor lizards (*Varanus niloticus*), to refrain from releasing their animals.

have very limited understanding of why people purchase exotic pets and what motivates them to release these pets. A better understanding of human motivations and behaviors is therefore critical for assessing invasion risks associated with the exotic pet trade. Research addressing this complex interplay of economics, human behavior, and biology is required to fully identify how risk manifests within the exotic pet trade and develop an evidence base for implementing policy solutions.

Third, even though exotic pets can become harmful invaders, such species are still compelling and desirable companion creatures to the general public. This emotional attachment means that public opposition to eradication or control programs can be fierce, making release prevention and rapid removal of released animals key to reducing invasion risk (Reaser and Meyers 2007). Although several such policy options have been implemented in limited geographical locations or trialed under specific contexts (Figure 5), very few have been evaluated within the framework of minimizing invasion risk in the exotic pet trade. Basing policy options on a strong evidence base is vital because the economic interest in maintaining a healthy and growing exotic pet market is strong, and public tolerance of failed eradication programs may be limited (Reaser and Meyers 2007).

Finally, a potentially important and difficult aspect of the exotic pet trade to evaluate is the black market. An economic perspective on black-market trade entails focusing on obscured costs, benefits, and uncertainties. The costs to participants of wildlife crime involve the direct cost of illicit transport, probability of detection by authorities, and legal consequences if caught. To practitioners, the latter two are highly uncertain, and the chances of detection and consequences may vary widely between countries. The benefits of illegal trade involve either sales revenue or personal enjoyment if the species are kept. These values are also highly uncertain given that the species involved are usually rare, preferences for species can change rapidly, and illicit markets usually have few participants and are poorly monitored. An efficient approach to deterrence may entail identifying which one (or combination) of the costs could be increased or how benefits could be decreased to discourage illegal trade. Although it might be tempting to focus additional effort on surveillance and enforcement, resources are already invested in these areas and there may be diminishing returns on additional investment (Challender *et al.* 2015). Interviewing illegal traders would provide insight into whether the driving factors in decision making are spikes in sale prices or changes in the likelihood of being caught.

Conclusion

The existing body of literature examining the exotic pet trade is spread across disciplines, and much of this research has focused on the exotic pet trade's contribution to extinction, while its contribution to invasions has largely been ignored. We have highlighted an evident and urgent need to understand, at a much more fundamental level, how the exotic pet trade contributes to invasions. The challenge is complex, given that a thorough understanding will necessarily include social perceptions, market forces, and ecology. Due to the industry's socioenvironmental scope, concerted interdisciplinary efforts are required to understand these aspects of the exotic pet trade in order to devise and implement strategies that mitigate its potential harmful impacts.

Acknowledgements

This work was supported by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the US National Science Foundation (DBI-1052875), and from Centre for Invasive Species Solutions project funding (PO1-I-002: "Understanding and intervening in illegal trade in non-native species").

References

Alves RRN, Nogueira EEG, Araujo HFP, *et al*. 2010. Bird-keeping in the Caatinga, NE Brazil. *Hum Ecol* **38**: 147–56.

APPA (American Pet Products Association). 2018. Pet industry market size & ownership statistics. Stamford, CT: American Pet Products Association Inc. www.americanpetproducts.org/press_industrytrends.asp. Viewed 27 Dec 2018.

Barroso de Magalhães AL and Jacobi CM. 2013. Invasion risks posed by ornamental freshwater fish trade to southeastern Brazilian rivers. *Neotrop Ichthyol* **11**: 433–41.

Blackburn TM, Cassey P, and Lockwood JL. 2009. The role of species traits in the establishment success of exotic birds. *Glob Change Biol* **15**: 2852–60.

Bradie J, Chivers C, and Leung B. 2013. Importing risk: quantifying the propagule pressure–establishment relationship at the pathway level. *Divers Distrib* **19**: 1020–30.

Bush ER, Baker SE, and Macdonald DW. 2014. Global trade in exotic pets 2006–2012. *Conserv Biol* **28**: 663–76.

Canlas CP, Sy EY, and Chng S. 2017. A rapid survey of online trade in live birds and reptiles in the Philippines. *TRAFFIC Bulletin* **29**: 58–63.

Capellini I, Baker J, Allen WL, *et al*. 2015. The role of life history traits in mammalian invasion success. *Ecol Lett* **18**: 1099–107.

Carrete M and Tella JL. 2008. Wild-bird trade and exotic invasions: a new link of conservation concern? *Front Ecol Environ* **6**: 207–11.

Cassey P, Delean S, Lockwood JL, *et al*. 2018. Dissecting the null model for biological invasions: a meta-analysis of the propagule pressure effect. *PLoS Biol* **16**: e2005987.

Collis AH and Fenili RN. 2011. The modern US reptile industry. Washington, DC: Georgetown Economic Services.

Challender DWS, Harrop SR, and MacMillan DC. 2015. Towards informed and multi-faceted wildlife trade interventions. *Global Ecol Conserv* **3**: 129–48.

Chang AL, Grossman JD, Spezio TS, *et al*. 2009. Tackling aquatic invasions: risks and opportunities for the aquarium fish industry. *Biol Invasions* **11**: 773–85.

Chen F. 2016. Poachers and snobs: demand for rarity and the effects of antipoaching policies. *Conserv Lett* **9**: 65–69.

CNN (Cable News Network). 2011. Live animals sold as key rings in China. Atlanta, GA: Turner Broadcasting System Inc. www.cnn.com/2011/WORLD/asiapcf/04/14/china.animal.keyring. Viewed 27 Dec 2018.

Deng Y. 2017. Can China become top dog in pet ownership? Beijing, China: Cheung Kong Graduate School of Business. http://knowledge.ckgsb.edu.cn/2017/06/21/consumers/pets-in-china-become-top-dog. Viewed 27 Dec 2018.

Ding J, Mack RN, Lu P, *et al*. 2008. China's booming economy is sparking and accelerating biological invasions. *BioScience* **58**: 317–24.

Duggan IC, Rixon CAM, and MacIsaac HJ. 2006. Popularity and propagule pressure: determinants of introduction and establishment of aquarium fish. *Biol Invasions* **8**: 377–82.

Essl F, Dullinger S, Rabitsch W, *et al*. 2011. Socioeconomic legacy yields an invasion debt. *P Natl Acad Sci USA* **108**: 203–07.

FDACS (Florida Department of Agriculture and Consumer Services). 2018. Ornamental fish and invertebrates. Tallahassee, FL: FDACS. www.freshfromflorida.com/Business-Services/Aquaculture/Ornamental-Fish-and-Invertebrates. Viewed 27 Dec 2018.

Gerson HB, Cudmore NE, Mandrak LD, *et al*. 2008. Monitoring international wildlife trade with coded species data. *Conserv Biol* **22**: 4–7.

Grein G and Chen J. 2018. Editorial. *TRAFFIC Bulletin* **30**: 1.

Hayes KR and Barry SC. 2008. Are there any consistent predictors of invasion success? *Biol Invasions* **10**: 483–506.

Holmberg RJ, Tlusty MF, Futoma E, *et al*. 2015. The 800-pound grouper in the room: asymptotic body size and invasiveness of marine aquarium fishes. *Mar Policy* **35**: 7–12.

Howeth JG, Gantz CA, Angermeier PL, *et al*. 2016. Predicting invasiveness of species in trade: climate match, trophic guild, and fecundity influence invasion success of nonnative freshwater fishes. *Divers Distrib* **22**: 148–60.

Hulme PE. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J Appl Ecol* **46**: 10–18.

Hulme PE, Bacher S, Kenis M, *et al*. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J Appl Ecol* **45**: 403–14.

Jepson P and Ladle RJ. 2005. Bird-keeping in Indonesia: conservation impacts and the potential for substitution-based conservation responses. *Oryx* **39**: 442–48.

Katsanevakis S, Zenetos A, Belchior C, *et al*. 2013. Invading European seas: assessing pathways of introduction of marine non-natives. *Ocean Coast Manage* **76**: 64–74.

Keller RP and Lodge DM. 2007. Species invasions from commerce in live aquatic organisms: problems and possible solutions. *BioScience* **57**: 428–36.

Kikillus KH, Hare KM, and Hartley S. 2012. Online trading tools as a method of estimating propagule pressure via the pet-release pathway. *Biol Invasions* **14**: 2657–64.

Knobel DL, Laurenson MK, Kazwala RR, *et al.* 2008. A cross-sectional study of factors associated with dog ownership in Tanzania. *BMC Vet Res* **4**: 5.

Kraus F. 2009. Alien reptiles and amphibians: a scientific compendium and analysis. Basel, Switzerland: Springer Nature.

Krysko KL, Burgess JP, Rochford MR, *et al.* 2011. Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: outlining the invasion process and identifying invasion pathways and stages. *Zootaxa* **3028**: 1–64.

Livengood EJ, Funicelli N, and Chapman NA. 2014. The applicability of the US Law Enforcement Management System (LEMIS) database for the protection and management of ornamental fish. *AACL Bioflux* **7**: 268–75.

Lyons JA and Natusch DJ. 2013. Effects of consumer preferences for rarity on the harvest of wild populations within a species. *Ecol Econ* **93**: 278–83.

McNeely JA, Kapoor-Vijay P, Lu Z, *et al.* 2009. Conservation biology in Asia: the major policy challenges. *Conserv Biol* **23**: 805–10.

Padilla DK and Williams SL. 2004. Beyond ballast water: aquarium and ornamental trades as a source of invasive species in aquatic ecosystems. *Front Ecol Environ* **2**: 131–38.

Ramsay NF, Ng PKA, O'Riordan RM, *et al.* 2007. The red-eared slider (*Trachemys scripta elegans*) in Asia: a review. In: Gherardi F (Ed). Biological invaders in inland waters: profiles, distribution, and threats. Dordrecht, the Netherlands: Springer.

Reaser JK and Meyers NM. 2007. Habitattitude™: getting a backbone about the pet release pathway. In: Witmer GW, Pitt WC, and Fagerstone KA (Eds). Managing vertebrate invasive species: proceedings of an international symposium. Fort Collins, CO: US Department of Agriculture.

Rhyne AL, Tlusty MF, Szczebak JT, and Holmberg RJ. 2017. Expanding our understanding of the trade in marine aquarium animals. *PeerJ* **5**: e2949.

Rhyne AL, Tlusty MF, Schofield PJ, *et al.* 2012. Revealing the appetite of the marine aquarium fish trade: the volume and biodiversity of fish imported into the United States. *PLoS ONE* **7**: e35808.

Rixon CAM, Duggan IC, Bergeron NMN, *et al.* 2005. Invasion risks posed by the aquarium trade and live fish markets on the Laurentian Great Lakes. *Biodivers Conserv* **14**: 1365–81.

Robinson JE, Griffiths RA, St John FAV, *et al.* 2015. Dynamics of the global trade in live reptiles: shifting trends in production and consequences for sustainability. *Biol Conserv* **184**: 42–50.

Romagosa C. 2014. Patterns of live vertebrate importation into the United States: analysis of an invasion pathway. In: Keller RP, Cadotte MW, and Glenn S (Eds). Invasive species in a globalized world: ecological, social, and legal perspectives on policy. Chicago, IL: University of Chicago Press.

Rosa CA, Curi NHA, Puertas F, *et al.* 2017. Alien terrestrial mammals in Brazil: current status and management. *Biol Invasions* **19**: 2101–23.

Shepherd CR, Compton J, and Warne S. 2007. In: Carew-Reid J, Salazar R, and Spring S (Eds). Transport infrastructure and wildlife trade conduits in the GMS: regulating illegal and unsustainable wildlife trade. Philippines: Asian Development Bank.

Smith KF, Behrens MD, Max LM, *et al.* 2008. US drowning in unidentified fishes: scope, implications, and regulation of live fish import. *Conserv Lett* **1**: 103–09.

Springborn M, Romagosa CM, and Keller RP. 2011. The value of non-indigenous species risk assessment in international trade. *Ecol Econ* **70**: 2145–53.

Springborn M, Keller RP, Elwood S, *et al.* 2015. Integrating invasion and disease in the risk assessment of live bird trade. *Divers Distrib* **21**: 101–10.

Strecker AL, Campbell PM, and Olden JD. 2011. The aquarium trade as an invasion pathway in the Pacific Northwest. *Fisheries* **36**: 74–85.

Stringham OC and Lockwood JL. 2018. Pet problems: biological and economic factors that influence the release of alien reptiles and amphibians by pet owners. *J Appl Ecol* **55**: 2632–40.

Su S, Cassey P, and Blackburn TM. 2014. Patterns of non-randomness in the composition and characteristics of the Taiwanese bird trade. *Biol Invasions* **16**: 2563–75.

Su S, Cassey P, Vall-llosera M, *et al.* 2015. Going cheap: determinants of bird price in the Taiwanese pet market. *PLoS ONE* **10**: e0127482.

Tella JL and Hiraldo F. 2014. Illegal and legal parrot trade shows a long-term, cross-cultural preference for the most attractive species increasing their risk of extinction. *PLoS ONE* **9**: e107546.

Vall-llosera M and Cassey P. 2017a. Leaky doors: private captivity as a prominent source of bird introductions in Australia. *PLoS ONE* **12**: e0172851.

Vall-llosera M and Cassey P. 2017b. Physical attractiveness, constraints to the trade and handling requirements drive the variation in species availability in the Australian cagebird trade. *Ecol Econ* **131**: 407–13.

van Ham C, Genovesi P, and Scalera R. 2013. Invasive alien species: the urban dimension – case studies on strengthening local action in Europe. Brussels, Belgium: International Union for Conservation of Nature, European Union Representative Office.

van Wilgen NJ, Wilson JRU, Elith J, *et al.* 2010. Alien invaders and reptile traders: what drives the live animal trade in South Africa? *Anim Conserv* **13**: 24–32.

Weigle SM, Smith D, Carlton JT, *et al.* 2005. Assessing the risk of introducing exotic species via the live marine species trade. *Conserv Biol* **19**: 213–23.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2059/suppinfo