UNITED STATES COMMERCE IN LIVE VERTEBRATES: PATTERNS AND CONTRIBUTION TO BIOLOGICAL INVASIONS AND HOMOGENIZATION

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UNITED STATES COMMERCE IN LIVE VERTEBRATES: PATTERNS AND CONTRIBUTION TO BIOLOGICAL INVASIONS AND HOMOGENIZATION

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Christina Margarita Romagosa, daughter of Alfredo Romagosa and Margarita Gavaldá Romagosa, was born in Ft. Lauderdale, Florida, on May 9, 1974. She is a first generation American, the daughter of Cuban immigrants. She earned her B.S. and M.S. degrees in wildlife ecology and conservation at the University of Florida. She is married to Matthew Williams, whom she met during their undergraduate days at the University of Florida.

DISSERTATION ABSTRACT

UNITED STATES COMMERCE IN LIVE VERTEBRATES: PATTERNS AND CONTRIBUTION TO BIOLOGICAL INVASIONS AND HOMOGENIZATION

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The trade in live vertebrates is a threat to biodiversity, homogenizing distinct flora and fauna, introducing invasive species and parasites, and depleting wild populations. Because records of live vertebrates imported or exported by the United States are maintained by the US Fish and Wildlife Service (USFWS), a complete record of species in trade can be generated for this country. I obtained USFWS records for 6 taxonomic groups (amphibians, turtles, lizards, snakes, birds, and mammals) from 1968 – 2006 and used these trade data to quantify patterns in trade over time, and assess its importance as an invasion pathway and contribution to biological homogenization. The United States transported over 4200 species of terrestrial vertebrates during 1968 – 2006. Because trade in live vertebrates is dynamic, there have been changes in the species used for trade, quantities of individuals traded, and trading countries. I found that trade in live vertebrates contributes to both mechanisms of biological homogenization, extinctions and introductions. Based on Monte Carlo sampling, the number of species traded, established, and threatened with extinction were not randomly distributed among vertebrate families. Vertebrate families that were traded preferentially were also more likely to be established or threatened with extinction, compared to families that were not traded preferentially. I followed this research with additional work that focused solely on introductions. I used USFWS trade data to estimate the number of species that have transitioned successfully through the five stages of the invasion process, and compared those transition rates to those expected by the "tens rule". I found that roughly 10% of all vertebrate species imported to the United States were introduced. Birds and snakes did not differ from what was expected by the "tens rule" for the establishment transition. Amphibians, lizards and snakes exhibited a high transition success at the establishment stage (~ 45%). All vertebrate species differed from the "tens rule" in the final spread stage, their transition success was approximately 40%. Finally, I used human influence variables (import pressure, previous invasion success elsewhere, monetary value, wild caught vs. captive bred) to assess their ability to predict introduction and establishment success among vertebrate species imported to the United States. Import pressure was measured as the average number of individuals imported and separated by time period into past and recent import pressure. Among the *a priori* models, those that included past import pressure were the best models consistently across all 6 vertebrate groups. For specific taxonomic groups, previous success elsewhere was the most important variable among the top models, and improved the prediction of introduction and establishment success.

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INTRODUCTION

Throughout history, humans have been responsible for altering the distribution of the world's flora and fauna by transporting plants, animals, and their associated pathogens (Bates 1956; Elton 1958; Coblentz 1990). Continual transport of species can lead to the eventual homogenization of ecological systems, especially those systems subject to anthropogenic disturbance (Soulé 1990; Jenkins 1996; McNeely 1999). Transportation of both people and goods is faster today than in years past, and the associated volume has increased enormously (Soulé 1990).

The live vertebrate trade is an important biological commodity that creates the global movement of millions of individuals annually (Fernandez & Luxmoore 1997). Although the trade in live vertebrates has a long history, the emphasis in collections of exotic animals was originally for novelty and exotic foods for the noble classes (Lever 1992). Today, the ability to obtain live vertebrates is no longer restricted to nobility, and species are traded widely for pet, food, medicinal, and research uses. Advances in air transport and shipping techniques have facilitated the movement of more species and individuals used for the live vertebrate trade than in the past (Roe et al. 2002; Fuller 2003).

There are several biological repercussions are associated with trade in live vertebrates. For example, global trade in vertebrates is widely cited as a major threat to biodiversity through depletion of wild populations and is the primary pathway for species introductions (Jenkins 1995; Kraus 2003). These threats to biodiversity can contribute to the two mechanisms of the homogenization process: extinctions and introductions (Olden & Poff 2004).

Extinctions

The collection of vertebrates from the wild often is not sustainable, and as a result, over-collection is thought to be an important cause of population declines in many species of vertebrates (Fitzgerald 1989; Thomsen & Mulliken 1992; Jenkins 1995; Hoover 1998; Wilcove 1998; Gibbons et al. 2000; Baillie et al. 2004). Because of this and other threats, such as habitat destruction and invasive species, approximately 20% of the terrestrial vertebrates evaluated by the International Union for the Conservation of Nature (IUCN) are considered as susceptible to extinction (Baillie et al 2004). Some vertebrate species have life history characteristics (i.e., long generation times and low reproductive output) which make the viability of their populations vulnerable to continual harvest. Identifying vulnerable species is important for prioritizing species whose trade should be closely monitored and regulated to prevent additional losses through extinction. However, it is difficult to monitor native populations of those vertebrates that are involved in trade, as well as the trade itself, which results in an inability to create truly sustainable levels at which continued trade might be maintained.

Introductions

The introduction of nonindigenous species contributes to global biodiversity loss and can have negative effects on ecosystem function, alter animal and human health, and cause economic losses (Wilcove et al. 1998; Kolar & Lodge 2001). For example, nonindigenous fishes, frogs, and turtles introduced from the food and pet trades have had negative effects on native species worldwide through direct predation and competition (Adams et al. 2003; Cadi & Joly 2004). Additionally, amphibians in the live animal trade are believed to be responsible for the spread of chytridiomycosis, an emerging fungal disease linked to the population decline of amphibians (Hanselmann et al. 2004; Weldon et al. 2004).

The primary reason for the importation of live vertebrates to the United States is for commercial use (i.e., pet and food trade). A growing market for exotic pets and food has created a source for introductions. For example, a boom in the avicultural trade beginning in the 1950s resulted in the proliferation of escaped birds (Long 1981). Intentional and unintentional release of pets and surplus commercial stocks are not limited to birds; the release of non-native fish, amphibians, and reptiles has occurred in North America (Wilson & Porras 1983; Butterfield et al. 1997; Fuller et al. 1999). In the last half of the century, the pet industry has seen a surge of interest for these latter groups (Hoover 1998; Padilla & Williams 2004). The increase in species introduced from these groups reflects the increase in their trade. Additionally, as people immigrate to the United States from around the world, they bring with them food or medicinal animals used in their native cultures, as most recently evidenced and widely publicized by the introduction of the Snakehead fish (*Channa* spp; Courtenay & Williams 2004).

Which species introductions succeed or fail is a debated topic (Williamson & Fitter 1996), but it cannot be denied that the first step to any success or failure begins with the transport of that species to a new range (Kolar & Lodge 2001; Duncan et al. 2003). What effects species have on native ecosystems cannot be known until they arrive, and often their populations and effects are not known for long periods of time after their establishment due to low detection and lag times (Crooks & Soule 1999). Regardless, the United States alone has experienced economic losses of approximately $137 billion from all nonindigenous species (Pimentel et al. 2000). These costs have encouraged a more proactive approach to research on the biology of invasions, and created a need for a more predictive science (Kolar & Lodge 2001).

Assessing trade in live vertebrates

Given the repercussions associated with the trade in live vertebrates, an assessment of global trade and its relationship to the homogenization process is timely. However, information on vertebrate species transported globally through trade is difficult to obtain. The United States, however, is unique among many countries because records of legal importation and exportation are available. The United States Fish and Wildlife Service (USFWS) requires that all wildlife imported to or exported from the United States be declared. This requirement creates records, maintained by the USFWS, which can be then used to assess trade in live vertebrates. The United States is among the top importers of live vertebrates in the world, being responsible for the movement of over 200 million individuals each year (Defenders of Wildlife 2007).

I obtained USFWS data on the importation and exportation for species within six vertebrate groups (amphibians, turtles, lizards, snakes, birds, and mammals). These data were then used to address the following objectives:

1) To assess how the live vertebrate trade has changed over time
2) To assess whether trade in live vertebrates contributes to biological homogenization
3) To estimate transition success for vertebrates at each stage of the invasion process
4) To determine whether human influence affects introduction and establishment success

Dissertation outline

Chapter 2 of the dissertation describes the dynamics of the live vertebrate trade over a period of 30 years. I determined that over 4200 vertebrate species were transported by the United States. The average number of individuals imported to the United States increased over time for amphibian, lizard and snake species; more than half of these individuals are currently wild-caught. Turtles, birds, and mammals showed a decrease in the average number of individuals imported over time. The average number of individuals exported has increased over time at least 3-fold for turtles, lizards, and snakes. Countries in Asia have become the most important trading partners for vertebrates imported to and exported from the United States.

Chapter 3 investigates the contribution of the live vertebrate trade to both mechanisms of the homogenization process. The USFWS importation and exportation data were used to estimate global trade. I used randomization procedures to determine whether the transport, susceptibility to extinction, and introduction success of vertebrate species were randomly distributed among all vertebrate families. I found that specific vertebrate families were more likely to be transported than expected, and that those families were also more likely to be introduced successfully outside of their native range or susceptible to extinction.

The live vertebrate trade is the most important pathway for the introduction of vertebrates (Elton 1958; Kraus 2003). Because of this importance, the final two chapters of the dissertation focus solely on the introduction mechanism of biological homogenization. All species that are transported outside of their native range have entered what is known as the invasion process (Kolar & Lodge 2001). The invasion process can be divided into a series of stages through which some species progress, while others do not. I define here these five stages that are used throughout the dissertation:

1) Global species pool stage. This stage refers to all species available for transport to a new location.

2) Transport stage. Refers to those species taken from one location and then transported to a new location outside of that species' native range.

3) Introduction stage. A subset of transported species may then be released into the wild in the new location; these species are considered to be introduced.

4) Establishment stage. A subset of species introduced will successfully establish breeding populations in the new location; these species are considered to be established or introduced successfully.

5) Spread stage. A subset of established species will spread from their original introduction site.

The probability of any species successfully transitioning to the next stage is thought to be low, based on a concept known as the “tens rule” (Williamson 1996). The “tens rule”, a statistical generalization used as a reference point for studying invasions, predicts that roughly 10% (5-20%) of species will transition between stages of the invasion process (Williamson 1996). Current research suggests that vertebrates have higher transition success rates than expected by the tens rule for the final two transitions (Jeshcke & Strayer 2005), but not much is known about success rates for the first two specifically because information on what species are transported is not available (Cassey et al. 2004). In Chapter 4, I use the USFWS importation data and information available from the published literature to estimate the transition success for vertebrates transported to the United States. I found that the transition from source pool to transport stage conforms to the tens rule for all groups except turtles, the transition from transport to introduction conforms to the tens rule for all groups, and the progression of species through the final two transitions (introduction-to-establishment and establishment-to-spread) does not conform to the tens rule consistently among vertebrate groups. This finding is valuable because it demonstrates that previous assumptions based on the “tens rule" underestimate the number of vertebrate species likely to establish and spread in the United States.

Finally, Chapter 5 assessed whether human-influenced variables predicted transition success to the introduction and establishment stages for species transported to the United States. I found that import pressure in the past (used as a surrogate for propagule pressure) predicted introduction and establishment success consistently across all vertebrate groups. Whether a species has a previous history of introduction or establishment success elsewhere also predicted introduction and establishment success in the United States, but this result was not consistent among all taxonomic groups. The effect of import pressure and previous success elsewhere on introduction and establishment success can be used to inform import screening decisions

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CHAPTER II

THE UNITED STATES TRADE IN LIVE VERTEBRATES: AN EXAMINATION OF TRADE DYNAMICS OVER TIME

INTRODUCTION

The United States is one of the largest global markets for the live vertebrate trade, with over 185 million individuals imported and 30 million individuals exported each year (United States Fish and Wildlife Service 2006, Defenders of Wildlife 2007). This anthropogenic transport of wildlife is now widely cited as a major threat to biodiversity, homogenizing distinct flora and fauna, introducing invasive species and parasites, and depleting wild populations (Wilcove et al 1998, Hanselmann et al. 2004, Sodhi et al. 2004). Over time, trade in vertebrates has increased substantially, and this increase can only aggravate further the ecological problems with which trade is associated. As a result, there is a need to better understand the scope of this trade before its cascading ecological consequences can be fully recognized.

The United States is unique among all countries because records of legal importation and exportation are available. Several studies have examined United States trade in live vertebrates by using these records (e.g., Nilsson 1990, Hoover 1998, Franke and Telecky 2001, Schlaepfer et al. 2005, Defenders of Wildlife 2007, Smith et al. 2008), but few have assessed changes in vertebrate trade patterns over time. We use available data to conduct a synthetic review of trade in live vertebrates by the United States over a period of 30 years. Here, we build on previous work and assess the scope and scale of trade over time for 6 vertebrate groups. In particular, we assess specific vertebrate trade dynamics by summarizing the cumulative number of species imported over time, comparing the magnitude of individuals imported and exported for available time periods, and summarizing geographic patterns in importation and exportation.

METHODS

Since 1967, the United States has required that a declaration form accompany any importation or exportation of wildlife transported into or out of the United States. These forms were maintained by the United States Fish and Wildlife Service only as hardcopy until 1997, when information from these forms was also entered into a computerized database (Law Enforcement Management Information System, LEMIS). As hardcopies and computerized storage of these forms are destroyed by the USFWS every 5-7 years, the only sources of these data prior to 2003 are from previous compilations (Table 1). Not all information from form 3-177 is included in these publications (Table 2). Recent data (5-7 years prior to the current date) can be obtained through a Freedom of Information Act (FOIA) request filed through the USFWS. Data from these forms must be considered as a minimum of legal trade, as it represents only shipments that wildlife dealers have declared.

We requested data from the USFWS for 6 taxonomic groups (amphibians, turtles, lizards, snakes, birds and mammals). Because we began requests in 2002 and concluded in 2007, our data covers the period from 1998 – 2006 and consists of more than 800,000 records. To our compilation of these data, we added importation and exportation information available through previous publications (availability of data varies by taxonomic group, Tables 1 & 2), and updated to current taxonomy where necessary (Romagosa et al. 2009).

From these data, we compiled the cumulative number of species imported into the United States for the available years from 1970 – 2006. We calculated the average number of individuals imported per year for three time periods: early (1970s), middle (late 80s – early 90s) and recent (2002 – 2006). For most taxonomic groups, each time period spanned 5 years. For the recent time period, the source of origin (Table 2) was available for most individuals transported by the United States. In order to estimate how many individuals were directly taken from the wild, we separated wild-caught individuals from those that were captive bred or of unknown source. We followed the procedure by Schlaepfer et al. (2005) and included ranched as well as those born in captivity of wild parents. Because of the considerable taxonomic uncertainty (i.e., large number of individuals not identified to species) found in similar assessments of LEMIS fish data (Smith et al. 2008), we also determined the proportion of individuals per taxonomic group that were identified to species for the recent time period.

In order to compare changes in the geographic pattern of transport we summarized the top five importing and exporting countries (Table 2) for each taxonomic group for the early and recent time periods. For the recent time period, country of origin (Table 2) was available for most individuals. We compared whether the top five importing and exporting countries were also declared as the country of origin.

RESULTS

Importation

The United States was responsible for the legal global transport of over 4200 species and almost 300 million individuals of terrestrial vertebrates in years we assessed during 1968-2006. By the 1970s the United States was already importing over 2000 species; this number almost doubled by 2006. Bird species account for over half of the vertebrate species imported into the United States during the entire time period 1970-2006. While the number of species imported over time has increased for all taxonomic groups, it has increased least for birds, and most for lizards (Figure 1). The number of species imported for each of these taxonomic groups by 2006 was 1.5 and 3 times, respectively, the number of species imported in 1971.

Over seven million individuals were imported annually to the United States during the recent time period (2002-2006). This number is double the approximately 3.5 million individuals imported annually during early time period (1968-1972). The difference between the two time periods is driven mostly by the substantial increase in the number of amphibians, and to a lesser extent, lizards, imported (Figure 2). The average number of individuals imported annually decreased in the recent time period compared to the early time period for turtles, birds, and mammals. As a result of these trends, the most heavily imported taxonomic group has shifted from turtles (1970s) to amphibians (2000s). Data from the middle time period available for reptiles and birds suggests that the greatest change seen in the annual average number of individuals imported for lizards, turtles, and birds occurred after the early 1990s. An increase in the amount of snakes imported occurred mostly between the 1970s and early 1990s.

Almost half of all vertebrates recently imported into the United States are wild caught (Figure 3). Not surprisingly, 78% of wild caught animals are amphibians, the most intensively traded taxonomic group. Within a taxonomic group, lizards and snakes have the greatest proportion of wild caught individuals imported (65% and 84%, respectively); birds have the fewest wild-caught individuals (16%). Most individuals imported into the United States are directly identified to the species level (Figure 4). Amphibians and lizards each comprise roughly 40% of the unidentified individuals.

The main change in geographic patterns from the 1970s to the 2000s was the number of countries from which the majority of animals were imported. In the 1970s, over 80% of all amphibians and reptiles were imported from only one country per taxonomic group. The majority of birds and mammals were imported from 2 countries per taxonomic group, each country contributing approximately 35% of the individuals imported into the United States. In the 2000s, the number of individuals imported per country was more evenly distributed among the top five countries for each taxonomic group. On average, no country contributed more than 19% of the animals imported into the United States. Additionally, countries in Asia have become more important trading partners over time, replacing the dominance of South America in the 1970s. The most important countries from which the United States imports animals were also the declared country of origin for individuals within five of the six taxonomic groups. The one exception was turtles, where the country of origin for all 5 most important countries was the United States itself. Turtles originating from the United States were primarily sliders (*Trachemys scripta*) and other Emydid species exported from the United States and then refused clearance by the recipient country. Removing all countries in which the United States is listed as the primary country of origin, changed the geographic pattern considerably.

Exportation

The United States exported more than 13 million vertebrates annually to other countries during the recent time period (Figure 7). The vast majority of these exports are turtles, which are mostly either *Trachemys scripta* (48% of all turtle exports) or unidentified pond turtles (44% of all turtle exports). Lizards and snakes experienced an almost 4-fold increase in the average number of individuals exported from the early 1990s to the mid 2000s. Turtle exports, although already heavily exported by the early 1990s, doubled between the two time periods. Export data for amphibians, birds, and mammals were only available for the recent time period, so comparisons to an earlier time period could not be made for these taxonomic groups.

About 42% of all vertebrates exported from the United States were of wild-caught origin (Figure 8). Because roughly 13 million turtles were exported a year, they make up nearly all wild caught individuals. Again, most of these turtles were individuals from the species *Trachemys scripta*. Within taxonomic groups, no group had less than 40% of the individuals taken from the wild; mammals (71%) and lizards (65%) had comparatively high proportions of wild-caught individuals. About 40% of wild caught mammals exported were black-tailed prairie dogs (*Cynomys ludovicianus*), and 57% of the wild-caught lizards were native and nonnative anoles (*Anolis carolinensis* and *Norops sagrei*) For most taxonomic groups, less than 10% of individuals were not identified to species (Figure 9). However, this trend does not apply to turtles, for which almost half of the individuals exported, approximately 5 million individuals, were not identified.

No one country imports more than 50% of animals exported from the United States . Canada is an important trading partner for amphibian, bird, and mammals that originate in the United States, importing on average 40% of individuals from these taxonomic groups. Asian countries dominate approximately 80% of the turtle export market. About 23% of lizards and snakes that originate in the United States are exported to Germany.

DISCUSSION

Although this study only analyzes a fraction of the global trade in live vertebrates, the quantity of individuals and species in the United States trade alone indicates the large magnitude at which vertebrates are traded globally. The United States trade data reveal several general patterns of the live vertebrate trade. We found that the trade in most vertebrate groups is increasing globally, a trend that has been corroborated by other research (Auliya 2003, Engler and Parry Jones 2007, Carrete and Tella 2008). Trade in live vertebrates, like all trade, is dynamic. What is traded from year to year is subject to the changes in supply and demand due to population busts and declines, trade restrictions, and human tastes. These trade-related dynamics have led to changes in the species used for trade, the individual quantities of those species traded, and where those species are traded.

Some trends have remained constant over the past 30 years, such as the high diversity of bird species found in trade. Because birds have been traded by humans for centuries, the number of species in trade should not be surprising, as more species should be accumulated over time (Fitzgerald 1989). With respect to the United States, the trade in wild birds already existed as early as 1865, and more than 200 species were imported in 1906 alone (Oldys 1907). In the last few decades of the 20th century, the pet industry in the United States and abroad has seen a surge of interest for amphibians and reptiles (Hoover 1998, Auliya 2003, Padilla and Williams 2004). This interest has led to more than a doubling of the amphibian and reptile species imported to the United States since the early 1970s. Turtles are particularly affected by this trend; this taxonomic group has only 300 species world-wide, and 62% of their global species richness has been imported to the United States to date. Turtles are not the only group intensely traded by humans. Within all the taxonomic groups, species within specific families are traded more than expected, suggesting that species used for trade are not randomly distributed among taxonomic groups (Romagosa et al. 2009).

Interest in a more diverse selection of amphibian and reptile species for pets has been accompanied by a greater demand for individuals from these taxonomic groups. The increase in the average number of individuals imported per year in the recent time period for lizards and snakes can be attributed to individuals imported for the pet trade. Most of these individuals belong to just a few species that are popular pet animals, such as iguanas (*Iguana iguana*), Chinese water dragons (*Physignathus cocincinus*), and boa and python species. The increase in amphibian imports, however, can be attributed to the food trade and education animals, as well as to the pet trade. More than half of the amphibians are from one species, *Rana catesbeiana* – a species native to the United States, but that is extensively "farmed" overseas in Asia and South America and then shipped back to the United States for food and education animals. Pet amphibian species such as fire-bellied toads and newts (*Bombina orientalis* and *Cynops orientalis*) and various species of African clawed frogs (*Hymenochirus* sp. and *Xenopus* sp.) contribute another 40% of individuals imported.

While the number of individuals imported increased for amphibian and most reptile groups between the two time periods, they decreased for turtles, birds and mammals. We attribute the decline in turtles to trade regulations enforced on foreign turtles, and the increased availability of native turtles for pets due to ranching operations (Thorbjarnarson et al. 2000). The United States Wild Bird Conservation Act of 1992 is likely responsible for the decrease seen in the average number of individuals imported per year for birds between the two time periods (Engler and Parry-Jones 2007). The United States was surpassed by the European Union as the most important foreign market for the bird trade following the enforcement of the Wild Bird Conservation Act. A recent ban on the import of wild birds enacted by the European Union in 2007 is expected to have the same effect on the number of birds imported to those countries as seen in the United States after 1992 (Carrete and Tella 2008). In the 1970s, 87% of the mammal trade was in primates used as research animals (Banks 1976). The decrease between the two time periods can also be attributed to stricter regulations regarding trade in primates, as well as increased availability of individuals from captive breeding programs established within the United States (Jorgenson and Jorgenson 1991). Country-specific restrictions in trade are the main cause for the shifts in geographic patterns seen over time (Fitzgerald 1989).

We expect that the same trade-related dynamics that affect importation of vertebrates into the United States also affect their export to other countries, with one major exception. The export of turtles from the United States has nearly doubled in the last decade. While approximately 12 million of the turtles exported are *Trachemys scripta* and unidentified pond turtles (*Pseudemys* sp.), nearly all of the remaining one-million individuals exported are species native to the United States. The primary export market for all turtles are countries in southern Asia, where they are mostly used for the food trade (Thorbjarnarson et al. 2000). The trade in North American turtles is largely unregulated, and concern over the amount of turtles exported to other countries has led to the ban or the proposition of a ban for wild collection in several states. Very few North American turtle species are monitored and regulated by the Convention for Trade in Endangered Species of Flora and Fauna (CITES). CITES is currently the only monitoring system of global trade for species that may be negatively affected by overexploitation (Ginsberg 2002) and has been credited as the most effective international treaty to reduce trade pressure on species that are listed among the CITES appendices (Jorgenson and Jorgenson 1991, Thomsen and Mulliken 1992, Ong 1998).

Many vertebrate species around the world are in decline, and over-exploitation has been cited as one of the most important causes of population declines for some vertebrate groups (Collar 1994, Gibbons et al. 2000). Some vertebrate species have life history characteristics, such as long generation times or low reproductive output, which make the viability of their populations vulnerable to continued harvest. In particular, with the decline in turtle populations at crisis stage (Jenkins 1995, Ginsberg 2002) the exploitation of species from this taxonomic group should not continue at the current rate. Identifying vulnerable species is important for prioritizing those species whose trade should be closely monitored and regulated to prevent additional losses through extinction.

Additional concerns exist regarding health risk through the transmission of disease to native animals and humans by vertebrate species in trade (Defenders of Wildlife 2007). For example, amphibians in the live animal trade are believed to be responsible for the spread of chytridiomycosis, an emerging fungal disease linked to the population decline of amphibians (Hanselmann et al. 2004, Weldon et al. 2004). The zoonotic disease transmission of monkeypox virus to humans from Gambian pouched rats (*Cricetomys gambianus*) and black-tailed prairie dogs kept as pets in the United States, led to a complete ban in their trade after 2004 by the Centers for Disease Control (Defenders of Wildlife 2007).

Finally, the live vertebrate trade is the most important pathway for vertebrate introductions (Kraus 2003). The introduction of nonindigenous species contributes to global biodiversity loss and can have negative effects on ecosystem function, alter animal and human health, and cause economic losses (Wilcove et al. 1998, Kolar and Lodge

2001). The number of vertebrate species imported to the United States is increasing over time, and concomitantly resulting in an increasing number of introductions (Temple 1992; Kraus, 2009). Additionally, those species with many individuals imported have a greater chance for establishment based on propagule pressure (Kolar and Lodge 2001). This concept is exemplified by the establishment worldwide of two heavily traded species, the bullfrog (*Rana catesbeiana*) and red-eared slider (*Trachemys scripta*) (Kraus 2009). Additional introductions will continue if there is no effort to stem the flow of species moved globally through this pathway.

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Table 2 -1. Availability of data from Form 3-177 by taxonomic group and year.

Taxonomic group	Years available	Import or Export	Reference
Amphibian	1970-1971	Import only	Busack 1974
	1998-2006	Import and export	This study
Reptile (turtles, lizards, snakes)	1970-1971	Import only	Busack 1974
	1989-1997	Import and export	Franke & Telecky 2001
	1998-2006	Import and export	This study
Bird	1968-1972	Import only	Banks 1970, Banks & Clapp 1972, Clapp & Banks 1972, Clapp & Banks 1973, Clapp 1975
	1977-1980	Import only	Nilsson 1977
	1986-1988	Import only	Nilsson 1990
	1998-2006	Import and export	This study
Mammal	1968-1972	Import only	Paradiso & Fisher 1972, Clapp 1973
	1998-2006	Import and export	This study

Table 2 - 2. Information from Form 3-177 used for this study.

	Description	Year available
Identity of species	(common name, scientific name)	All years
Quantity of individuals		All years
Source of origin	whether captive bred or wild caught	1998-2006
Country of origin	Where animal was taken from the wild or was born	1998-2006
Importing or exporting country	Country to which or where from the animal was transported	1968-1972, 1998-2006

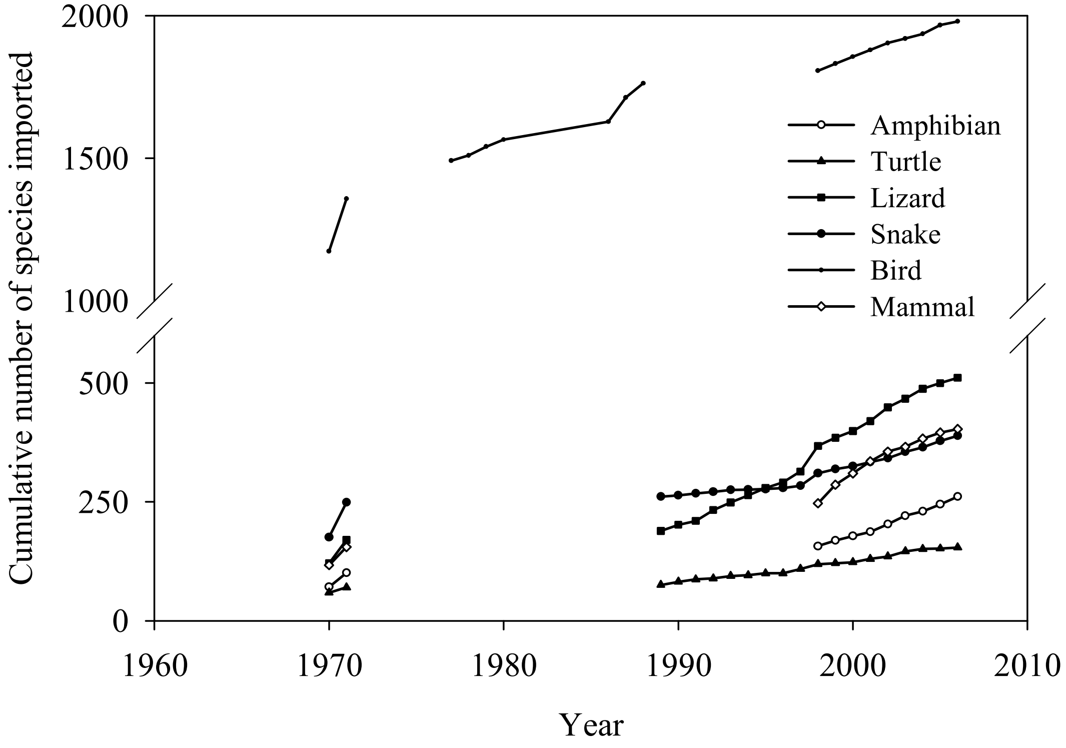

Figure 2 - 1. Cumulative number of species imported by the United States over time (1970 – 2006) for six vertebrate groups.

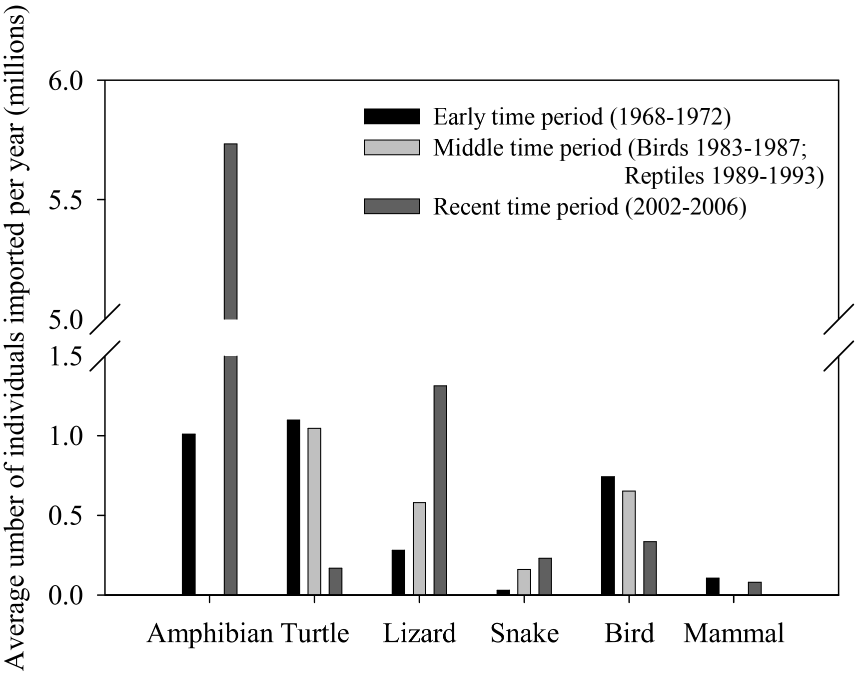

Figure 2 - 2. Average number of individuals imported per year by the United States for early, middle, recent time periods.

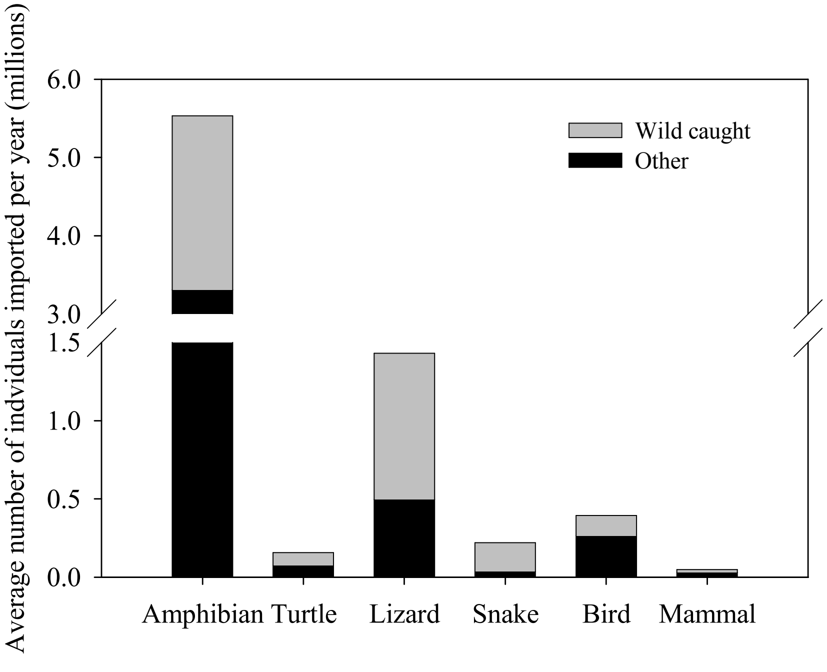

Figure 2 - 3. Average number of individuals imported per year that were declared as wild caught for recent time period (2002-2006). The category “other” contains individuals that were declared as any other source of origin (captive bred, unknown).

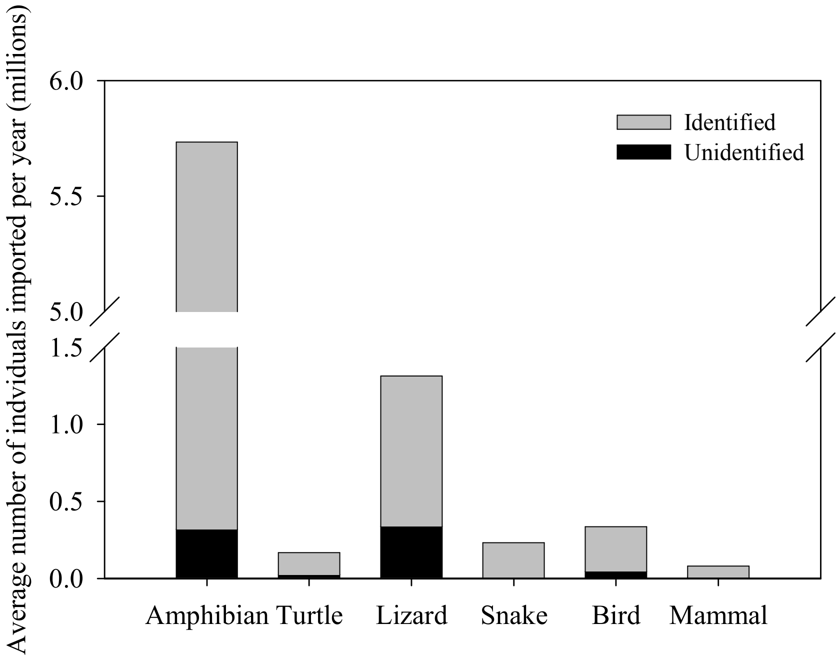

Figure 2 - 4. Average number of individuals imported per year that were and were not identified to species for recent time period (2002-2006).

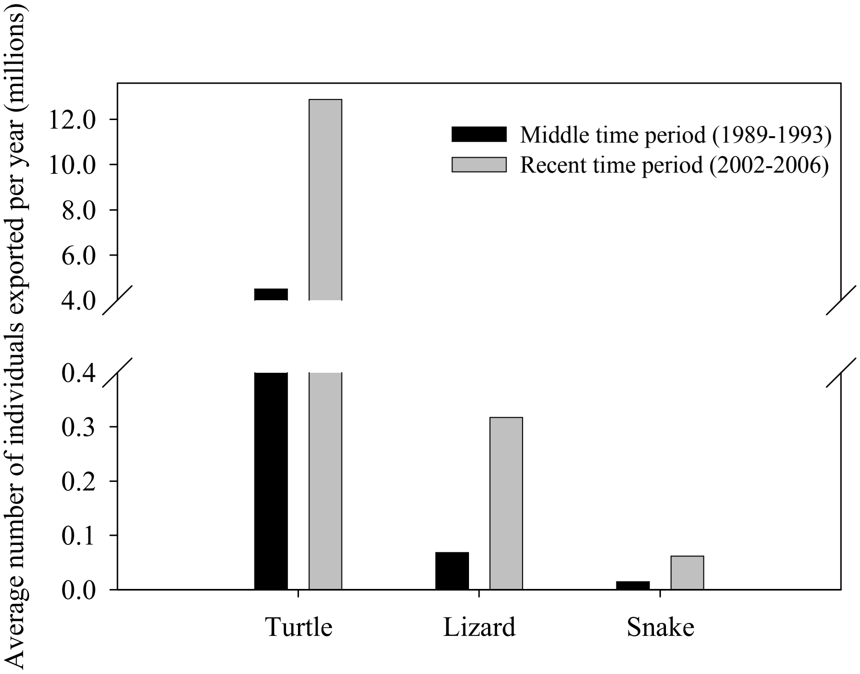

Figure 2 - 5. Average number of individuals exported per year for middle and recent time periods. Data on exports for both time periods were only available for reptiles.

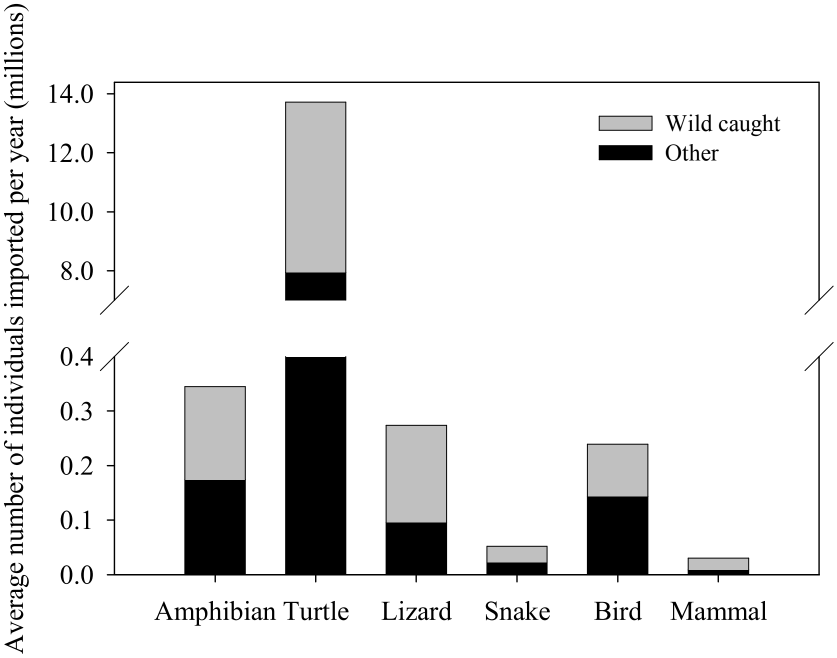

Figure 2 - 6. Average number of individuals exported per year that were declared as wild caught . for recent time period (2002-2006). The category “other” contains individuals that were declared as any other source of origin (captive bred, unknown).

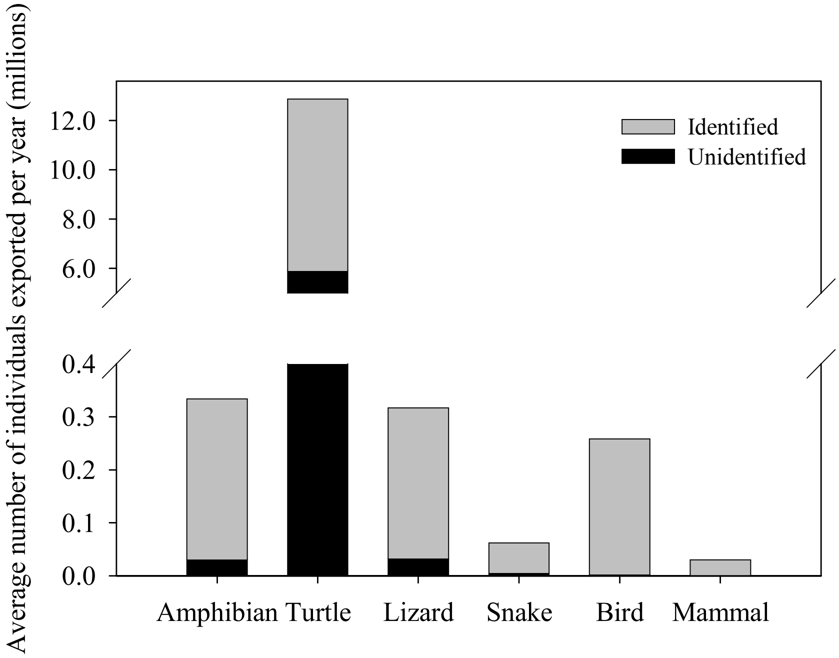

Figure 2 - 7. Average number of individuals exported per year that were and were not identified to species for recent time period (2002-2006).

CHAPTER III

CONTRIBUTION OF THE LIVE VERTEBRATE TRADE TOWARD TAXONOMIC HOMOGENIZATION

INTRODUCTION

Taxonomic homogenization—the process by which taxonomic similarity increases among geographic areas—is often driven by a breakdown of dispersal barriers through anthropogenic means (McKinney & Lockwood 1999; Olden & Poff 2003). The process of homogenization results from the interplay of two mechanisms: extinctions, the way members within distinct communities are lost, and introductions, the process through which cosmopolitan communities are created. Disagreements abound over the magnitude and long-term consequences of homogenization, but it is generally agreed that the process is expected to yield a decrease in global diversity (Sax & Gaines 2003). Although it would be impossible to homogenize the global flora and fauna completely because of climatic and geographical differences among regions (Collins et al. 2002), even small shifts in species composition can have profound impacts on ecosystem function, resiliency, and stability (Sax & Gaines 2003).

Although barriers to dispersal do exhibit natural variation in their porosity over time and space, the process of taxonomic homogenization is clearly accelerated by human-mediated transport of species. The homogenization process can be expected to increase with global trade (Olden & Poff 2004) because wildlife can be transported more quickly and easily now than in the past (McNeely 1999). Trade in live vertebrates, one aspect of this increased transport, is a major pathway for introductions and contributes to declines of wild populations due to overharvesting (e.g., Jenkins 1995; Kraus 2003; Cassey et al. 2004). By quantifying particular aspects of trade in live vertebrates, assessment of the contribution of trade to the process of homogenization of vertebrates may be possible. Measurement of the magnitude of this contribution can provide an upper limit as to what can be expected if the process continues.

Records of trade in live vertebrates, lists of species of global conservation concern, and observations of vertebrate introductions provide information from which the relationship between trade and species extinctions and introductions can be explored. When examined across taxonomic groups, such data should highlight the contribution of vertebrate trade to the homogenization process and should allow conservation efforts to be concentrated on taxonomic groups that are particularly problematic. Transport, extinction, and introduction of species are likely not random processes among higher taxonomic groups. Taxonomic biases have been identified in the homogenization mechanisms in families of birds and amphibians (extinction: Bennett & Owens 1997; Bielby et al. 2006; introduction: Lockwood 1999; Blackburn & Duncan 2001; introduction and extinction: Lockwood et al. 2000), but these characteristics have not been assessed among reptile groups. Additionally, the taxonomic biases seen in bird families for both homogenization mechanisms may be driven by additional bias in their transport (Lockwood et al. 2000). Because information on the number of vertebrate species transported globally through trade is difficult to obtain (Cassey et al. 2004), no one has assessed taxonomic biases in the trade of live vertebrates and its contribution to the homogenization process.

We used records of species transported to and from the United States as a proxy for the pool of species traded globally and addressed the concept of taxonomic homogenization specifically through the lens of trade. The United States is a major trader of live vertebrates, with more than 2000 species and over 200 million individuals imported each year during 2000–2004 (Defenders of Wildlife 2007). Although these data provide a minimum estimate of the global trade in live vertebrates, the dominance of the United States in global trade volume and the completeness of the records suggest that they are an informative sample of global live-vertebrate trade. In examining these records, our objectives were to assess whether trade, extinction, and introduction are taxonomically biased and to explore how taxonomic biases in trade in live vertebrates contribute to the biological mechanisms that drive biotic homogenization. Specifically, we expected that if trade contributes to the processes of homogenization, then families that are traded preferentially should also have more species that are threatened with extinction or that are established outside their native range than species that are not traded preferentially.

METHODS

Data Sources

Data documenting importation and exportation of six major vertebrate groups (amphibians, turtles, lizards, snakes, birds, and mammals) into or out of the United States were obtained from a U.S. Fish and Wildlife Service (USFWS) declaration form that documents importation or exportation of fish or wildlife form. This form (Form 3–177) must accompany any import or export of live or dead fish and wildlife and their products. We accessed recent data from these forms through a Freedom of Information Act request filed through the USFWS Law Enforcement Management Information System (LEMIS).Only data from 5 years prior to the date of the request are usually available. We requested data for 1998–2006. For information before 1998, we extracted data from published compilations and USFWS reports (e.g., Clapp & Banks 1973; Hoover 1998; Franke & Telecky 2001). An additional description of these data and their potential shortcomings is provided in Schlaepfer et al. (2005). We considered all species; thus, we assumed if a species was recorded in the USFWS data, then it was capable of being transported live to a new location. We updated taxonomic names to conform to current taxonomy (Wilson & Reeder 2005; Clements 2007; Frost 2007; Uetz 2007).

The International Union for Conservation of Nature (IUCN) Red List is the only source that estimates extinction risk rigorously and consistently. Therefore, the IUCN Red List has been used to assess the potential for species extinctions (e.g., Bennett & Owens 1997; Russell et al. 1998; McKinney 1999). We used the 2007 IUCN Red List (IUCN 2007) to estimate the likelihood of extinction for each species traded by the

United States. Following Bennett and Owens (1997), we categorized species as sensitive to the extinction process if they were listed in any of the following five categories: extinct, extinct in wild, critical, endangered, or vulnerable. Henceforth, the term IUCN listed indicates species assumed to be vulnerable to extinction.

We obtained information on species establishment from published sources (Long 1981; Lever 1987; Lever 2003; Long 2003; Pranty 2004; Bomford et al. 2005).

Analyses

We compiled data on global species richness, number of species traded by the United States, number of established species, and number of IUCN-listed species for families within all vertebrate groups. To assess whether trade has an effect on the processes of homogenization, we first identified which vertebrate families were traded, established, and IUCN listed more than expected. We determined taxonomic biases among vertebrate families with randomization procedures as described by Lockwood et al. (2000). We performed these randomization procedures by combining families from all six vertebrate groups into a single pool or by analyzing each vertebrate group as a separate pool. Because the results from each approach were similar, we only describe the randomization procedures performed for the combined pool. (The analytical details and results for the randomization procedures with each vertebrate group considered separately are available upon request from C.M.R.) We generated empirical frequency distributions with Monte Carlo sampling for each of three categories (number of species traded, established, and IUCN listed). These distributions were derived by a random draw of species, without replacement, from the global pool of vertebrate species until the total draws equaled the observed number of traded species. The number of species randomly selected from each family was then counted as a single estimate of expected numbers and compared with the observed numbers. This process was repeated 99,999 times. For the established and IUCN-listed categories, we performed a similar randomization process, except that we took the observed number of species per category and randomly selected an identical number of species from the pool of all vertebrate species known to have been traded.

We used the randomization-based empirical distributions to estimate one-tailed statistical probability of the actual observed values. For the upper tail, we divided the number of randomizations that had a value greater than or equal to the observed number by the number of iterations (99,999) to obtain a p value. We did not adjust α for multiple comparisons because these adjustments have been increasingly criticized (Moran 2003). Instead, we judged statistical significance for this test at both $\alpha = 0.01$ and 0.05. This method resulted in two separate family lists for the three categories of interest.

Finally, we used two separate goodness-of-fit tests to evaluate whether trade had an effect on the homogenization process. Each test was conducted twice, once with the family list generated from $\alpha = 0.05$ and once with the list generated from $\alpha = 0.01$. The first pair of tests was used to determine the relationship between trade status (preferentially or nonpreferentially traded) and extinction risk (IUCN listed more than expected or not IUCN listed more than expected), and the second pair of tests evaluated the relationship between trade status and establishment (established more than expected or not established more than expected).

RESULTS

We examined 4202 species from 344 vertebrate families traded by the United States, representing approximately 14% of species and 75% of families from the global fauna. Of these traded species, 387 species from 122 families are established and 484 species from 145 families are IUCN listed. The observed numbers of species that are traded and then become established or are IUCN listed were not randomly distributed among vertebrate families within the major vertebrate groups we analyzed (Tables 1 & 2). For the family list created at $\alpha = 0.05$, 100 of 344 (29%) vertebrate families were traded preferentially. These families were four times more likely to be either IUCN listed or established than families that were not traded preferentially (Table 3). At $\alpha = 0.01$, 74 families (22%) were traded preferentially and were six times more likely to be IUCN listed or established than families not traded preferentially (Table 3). Most families were susceptible to only one homogenization mechanism; however, four families (Emydidae, Iguanidae, Phasianidae, Psittacidae) were susceptible to both mechanisms of the homogenization process.

Families traded more than expected were also established ($G=7.23$, $p=0.007$ for overall test) or IUCN listed ($G = 21.37$, $p < 0.0001$) more than expected when those families were evaluated at $\alpha = 0.05$. This interaction with trade remained for those families that were IUCN listed more frequently than expected when $\alpha = 0.01$ ($G = 18.38$, $p < 0.00001$); this did not hold for families established more frequently than expected when $\alpha = 0.01$ ($G = 1.78$, $p = 0.18$).

DISCUSSION

The live-vertebrate trade is correlated with global and taxonomic patterns of homogenization. Although results of other studies suggest such a trend, it has proven difficult to evaluate (Lockwood et al. 2000). Our use of U.S. trade data allowed us to assess the effect of live-vertebrate trade on the homogenization process for the families we analyzed. Vertebrate families that were traded preferentially were more susceptible to either mechanism of the homogenization process than families that were not traded preferentially. This finding is consistent with the hypothesis that trade in live vertebrates is an important introduction pathway and an important factor regarding the sustainability of wild populations. Most vertebrate families were affected by only one of the two homogenizing mechanisms. Thus, the contribution of trade to homogenization of the global vertebrate fauna may not occur at an equal rate through both mechanisms for all vertebrate groups. The number of species used by humans is increasing (Russell et al. 1998; Jeschke & Strayer 2005), which means that over time additional species will be affected by either or both homogenizing mechanisms of introduction and extinction. We propose that our method be repeated in the future to determine those families that are most affected by continuing increases in vertebrate trade.

Data that we used for species currently affected by the homogenization process should be considered as a minimum for introductions and a maximum for extinctions for most vertebrate groups. Because all established species are not always detected and because there is a time lag for species to establish after their introduction (Crooks & Soul´e 1999; Jeschke & Strayer 2005), the number of established species should be greater than what we observed. Conversely, the IUCN Red List is generated from an analysis of extinction risk, and if conservation efforts are focused on those threatened species, then the actual number of species that do go extinct should be lower than what we assumed (Russell et al. 1998). This trend, however, may not be applicable to all vertebrate groups. An additional consideration with the IUCN Red List is the paucity of species assessed within lizards and snakes. We believe the scant attention paid to the families within these groups caused them to appear insensitive to the extinction mechanism. Although this insensitivity may be an actual trend, a reanalysis of our data following the completion of the Global Reptile Assessment, launched in 2004 (Baillie et al. 2004) and stalled because of funding shortages (S.N. Stuart, personal communication), may show more families within these vertebrate groups are susceptible to this particular homogenization mechanism.

Because we only considered vertebrate species that are known to be traded, our results of taxonomic bias among amphibian and bird families affected by homogenization differs in some cases from those of other authors (Lockwood et al. 2000; Bielby et al. 2006). Our results were equivalent to those found by Lockwood et al. (2000) for only three of the 13 bird families with more IUCN-listed species than expected (Gruidae, Phasianidae, Psittacidae) and for five of the seven families with more established species than expected (Anatidae, Estrilididae,Odontophoridae, Phasianidae, and Psittacidae). Of the seven families Bielby et al. (2006) identified as being IUCN listed more than expected, we found only one (Plethodontidae) that fit this description. Additionally, another family that was IUCN listed more frequently than expected, Mantellidae, was found by Bielby et al. (2006) to be IUCN listed less frequently than expected. These differences imply that when homogenization is assessed within the restricted window of trade, certain families are susceptible to the mechanisms of the homogenization process, whereas in other families a medium other than trade likely drives homogenization. Homogenization is a problem with multiple causative forces, and recognizing trade's contribution should promote awareness of the need for trade regulation.

When making conservation recommendations regarding regulation of trade, specific attention should be given to those vertebrate families listed in Tables 1 and 2. For example, trade in several turtle families contributed to their homogenization mostly through extinction. This result corroborates recent discussions regarding the global crisis in the decline of turtles due to their trade (Gibbons et al. 2000; Nijman & Sheperd 2007) and emphasizes a need for trade restrictions on this vertebrate group. Additionally, the observation that some families are already experiencing the effects of homogenization regardless of their level of trade, implies that trade does not drive their homogenization or that those groups do not need to be intensely traded to be susceptible to either mechanism of the homogenization process. These effects may be intensified should their trade continue to increase.

We do not contend that complete homogenization will occur through trade in live vertebrates; rather, we emphasize that trade is an important contributing factor to the global decline in diversity. Homogenization of higher taxa (e.g., family level) could result in a disproportionately large loss in vertebrate diversity (McKinney & Lockwood 2001). Additionally, biotic differentiation, a process in which taxonomic similarity decreases among geographic areas, is also driven by introductions and extinctions (Olden & Poff 2003). Because homogenization and differentiation share the same mechanisms, we expect species within the families susceptible to the homogenization process also could contribute to biotic differentiation.

The live-vertebrate trade contains specific pathways (i.e., pets, live food, and research) that could exert varying pressure on establishment success or populations declines. Future work should consider these different aspects of live-vertebrate trade and the significance of their relative effects on the homogenization process. We focused only on direct trade as a factor and not on the effect of the loss or gain of species, and their associated pathogens, on native fauna. Quantifying these effects on global ecosystems is important, but difficult to assess. In lieu of this knowledge, recognizing which taxonomic groups could be affected by the homogenization process at disproportionate rates can be a first step to help direct further study on the functional roles of those groups in structuring communities.

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Table 3 - 1. Observed and expected number of species within vertebrate families that are traded by the United States and have become established outside their native range.[a]

Vertebrate group	Family	Observed established species	Expected established species	Observed traded species	Expected traded species	Global species richness[b]
Amphibia	Alytidae	2**	0.14	2	1.50	11
	Bombinatoridae	2*	0.28	3	1.43	10
	Dicroglossidae	3*	0.83	9	23.51	164
Testudines	Emydidae	7*	3.12	34**	5.87	41
Sauria	Iguanidae	4*	1.20	13**	5.16	36
	Polychrotidae	6**	1.19	13	56.35	393
Aves	Estrildidae	15**	7.18	78**	20.20	141
	Fringillidae	10*	5.34	58**	25.24	176
	Mimidae	2*	0.18	2	5.02	35
	Odontophoridae	3*	0.55	6	4.44	31
	Phasianidae	11**	5.07	55**	22.23	155
	Psittacidae	30*	21.74	236**	49.60	346
	Tetraonidae	4**	0.65	7*	2.72	19
Mammalia	Castoridae	2*	0.18	2*	0.28	2
	Cervidae	12**	1.38	15**	7.31	51
	Leporidae	3**	0.46	5	8.88	62
	Macropodidae	7**	1.66	18**	9.30	65
	Muridae	5**	1.29	14	104.66	730
	Procyonidae	3*	0.64	7**	2.01	14
	Sciuridae	7*	2.67	29	39.90	278

[a] Families that have significantly more established species than expected are based on randomization procedures (* $\alpha = 0.05$, ** $\alpha = 0.01$) in which selection was made from a pool containing species from all vertebrate families combined. Families that were also traded more than expected based on randomization procedures are marked with an asterisk (* $\alpha = 0.05$, ** $\alpha = 0.01$) within the Traded species column.

[b] Provided for reference.

Table 3 - 2. Observed and expected number of species within families that are traded by the United States and considered vulnerable to the extinction process by the IUCN (International Union for Conservation of Nature) Red List.[a].

Vertebrate group	Family	Observed IUCN-listed species	Expected IUCN-listed species	Observed Traded species	Expected Traded species	Global species richness[b]
Amphibia	Mantellidae	10**	1.95	17	23.81	166
	Petropedetidae	2*	0.35	3	2.29	16
	Plethodontidae	5**	1.38	12	54.19	378
Testudines	Cheloniidae	5**	0.57	5**	0.86	6
	Emydidae	10**	3.92	34**	5.87	41
	Geoemydidae	32**	5.43	47**	9.90	69
	Podocnemididae	5**	0.81	7**	1.16	8
	Testudinidae	24**	4.39	38**	7.31	51
	Trionychidae	9**	1.84	16**	4.31	30
Sauria	Iguanidae	6**	1.49	13**	5.16	36
Aves	Casuariidae	2*	0.35	3**	0.43	3
	Drepanididae	3**	0.34	3	3.02	21
	Gruidae	8**	1.49	13**	2.15	15
	Phasianidae	12*	6.32	55**	22.23	155
	Psittacidae	44**	27.20	236**	49.60	346
	Spheniscidae	4*	1.15	10**	2.43	17
Mammalia	Bovidae	16*	8.98	78**	20.51	143
	Cercopithecidae	8**	3.11	27*	18.88	132
	Chinchillidae	2*	0.35	3	1.01	7
	Elephantidae	2*	0.23	2	0.43	3
	Equidae	3*	0.58	5**	1.15	8
	Eupleridae	3**	0.35	3	1.15	8
	Felidae	8**	2.65	23**	5.73	40
	Hippopotamidae	2*	0.23	2*	0.28	2
	Hominidae	4**	0.46	4*	1.01	7
	Hylobatidae	5**	0.80	7**	2.00	14
	Lorisidae	2*	0.23	2	1.29	9
	Rhinocerotidae	2*	0.35	3*	0.72	5
	Ursidae	4**	0.81	7**	1.14	8

[a] Vertebrate families that have significantly more IUCN-listed species than expected are based on randomization procedures (* $\alpha = 0.05$, ** $\alpha = 0.01$) in which selection was from a pool containing species from all vertebrate families combined. Families that were also traded more than expected based on randomization procedures are marked with an asterisk (* $\alpha = 0.05$, ** $\alpha = 0.01$) within the traded-species column.

[b] Provided for reference.

CHAPTER IV

TENS RULE AND THE PROGRESSION OF VERTEBRATES IN TRADE THROUGH THE INVASION PROCESS

INTRODUCTION

Growth and development of trade has led to an increased volume of commodities exchanged among countries. This increased global trade has been linked with an increase in intentional and unintentional species introductions worldwide for several taxonomic groups (Dehnen-Schmutz et al. 2007; Levine & D'Antonio 2003; Westphal et al. 2008). For many vertebrate groups, trade in live specimens is thought to be the most important pathway related to their introduction because millions of individuals are transported annually and many of these species have become established outside their ancestral ranges (Kraus 2003; Lockwood et al. 2000; Padilla & Williams 2004; Semmens et al. 2004). Nevertheless, few studies have quantified trade in live vertebrates because the number of species and individuals that enter and progress through the invasion process by this pathway is difficult to ascertain.

The biological invasion process has been divided into five stages (Fig. 1; Kolar & Lodge 2001; Williamson 1996) that allow for a more precise analysis of species invasions, and a better prediction of factors that influence successful transitions between stages. The base rate (sensu Smith et al. 1999), or the proportion of species that successfully transition through each stage of the invasion process, is expected to be small, based on a concept known as the tens rule (Fig. 1; Williamson & Brown 1986; Williamson & Fitter 1996; Williamson 1996). The tens rule predicts that, on average, 10% (5-20%) of species will transition from one stage to the next as those species are sampled from the world's fauna, transported to a new locality, released, become established, and eventually spread from the introduction site (Williamson 1996). The tens rule is a simplistic statistical generalization whose reference base rates are used as a yardstick to which biological invasions can be compared (Smith et al. 1999; Williamson 2006). Because the base rate of transitions expected by the tens rule is low, the prevalence of species transitioning from one stage to the next is thought to be too low to be accurately predicted (Smith et al. 1999). Continued examination of the tens rule can provide for a better understanding of biological invasions by highlighting taxonomic groups that may be unusually successful (Byers et al. 2002). Those taxonomic groups with higher base rates would be the best candidates for creation of risk assessment methods to prevent them from progressing through subsequent stages.

Although the tens rule has been shown to apply generally to plants and some animal groups (Williamson & Fitter 1996), current research suggests that it may not be applicable to all animal invasions (Cassey et al. 2004; Garcia-Berthou et al. 2005; Jeschke & Strayer 2005; Keller et al. 2007), and may differ depending on the source pathway (Williamson & Fitter 1996). Vertebrates appear to have higher transition success rates than expected by the tens rule for the introduction-to-establishment and establishment-to-spread transitions (Williamson 1996; Kraus 2003; Cassey et al. 2004; Garcia-Berthou et al. 2005; Jeshcke & Strayer 2005), but not much is known about success rates for the first two transitions. A statistical generalization for transition success has never been made for the first transition (source pool-to-transport) because information on the number of species entrained in the transport stage is difficult to obtain (Cassey et al. 2004), although we assume that the proportion of species in this transition should be similarly small. Additionally, most previous attempts to evaluate the generality of the tens rule as it relates to the second transition (transport-to-introduction) are inaccurate because of the concatenation of the first two transitions (Cassey et al. 2004; Jeschke & Strayer 2005).

However, data available on the importation of vertebrates maintained by the United States Fish and Wildlife Service (USFWS) provide a method by which species and individuals that have been transported to the United States through this pathway can be quantified and additional information is available to assess their progression through stages of the invasion process. Here, we use these data to estimate transition probabilities between each stage for six vertebrate groups (amphibians, turtles, lizards, snakes, mammals, birds) and also for families within each vertebrate group; we then compare these estimates to probabilities predicted by the tens rule.

METHODS

Data documenting importation of nonindigenous amphibians, turtles, lizards, snakes, mammals, and birds into the United States were obtained from declaration forms for importation or exportation recorded by the USFWS (Form 3-177). We obtained data for 1998-2006 through a Freedom of Information Act request filed through the USFWS Law Enforcement Management Information System. For data before 1998, we relied on information extracted from published USFWS reports and compilations of Form 3-177 (Banks 1970; Banks & Clapp 1972; Busack 1974; Clapp 1973; Clapp 1975; Clapp & Banks 1972; Clapp & Banks 1973; Franke & Telecky 2001; Nilsson 1977; Nilsson 1990; Paradiso & Fisher 1972); for all sources we updated taxonomic names to conform to current taxonomy (Clements 2007; Frost 2007; Uetz 2007; Wilson & Reeder 1993). The data from Form 3-177 represent a minimum of species imported by the United States, and although these data have inherent problems (see Schlaepfer et al. 2005), they are the most complete records available of species found in the transport stage. We obtained information on species introductions to the continental United States (excluding Hawaii) from published sources (Bomford et al 2005; Long 1981; Lever 2003; Long 2003; Pranty 2004).

We considered the source pool to be global species richness minus US natives for each taxonomic group; we considered the transport pool to be all species known to have been imported to the United States. We then determined which species from the transport pool were introduced, which species from the introduced pool have established, and which species from the pool of established species spread from their site of establishment. The number of species within the transport and introduction pools must be considered a minimum, as some species may not be captured by the USFWS data for the years we analyzed, and record of failed introductions are not always noted (Kark & Sol

2005). Williamson (1986) defines the species that transition to the final stage as pests; we follow Jeshcke and Strayer's (2005) definition of species in the final stage as those species that spread beyond their point of introduction. Base rate at each transition was calculated as the proportion of the species pool from the previous stage that successfully transitioned to the next stage of the invasion process. These base rates were calculated on all species within each of the six vertebrate groups. Additionally, we calculated base rates for replicate families within each group with ten or more species in the source and transport pools to assess possible variation in transition probabilities within each group. All statistical tests were based on pooling of all species within the taxonomic group in question.

In order to have a baseline with which we could identify taxonomic groups that were particularly successful, we used the reference base rates predicted by the tens rule and compared our observed base rates at each transition among the six major vertebrate groups. We included the first transition (source pool-to-transport) in these comparisons because there is no statistical generalization available and we have no *a priori* reason to assume that the base rate for this transition would not be within the 5-20% predicted by the tens rule. We performed four separate Goodness of Fit tests (one for each of the four transitions in Fig. 1), each of which accounted for the main effects of model (observed vs expected), outcome (successful transition vs unsuccessful transition), and taxon (six major vertebrate groups). Thus our design was of a 2x2x6 contingency table (Zar 1999). Our null expectation was that the proportion of all observed species that successfully transitioned to the next stage in the invasion process would not differ from 0.10 (tens rule) and that this proportion would be consistent among all vertebrate groups. If the observed proportion differed significantly from this hypothesis, then we reset the expected proportion to 0.05 or 0.20, the lower and upper limits proposed for the tens rule, and re-ran the test. When the proportion of species transitioning to a stage differed among vertebrate groups, we removed outlying groups, and re-ran tests until groups analyzed did not differ from each other.

We used the above analysis to create two new groups of families among the major vertebrate groups, separating taxa that conform to the tens rule from those that do not. Using families as replicates, we then generated frequency distributions for the proportion of species within families that successfully transitioned to the next stage in the invasion process. Each distribution was tested for normality, skewness, and kurtosis to explore how transition probabilities differ among families within the vertebrate groups that do and do not conform to the tens rule, and whether those probabilities aggregate near a mode. The skewness and kurtosis coefficients were considered significant if the absolute value of skewness divided by its standard error was greater than two (Reed & Boback 2002). We expected that transition probabilities for most families within vertebrate groups that conformed to the tens rule would cluster around those expected by the tens rule (0.05 – 0.20), and that families in nonconforming groups would not cluster around those probabilities.

RESULTS

We compared observed transition successes to those expected by the tens rule for all vertebrate groups, and also generated distributions of observed transition probabilities using vertebrate families as replicate observations. When results indicated no differences among major vertebrate groups only a single distribution for all vertebrate families was created; and when results indicated differences among major groups, we generated two distributions, one for families within vertebrate groups that differed from the tens rule and the other for families that did not differ from the tens rule.

The proportion of global species richness transported by humans does conform to the tens rule (Fig. 2; $G = 0.13$, $P = 0.72$), but not consistently among all vertebrate groups ($G = 616.51$, $P < 0.001$). The latter result emerges because turtles are significantly more likely to be transported than are the other major taxonomic groups. The frequency distribution of transition probabilities for turtle families does not differ from a normal distribution (Kolmogorov-Smirnov Statistic = 0.208, $P > 0.15$), and is composed of high transition rates, suggesting a consistently high preference for trade in all turtles (Fig. 3*A*). The frequency distribution of transition probabilities for families in all other groups differs significantly from normal (Kolmogorov-Smirnov Statistic = 0.181, $P < 0.01$) because of a positive skew (skewness = 1.81, SE = 0.15), and the presence of a single mode centered within the range of values expected of the tens rule (Fig. 3*A*). The skewness results from a few families within each major vertebrate group (e.g. parrots within birds, and chameleons within lizards) that are transported at a level comparable to that exhibited for turtles (Fig. 3*A*). This result is the first attempt to characterize the source-pool-to-transport transition and indicates that this transition typically conforms to the tens rule.

For our data set, the transport-to-introduction transition is remarkably consistent with the tens rule (Fig. 2), but due to a low transition rate for snakes, the fit to the tens rule differs among the vertebrate groups ($G = 17.01$, $P = 0.004$). Nevertheless, snake transition probabilities do not differ from the lower bound (5%) of the tens rule ($G = 1.81$, $P = 0.18$). Further evidence that this rule is general for the transport-to-introduction transition is evident from the distribution of values among families. Overall, the frequency distribution is significantly different from normal (Fig. 3*B*, Kolmogorov-Smirnov Statistic = 0.137, $P < 0.01$), positively skewed (skewness = 1.56, SE = 0.26), and aggregated near the mode (kurtosis = 2.45, SE = 0.52).

For the final two transitions, the tens rule does not hold consistently among vertebrate groups. Although the proportion of birds and snakes transitioning from introduction to establishment do not differ from the tens rule (Fig. 2; $G = 0.62$, $P = 0.43$), or from each other ($G = 0.02$, $P = 0.89$), the majority of species within families of these two groups are unsuccessful in making this transition, creating a distribution that is non-normal (Kolmogorov-Smirnov Statistic = 0.192, $P < 0.01$) because it is positively skewed (skewness = 1.55, SE = 0.37, Fig. 3*C*). Thus, there is no strong evidence that the tens rule explains establishment of snakes and birds and there is no tendency for the data at the family level for these two groups to point to a replacement rule. The probabilities of successful establishment for the remaining vertebrate groups fail to correspond with the tens rule (Fig. 2; $G = 12.05$, $P = 0.0005$) because the distribution of transition probabilities at the family level for these groups spans the entire range of possible probabilities and the majority of families fall outside the probabilities expected of the tens rule (Fig. 3*C*). Similarly, the transition from establishment to spread differs significantly from the upper bound of the tens rule (Fig. 2; $G = 4.33$, $P = 0.04$ for expected proportion of 0.2), but is consistent among vertebrate groups ($G = 1.17$, $P = 0.88$) and has a distribution of transition probabilities among families that spans the range of possible values (Fig. 3*D*). These features suggest that establishment and spread are more likely in vertebrates than predicted by the tens rule, but an obvious replacement for the tens rule does not exist for these stages.

DISCUSSION

Our estimates of vertebrate transition success in the invasion process differ in some cases from those of other studies (Jeschke & Strayer 2005; Kraus 2003; Shieh et al. 2006). While some of the differences likely result from our refined method of pathway specification, a more general explanation is variation in the definition of source and recipient geographic regions of interest. For example, Jeschke and Strayer (2005) estimated transition success of vertebrates, restricting their analyses to introductions to and from North America and latitudinally-similar areas of Europe. Our estimates of establishment success and spread rates are lower than those found by Jeschke and Strayer (2005) because we used the global species pool in our analyses, which includes species from source regions at all latitudes. Additionally, human influence, known to be an important and confounding factor in studies regarding biological invasions (Duncan et al.

2003; Lockwood 1999), also can affect differences in transition success seen among studies. An example of this influence is seen in Taiwan, where the high rate of success for bird species in the rarely-assessed transport-to-introduction transition was attributed to the religious cultural practice of releasing birds in prayer rituals (Shieh et al. 2006). No such rituals are known to affect the invasion process in North America; therefore, we suggest that our values are not biased in their ability to detect general trends that are the focus of our study.

Our inclusion of a wide variety of taxa (ecto- and endotherms, oviparous and viviparous reproductive modes, primary consumers and top predators) and the fact that a few families are unusually likely to be introduced are consistent with arguments presented by Williamson (1996) in generating the tens rule and arguing for its generality. However, the near-uniform distribution of transition probabilities to the establishment and spread stages emphasizes the importance of preventing vertebrates in families at the upper end of the distribution from reaching these stages.

Traditional efforts to manage species once they reach these stages, such as eradication and control, are costly and often ineffective (Leung et al. 2002; Lodge et al. 2006). The most effective prevention is possible only during the early stages of the invasion process, before a species enters a pathway and is transported to a new location (Lodge et al. 2006). Unfortunately, the vertebrate groups assessed here consistently have remarkably low success in the first two transitions, making it difficult to argue for limited trade in vertebrates (Keller et al. 2007; Smith et al. 1999). However, because rates of establishment and spread of several vertebrate families are high and economic and ecological costs associated with these species can be substantial, the accuracy of prediction for these stages and the benefits of prevention increase (Keller et al. 2007). As an efficient, proactive management strategy, information on species that successfully transition to those latter stages could be used to build predictive risk assessments and in turn could be applied to species in a pre-import screening process. Preventing species transport in the first place is likely to be the key to minimizing the number of additional invasive species. With every vertebrate species that has its transport limited, the potential invasive species pool and number of subsequent introductions could be lowered (Vander Zanden 2005).

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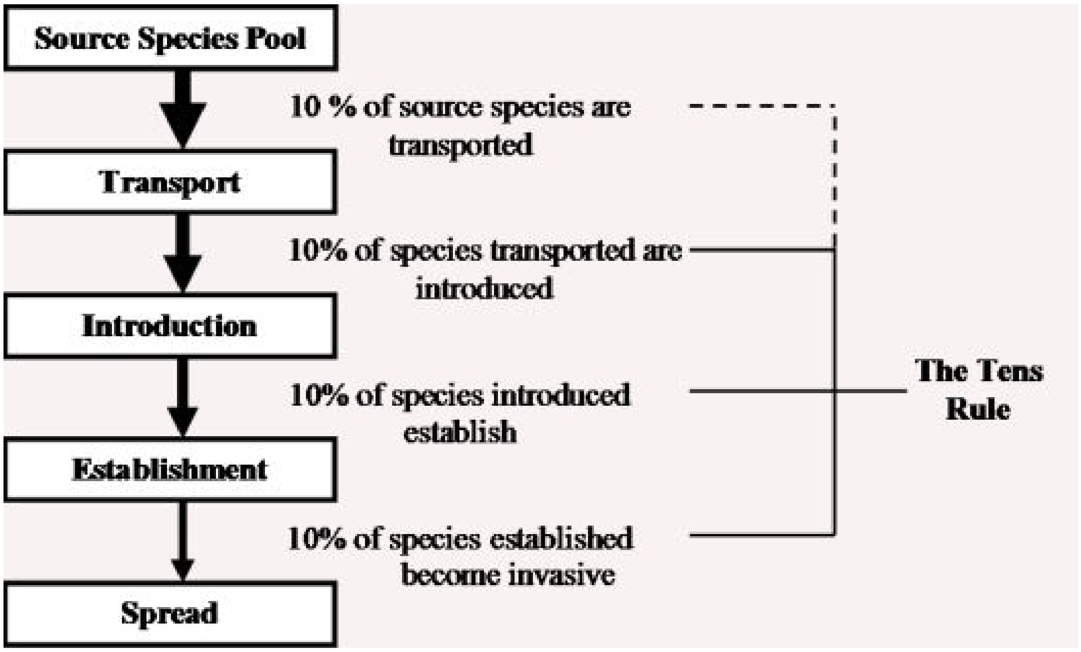

Figure 4 - 1. A model of the invasion process (Kolar & Lodge 2001) and predictions of the tens rule (after Williamson 1996, solid lines; or inferred by us, dotted line). Boxes represent stages of the invasion process; each stage is a subset of the previous stage. Arrows represent transition from one stage to the next. Species in the transport stage are those traded as live animals.

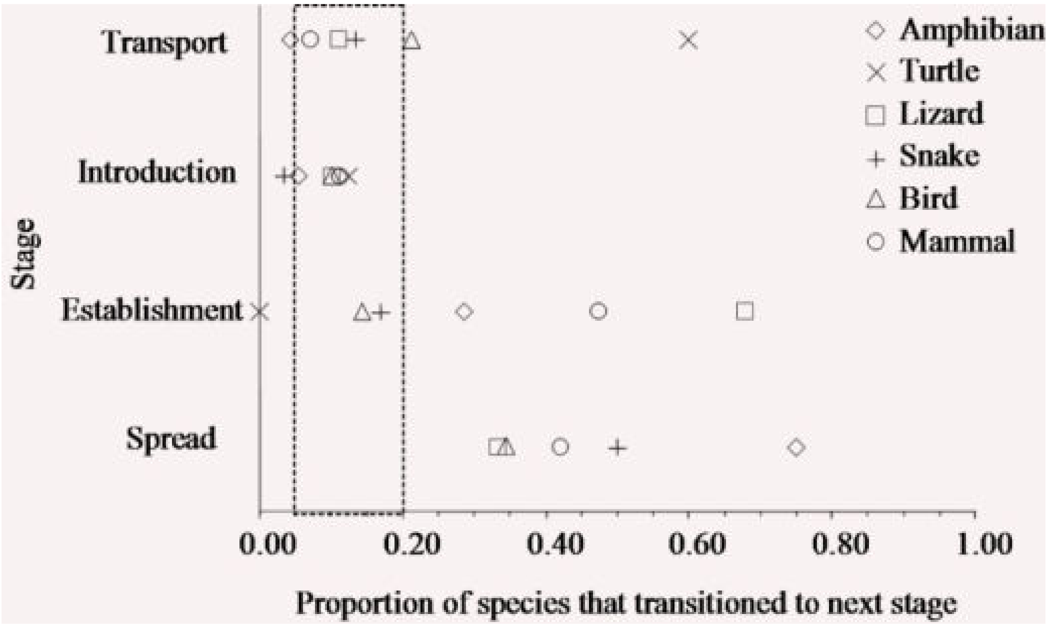

Figure 4 - 2. Proportion of species that successfully transitioned from one stage to the next in the invasion process. Stages of the invasion process are displayed on the y-axis. Points indicate transition success rates for each vertebrate group. Region bordered by dotted line indicates the range predicted by the tens rule.

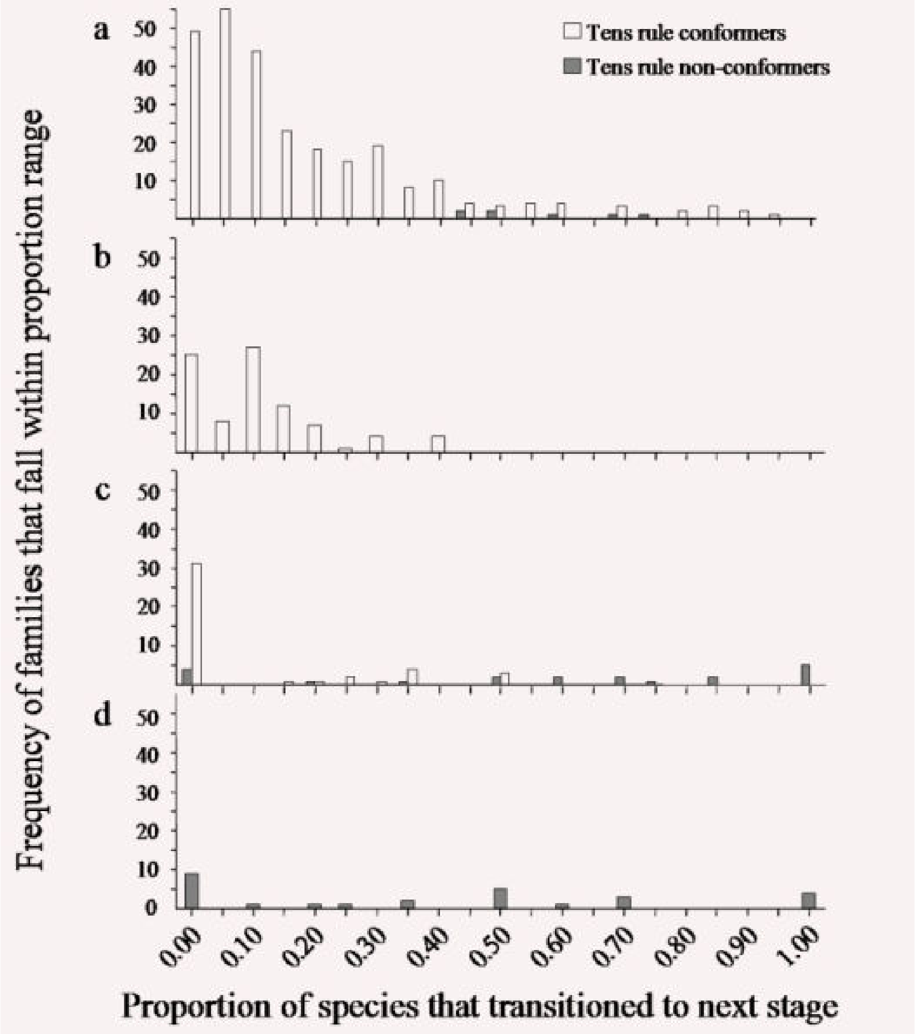

Figure 4 - 3. Frequency distribution of transition success among vertebrate families within taxonomic groups that conformed (open) and did not conform (shaded) to the tens rule. a, Source pool-to-transport transition (conformers are families within amphibians, lizards, snakes, birds, and mammals; non-conformers are turtles), b, Transport-to-introduction transition (all vertebrate groups are conformers); c, Introduction-to-establishment transition (conformers are families within snakes and birds; non-conformers are families with amphibians, mammals, lizards, and turtles); d, Establishment-to-spread transition (all vertebrate groups are non-conformers).

CHAPTER V

IMPORT PRESSURE AND HUMAN INFLUENCE PREDICTS INTRODUCTION AND ESTABLISHMENT OF NONINDIGENOUS VERTEBRATES IN THE UNITED STATES

INTRODUCTION

Global commerce in live plants and animals has been linked to biological invasions worldwide (Lodge et al. 2006). For some vertebrate groups, the live-animal trade is the most important pathway related to their introduction (Temple 1992; Kraus 2003). Though many species introduced to a location outside their native ranges subsequently do not establish self sustaining populations (Williamson 1996), a large proportion of vertebrates do establish and spread widely (~50 %; Jeschke & Strayer 2005; Chapter 2), sometimes after a lag phase of many years in which populations remain small and localized. Once a species is established and spreads, its potential to cause ecological and economic damage increases greatly (Lodge et al. 2006); and such species are often difficult and costly to eradicate (Mack et al. 2000).

Currently, the United States does not place strong restrictions on the import and transport of live non-indigenous organisms, and as a result, the number of invasive species introduced through this medium continues to increase (Keller & Lodge 2007).

However, greater awareness among policymakers of the economic and environmental impacts of invasive species has led to the proposition of at least one bill designed to minimize these effects. Additionally, a position paper of the Ecological Society of America describing US policy and management of biological invasions recommends the application of pre-import screening and risk analysis methods to all species proposed for import before entry is granted (Lodge et al. 2006). To be most effective, these methods must be repeatable and scientifically supportable, time and cost effective, and usable across all agencies (National Resource Council 2002). This approach has encouraged a more proactive approach to research on biological invasions, and created a need for a more predictive science using quantitative, statistically sound methods (Kolar & Lodge 2001, National Resource Council 2002). Coarse risk screening efforts have been conducted for the United States (Defenders of Wildlife 2007), but quantitative assessments of risk are still needed.

The biological invasion process has been separated into a series of stages: transport, introduction, establishment, and spread (Williamson 1996, Kolar & Lodge 2001). Recognition of these stages allows for a better prediction of the factors that drive successful transitions between stages. Studies that compare successful and failed species offer the most powerful test to differentiate the two groups at a given stage in the invasion process (Kolar & Lodge 2001). Each stage should be addressed separately, as the biological and social factors that favor success in any one stage may or may not be the same factors favoring success among other stages (Kolar & Lodge 2001).

While biological and ecological factors are important determinants for predicting transition success, there is another set of factors associated with human interest that are particularly important in the early stages of the invasion process (Mack 2003; Williamson 2006). Hayes and Barry (2008) examined several studies that identified correlates of establishment success across several animal groups and found that two of the three characteristics consistently associated with establishment were associated with human effort: previous establishment success elsewhere and propagule pressure (also known as introduction effort). It has been suggested that these human-associated factors may mask underlying biological characteristics, and should be analyzed separately (Marchetti et al. 2004). This seems particularly important when considering an intentional transport pathway, such as the live-animal trade. Unlike other pathways, such as ship ballast, the majority of species within this pathway are specifically selected by humans for transport (although unintentional transport of species is also possible, see Keller & Lodge 2007). Because of this selectivity, species that are transported are not a random sample of the global species pool (Lockwood 1999, Romagosa et al. 2009), and may therefore affect the trends in how species progress through the early stages of the invasion process.

Few studies have assessed transport-to-introduction transition because information on the number of species entrained in the transport stage is difficult to obtain (Cassey et al. 2004). However, records maintained by the USFWS that inventory vertebrates transported to the United States provide an estimate of species available for this first transition. Here, we use these data to examine the importance of human-associated factors to the successful transition to the introduction and establishment stages by six vertebrate groups (amphibians, turtles, lizards, snakes, mammals, birds). We include the human-associated factors, propagule pressure and previous success elsewhere, in our analyses. In addition, we consider two other human-associated factors shown to be related to establishment success, primary source of origin and monetary value. Primary source of origin refers to whether a species is primarily wild caught or captive bred for the live animal trade; and it has been shown that wild caught species have greater success in establishment than species that are primarily captive bred (Griffith 1989, Carrete & Tella 2008). Monetary value and its relationship to introduction and establishment is likely a reflection of consumer behavior. People are more likely to purchase inexpensive animals, and then dispose of those animals when they become cumbersome to keep (Robinson 2000, Franke & Telecky 2001); the same principle could apply to importers when inexpensive stock animals become a monetary loss, leading to the release of excess animals.

Despite the likely importance of propagule pressure as a predictive variable, data on this factor are lacking. Many authors have suggested use of a surrogate for propagule pressure (Sol et al. 2008), and some trade-related proxies have been utilized (Drake & Lodge 2004; Rixon et al. 2004; Semmens et al. 2004; Dehnen-Schmutz et al. 2007a, 2007b). Information on import pressure and market presence has been used as an approximate estimator of the number of individuals per species “available” for introduction (Semmens et al. 2004; Duggan et al. 2006; Dehnen-Schmutz et al. 2007a, 2007b). We used the average number of individuals imported per year to create variables associated with import pressure. These variables were used as proxies for propagule pressure. Because there may be a temporal effect of importation patters on establishment

(Pemberton & Liu 2009), we separated the average number of individuals imported per year into past and recent periods.

METHODS

Data Sources

Data documenting importation of nonindigenous amphibians, turtles, lizards, snakes, mammals, and birds into the United States were obtained from compilations of USFWS importation declaration forms for the available years between 1968–2005. For a full description of the data see Chapter 2. From data compilations before 1998, only the number of individuals imported per year was available. After 1998, various trade-related variables, including the number of individuals imported, are available. We compiled the following for each species imported into the United States: average number of individuals imported per year for the available years, primary source of origin (wild caught or captive bred), and declared monetary value per individual.

We summarized information from the literature on species that were imported into the United States that successfully or unsuccessfully transitioned from the transport-to-introduction stage and from the introduction-to-establishment stage, within and outside the continental United States (Long 1981; Lin 2001; Eterovic & Duarte 2002; Lever 2003; Long 2003; Pranty 2004; Bomford et al 2005; Shieh et al. 2006; Agoramoorthy & Hsu 2007; Carrete & Tella 2008). The number of species imported and introduced must be considered a minimum, as some species may not be captured by the USFWS data for the years we analyzed, and records of failed introductions are rare (Kark & Sol 2005).

Model development

We examined the influence of five variables that measured import effort and human influence (Table 1) on the successful transition of vertebrates between the introduction and establishment stages. We did not have sufficient sample size to assess the establishment-to-spread stage. Accordingly, we used these variables to build an a priori set of candidate statistical models that reflect biological hypotheses (Table 2; Burnham and Anderson 2002). We tested for multicollinearity among our continuous explanatory variables (past and recent average, declared monetary value) before constructing multivariate models and found that these 3 variables were not highly correlated (Pearson correlation < 0.65) and the estimated variance inflation factor was low (VIF < 2.2). We began with our most complex model (e.g., all variables), followed by progressively less complex models. These models were evaluated for both the introduction and establishment stages of the invasion process.

For species (all 6 taxonomic groups) involved in the transport-to-introduction transition, we created 17 models. These models include a global model with all five explanatory variables (all import pressure and human influence variables; model 1). The remaining models are based on the following hypotheses: (1) Import pressure + monetary value models (models 2a-c). Introduction is related to either or both import pressure variables and only the human influence variable monetary value. Each import pressure variable is assessed iteratively for these models and the following models that contain import pressure variables, because time period may have an effect on introduction, or its effect may be additive. (2) Import pressure + source models (models 3a-c). Introduction is related to either or both import pressure variables and only the human influence variable source. (3) Import pressure + previous success models (models 4a-c). Introduction is related to either or both import pressure variables and previous introduction success elsewhere. (4) Import pressure models (models 5a-c). Introduction is related to either or both measures of import pressure (5) Full human influence model (model 6). All three human influence variables best predict introduction success. (6) We did not assess human influence variables iteratively because we have no *a priori* reason to assume that any particular combination of these variables would best describe introduction success. Therefore, models 7-9 assess the relationship of each human influence variable to introduction success.

For species involved in the introduction-to-establishment transition, we again used the above described models, but substituted previous establishment success elsewhere for previous introduction success elsewhere. We only had sufficient data to test these models on two taxonomic groups, birds and lizards.

All models were tested using either uni- or multivariate logistic regression (Mystat 12), with introduction or establishment as the binary response variable. We used Akaike's information criterion adjusted for sample size (AICc) and Akaike weights (w_i, Burnham & Anderson 2002) to evaluate the amount of support in our data for each model in our candidate list (see above). We considered the best approximating model to be that with the lowest AICc value and highest Akaike weight (Burnham & Anderson 2002). When no single model was superior to others in a set, a model-averaging approach was used, where inferences were based on the entire set of models, and model coefficients were weighted using Akaike weights. Additionally, Akaike weights were used to gauge the importance of each variable for predicting introduction and establishment. We assessed fit of the logistic regression models based on response operator curve (ROC) values.

RESULTS

While no particular introduction model was consistently the best approximating model among all taxonomic groups, models that considered both measures of import pressure and previous introduction success elsewhere were among the top ranking models (ΔAICc < 2) for five out of six taxonomic groups (Table 4). Turtles were the exception, for which the top ranking models included only import pressure (Table 4). The pattern for birds was best described by the global model. For the establishment models, the best approximating model for both lizards and birds was one that considered past average number of individuals imported per year and establishment success elsewhere (model 4b, Table 5). The predictive success of the highest ranking models, as evaluated by ROCs, ranged between AUC = 0.68 and 0.885 (Tables 4 & 5), indicating an acceptable to excellent fit of the models to the original data (Hosmer and Lemeshow 2000).

The relative importance of variables was examined using the information-theoretic approach by summing the Akaike weights for each variable across all models considered (ΔAICc < 4) that contain that variable (Burnham & Anderson 2002). Among these introduction models, past average was the most consistently important predictor for all taxonomic groups (variable importance > 0.70, Table 6). Recent average (variable importance 0.320 < variable importance < 1) and previous introduction success (0.218 < variable importance < 1) were also important predictors, although their importance varied among taxonomic groups (Table 6). With the exception of birds, where all 5 variables were important, we found limited support that declared value and primary source were related to introduction success.

Past average and previous establishment success elsewhere occurred in all high ranking establishment models (Table 7; variable importance > 0.596), suggesting that both variables are important predictors for establishment. Recent average was not an important predictor, and there was little or no effect of final source or declared monetary value on establishment (variable importance < 0.158).

For most taxonomic groups the Akaike weights for the top models ($0.278 < w_i < 0.472$; Tables 4 & 5) in both sets of models (introduction or establishment) suggested model uncertainty, which indicated that a model-averaging approach was appropriate. The difference in Akaike weights between the first and second ranked models varied from 0.053 to 0.262. We did not include birds and lizards from the introduction models in the model-averaging approach because model weight of the best approximating model was > 0.835. The model-averaged logistic regression coefficients were calculated together with unconditional standard errors (Tables 6 & 7). An unconditional standard error of a variable that was comparable or larger than the model-averaged coefficient for that variable (Tables 6 & 7), suggests that considerable uncertainty existed as to the true effect of the variable on the pattern of introduction and establishment. For all taxonomic groups, the estimated model-averaged coefficients for the past average variable indicate that species that were imported in large quantities in the 1970s are more likely to be introduced. Additionally, with the exception of turtles, the estimated model-averaged coefficients for previous introduction success elsewhere indicate that species that have been introduced in other countries are more likely to be introduced to the United States as well. In the establishment models, the model-averaged coefficients for past average and previous establishment success elsewhere were the only variables that indicated a significant effect on the establishment of birds and lizards in the United States.

DISCUSSION

Among the human-associated factors we assessed, we found that propagule pressure and a history of previous success elsewhere are the most important factors related to the introduction and establishment of nonindigenous vertebrates imported into the United States. These factors have been shown to be important predictors for various stages of the invasion process for several plant and animal groups found in trade (Lockwood 1999; Cassey et al. 2004; Rixon et al. 2004; Semmens et al. 2004; Dehnen-Schmutz et al. 2007a, 2007b). Our recognition of their importance supports a growing literature on these aspects of human behavior; and we found that importation records maintained by the USFWS can be used to create informative surrogates of propagule pressure in the form of import pressure. Similar data on US tropical marine fish imports from the Global Marine Aquarium Database showed a link between the magnitude of importation and the probability of introduction to waters off the eastern coast of Florida (Semmens et al. 2004). Our use of importation records for 6 additional taxonomic groups suggests that this proxy for propagule pressure is informative across all vertebrate groups. Additionally, we show that the intensity of importation in the past has a significant effect on whether an imported species will be released or established in the United States. While our data supporting this claim are correlative, we argue that propagule pressure (here, our measure of import pressure) is the primary driver for introduction and establishment success of vertebrates in the United States. We suggest that any studies that assess the relationships between species-specific characteristics of vertebrate species in trade and success at any stage of the invasion process consider the confounding effects of propagule pressure noted by Colautti et al. (2006).

The temporal effect we observed is mostly likely related to another dimension of propagule pressure known as residence time, or how long a species is present in a region (Pyšek & Jarošík 2005). Several studies have reported significant positive relationships between residence time and invasion success in plants (Rejmánek 2000; Castro et al. 2005; Wilson et al. 2007). In the present study, we use residence time to refer to how long a species has been imported into the United States, and assume that import pressure increases with time as more individuals are imported. Longer residence times can allow species to overcome lag phases that are often associated with biological invasions (Richardson & Pyšek 2006). Lag phase refers to the period of time between the first introduction of a species and its population increase and subsequent range expansion (Crooks & Soulé 1999). This lag phase may explain the importance of past average in the establishment of birds and lizards; we suggest that a lag phase also may be evident in the time to introduction after first importation. This time lag in transport to introduction may exist for several reasons, some of which are applicable to the lag time seen between introduction and establishment. First, it may be that the time lag observed between a species' first import and its introduction may be due to detection probability, where these species must first obtain a mass in the environment before being detected and subsequently reported. Second, in the case of introduction through a consumer medium such as the pet or food trades, a species may need to be present in trade for a time period that is long enough and be traded in sufficient numbers to be widely purchased and regularly released. Finally, over time, a species' genetic diversity may increase with additional influx of genes as more individuals are imported. Eventually, individuals of that species may arrive with a genotype that is suitable for introduction and establishment success (Shigesada & Kawasaki 1997; Crooks & Soulé 1999).

That previous introduction or establishment success can predict introduction and establishment of vertebrate species in the United States is not surprising. Species are introduced because of some association with humans; this association is direct for species in the live animal trade because they are specifically selected for transport. Humans select species for transport for a variety of reasons such as for companion animals, food sources, and for hunting. The biological traits inherent to these species for such human uses may be more diverse than, but are also related to, the biological traits that predispose a species for successful progression through all stages of the invasion process (Lockwood 1999). For example, hardiness, high fecundity, diet breadth, and large body size are all species-specific traits that make for good pet, food, or game animals, and can also be related to establishment success (Lockwood et al. 2005).

Although previous import pressure and introduction success elsewhere best predicted introduction of vertebrate species to the United States, some differences seen among the taxonomic groups are worth discussing. For example, the average number of individuals imported recently also has an effect on whether a lizard or snake species is introduced. For these two groups, the average number of individuals imported has increased between the two time periods for all species, but more so for species that are currently introduced to the United States. Because of this trend, both the past and recent average number of individuals imported had an effect on introduction. For the other taxonomic groups, the average number of individuals imported either decreased between the two time periods or increased only for species that are not introduced. This result suggests that for amphibians, birds, mammals, and turtles, only import pressure exerted in the 1970s predicted what species are seen in the wild today.

We found that introduction success elsewhere was not an important predictor for turtle introductions to the United States. Although turtles experience significant trade, their introduction is not as common as other taxonomic groups (Kraus 2009). In fact, most global introductions of turtles are of one species (*Trachemys scripta*) that is native to the United States. But in particular, it appears that the turtles introduced to other parts of the world are not consistently introduced to the United States.

Our other two measures human influence, declared value and final source, were not important predictors of introduction or establishment success. Other studies that have used monetary value found that it is a good predictor for introduction and establishment (Dehnen-Schmutz et al. 2007). Although our results did not reflect this effect, this variable, as we measured it, may become important in future analyses of introduction and establishment success. We based this variable on current monetary value and because the past average number of individuals imported was the most informative predictor variable for import effort in this study, the monetary value for each species in the past time period might have been be more informative. Unfortunately, past monetary value was not available. We do not believe that a lack of effect is due to our use of declared value, a value that is provided by the importer on Form 3-177, rather than market value. Market value for the consumer reflects the declared value for an importer, and both values are highly correlated (CMR unpublished data).

Our measure of whether a species was wild caught or captive bred was also obtained from current information, and it may be that current trends we observed may not reflect trends in the past time period. Again, the information on which species were primarily wild caught versus captive bred were not available for the past time period. We can assess the trends have changed for birds, where approximately 82% of all birds imported in the 1970s were wild caught (Banks 1976), as compared to 40% in our data. However, we assert that trends between the two time periods likely have not changed much for reptiles and amphibians, and that most species from these taxonomic groups are wild caught now as they were in the 1970s. Regardless of the differences in trends between the time periods, it may be that sufficient import pressure masks any biological effect created by the originating source.

Because we limited our analyses within specific taxonomic groups, we did not have sufficient sample size to assess the role of import pressure and human influence on the establishment-to-spread transition. While past import pressure is an important variable that predicts which species get to this transition, it may not be as important in differentiating those species that spread from those that do not spread. The human influence variable, previous *spread* elsewhere, would be a more powerful predictor at this stage if this information were available. What allows a species to spread successfully is likely a combination of biological traits that allow it to continue to overcome Allee effects, should those effects be present, and if enough suitable habitat exists for the species to persist and disperse (Taylor & Hastings 2005). We believe that analyses that include these variables would be most informative at the establishment-to-spread transition because the effects of propagule pressure would be minimized.

The diversity of species in the live animal trade is rising through time (Jeschke 2008). We have documented the importation of over 4000 tetrapod species into the United States from 1968 to 2005; and since 1998, approximately 85 new species and 7 million more individuals are imported each year. It can be expected that the number of species that are released and establish populations will also increase because of the relationship to import pressure. Reducing the risk of additional introductions and establishment from the live animal trade will require changes in the species used and in the ways that the industries and their consumers acquire, keep, and dispose of those organisms (Keller et al. 2007).

A major criticism of risk assessment for biological invasions is the lack of quantitative variables that are consistent predictors across all taxonomic groups. We have shown that past import pressure and previous success elsewhere apply across all the taxonomic groups we assessed. Knowledge of which and how species are traded and whether those species are successfully introduced or established elsewhere can help inform import screening decisions. If past import pressure predicts current introductions and establishment, then current import pressure should predict future introductions and establishment. This variable could be particularly useful when knowledge of previous introduction or establishment does not exist because a species is new to trade and may not have been transported before. Characterizing the supply of propagules, such as the number of individuals imported per year in the case of the live animal trade, is essential for understanding invasion risk and developing effective management strategies (Verling et al. 2000). Because time and resources for conducting risk assessments of every species imported to the United States is limited, a coarse-meshed screening method could use import pressure and previous success elsewhere, if it is available, to identify those species currently imported that are at highest risk for introduction and establishment. Those species could then be candidates for more species-specific risk assessments for invasion that use climate matching models, and assessment of biological traits after the effects of propagule pressure have been considered.

Even for preliminary screening methods, there is a need for global dissemination of invasive species information (Ricciardi et al. 2000). There is a shortage of scientific information on species that have transitioned through any of the stages of the invasion process and their subsequent management (Browne& De Poorter 2009). Most of this information is difficult to obtain because it requires searching through a wide variety of disciplinary journals or obscure sources and is often of variable quality (Ricciardi et al.

2000). In order to most efficiently and effectively implement risk assessment methods as outlined by Lodge et al. (2006), this information needs to be readily accessible. The development and maintenance of invasive species databases within Global Invasive Species Information Network (www.gisinetwork.org) helps to meet this need (Graham et al. 2008). In addition to the species-specific information on biological invasions, we suggest that information on global trade in these species be included in order to provide an estimate for potential propagule pressure. Because the USFWS currently purges importation records every 5-7 years, maintaining these data within a global information network would secure their availability for future research on biological invasions. Strategies to identify and reduce propagule supply, whether through regulation or education, should help to prevent future invasions through the live animal trade.

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Table 5 - 1. Name, description, and data type of variables used in the models.

	Variables used	Variable name	Type
Measures of import pressure	Average number of individuals imported per year in "past" time period (1968-1977)	LOGPASTAVG	Continuous ($\log_{10}$ transformed)
	Average number of individuals imported per year in "recent" time period (1998-2005)	LOGRECENTAVG	Continuous ($\log_{10}$ transformed)
Measures of human influence	Declared monetary value per individual	LOGDECVALUE	Continuous ($\log_{10}$ transformed)
	Primary source of origin for species (wild caught vs. captive bred)	FINALSOURCE	Categorical
	Introduction success elsewhere	INTRODELSE	Categorical
	Establishment success elsewhere	ESTABELSE	Categorical

Table 5 - 2. Introduction model name, number and variables included in each model.

Introduction models	Model number	Variables
Global (import pressure + human influence)	1	LOGRECENTAVG+LOGPASTAVG+ LOGDECVALUE+FINALSOURCE+ INTRODELSE
Import pressure + monetary value	2a	LOGRECENTAVG+LOGPASTAVG+ LOGDECVALUE
Import pressure + monetary value	2b	LOGPASTAVG+LOGDECVALUE
Import pressure + monetary value	2c	LOGRECENTAVG+LOGDECVALUE
Import pressure + source	3a	LOGRECENTAVG+LOGPASTAVG+ FINALSOURCE
Import pressure + source	3b	LOGPASTAVG +FINALSOURCE
Import pressure + source	3c	LOGRECENTAVG +FINALSOURCE
Import pressure + previous success	4a	LOGRECENTAVG+LOGPAST AVG+INTRODELSE
Import pressure + previous success	4b	LOGPASTAVG+INTRODELSE
Import pressure + previous success	4c	LOGRECENTAVG+INTRODELSE
Import pressure	5a	LOGRECENTAVG+LOGPASTAVG
Import pressure	5b	LOGPASTAVG
Import pressure	5c	LOGRECENTAVG
Full human influence	6	LOGDECVALUE+FINALSOURCE+ INTRODELSE
Monetary value	7	LOGDECVALUE
Source	8	FINALSOURCE
Previous success	9	INTRODELSE

Table 5 - 3. Establishment model name, number and variables included in each model.

Establishment models	Model number	Variables
Global (import pressure + human influence)	1	LOGRECENTAVG+LOGPASTAVG+ LOGDECVALUE+FINALSOURCE+ ESTABELSE
Import pressure + monetary value	2a	LOGRECENTAVG+LOGPASTAVG+ LOGDECVALUE
Import pressure + monetary value	2b	LOGPASTAVG+LOGDECVALUE
Import pressure + monetary value	2c	LOGRECENTAVG+LOGDECVALUE
Import pressure + source	3a	LOGRECENTAVG+LOGPASTAVG+ FINALSOURCE
Import pressure + source	3b	LOGPASTAVG +FINALSOURCE
Import pressure + source	3c	LOGRECENTAVG +FINALSOURCE
Import pressure + previous success	4a	LOGRECENTAVG+LOGPAST AVG+ESTABELSE
Import pressure + previous success	4b	LOGPASTAVG+ESTABELSE
Import pressure + previous success	4c	LOGRECENTAVG+ESTABELSE
Import pressure	5a	LOGRECENTAVG+LOGPASTAVG
Import pressure	5b	LOGPASTAVG
Import pressure	5c	LOGRECENTAVG
Full human influence	6	LOGDECVALUE+FINALSOURCE+ ESTABELSE
Monetary value	7	LOGDECVALUE
Previous success	8	ESTABELSE
Source	9	FINALSOURCE

Table 5 - 4. Summary of model selection statistics for evaluating introduction success for vertebrates imported to the United States.

Taxonomic group	Model no.	Variables	ROC	lnL	K	AICc	ΔAIC	w_i
Amphibian N=35	4b	LOGPASTAVG +INTRODELSE	0.809	-13.200	3	33.174	0.000	0.471
	5b	LOGPASTAVG	0.707	-15.213	2	34.801	1.627	0.209
	4a	LOGRECENTAVG +LOGPASTAVG +INTRODELSE	0.811	-13.168	4	35.669	2.495	0.135
	4c	LOGRECENTAVG +INTRODELSE	0.768	-14.678	3	36.130	2.956	0.108
	5a	LOGRECENTAVG +LOGPASTAVG	0.694	-15.014	3	36.802	3.628	0.077
Bird N = 259	1	LOGRECENTAVG +LOGPASTAVG+ LOGDECVALUE+ FINALSOURCE+ INTRODELSE	0.808	-121.505	6	255.343	0.000	1.000
Lizard N = 89	4a	LOGRECENTAVG +LOGPASTAVG +INTRODELSE	0.869	-38.396	4	85.268	0.000	0.835
	1	LOGRECENTAVG +LOGPASTAVG +LOGDECVALUE +FINALSOURCE +INTRODELSE	0.874	-37.746	6	88.516	3.248	0.165
Mammal N = 96	4b	LOGPASTAVG +INTRODELSE	0.836	-34.200	3	74.661	0.000	0.472
	4a	LOGRECENTAVG +LOGPASTAVG +INTRODELSE	0.857	-33.376	4	75.192	0.531	0.362
	4c	LOGRECENTAVG +INTRODELSE	0.822	-35.251	3	76.763	2.102	0.165

Table 5 - 4 (continued).

Taxonomic group	Model no.	Variables	ROC	lnL	K	AICc	ΔAIC	w_i
Snake N = 100	5a	LOGRECENTAVG +LOGPASTAVG	0.871	-24.627	3	55.504	0.000	0.323
	4b	LOGPASTAVG +INTRODELSE	0.882	-24.806	3	55.862	0.358	0.270
	4a	LOGRECENTAVG +LOGPASTAVG +INTRODELSE	0.885	-24.048	4	56.517	1.013	0.195
	5b	LOGPASTAVG	0.863	-26.484	2	57.092	1.588	0.146
	2a	LOGRECENTAVG +LOGPASTAVG+ LOGDECVALUE	0.880	-24.012	5	58.662	3.158	0.067
Turtle N = 46	5b	LOGPASTAVG	0.698	-24.686	2	53.651	0.000	0.278
	5a	LOGRECENTAVG +LOGPASTAVG	0.724	-23.827	3	54.225	0.574	0.208
	5c	LOGRECENTAVG	0.696	-25.169	2	54.617	0.966	0.171
	4b	LOGPASTAVG +INTRODELSE	0.691	-24.647	3	55.865	2.214	0.092
	4a	LOGRECENTAVG +LOGPASTAVG +INTRODELSE	0.728	-23.814	4	56.604	2.953	0.063
	2a	LOGRECENTAVG +LOGPASTAVG+ LOGDECVALUE	0.727	-23.819	4	56.614	2.963	0.063
	4c	LOGRECENTAVG +INTRODELSE	0.684	-25.023	3	56.617	2.966	0.063
	7	LOGDECVALUE	0.634	-26.191	2	56.661	3.010	0.062

ROC receiver operating characteristic, lnL maximized log-likelihood function, *K* number of parameters, ΔAIC difference from best AICc model, w_i Akaike weights.

Table 5 - 5. Summary of model selection statistics for evaluating establishment success for vertebrates imported and introduced to the United States.

Taxonomic group	Model no.	Variables	ROC	lnL	K	AICc	ΔAIC	w_i
Bird N = 80	4b	LOGPASTAVG +ESTABELSE	0.774	-35.921	3	78.158	0.000	0.390
	5b	LOGPASTAVG	0.752	-37.538	2	79.232	1.074	0.228
	4a	LOGRECENTAVG +LOGPASTAVG +ESTABELSE	0.773	-35.800	4	80.133	1.976	0.145
	2b	LOGPASTAVG+ LOGDECVALUE	0.754	-37.534	3	80.924	2.766	0.098
	5a	LOGRECENTAVG +LOGPASTAVG	0.753	-37.534	3	81.384	3.226	0.078
	1	LOGRECENTAVG +LOGPASTAVG +LOGDECVALUE +FINALSOURCE +ESTABELSE	0.802	-34.369	6	81.889	3.731	0.060
Lizard N = 33	4b	LOGPASTAVG +ESTABELSE	0.831	-15.707	3	38.242	0.00	0.627
	4a	LOGRECENTAVG +LOGPASTAVG +ESTABELSE	0.829	-15.300	4	40.029	1.787	0.256
	9	ESTABELSE	0.696	-18.600	2	41.600	3.358	0.117

ROC receiver operating characteristic, lnL maximized log-likelihood function, *K* number of parameters, ΔAIC difference from best AICc model, w_i Akaike weights.

Table 5 - 6. Variable importance (based on cumulative Akaike weights), model-averaged coefficients and unconditional standard errors for variables in introdction models ΔAIC < 4 and recommended for inference based on Akaike weight (w_i).

		Variable				
Taxonomic group		Constant	RECENTAVG	LOGPASTAVG	LOGDECVALUE	INTRODELSE
Amphibian	Variable importance	-	0.320	0.892	-	0.714
	Model-averaged coefficient	-2.605	0.072	0.697	-	1.487
	Unconditional SE	1.456	0.164	0.356	-	1.258
Mammal	Variable importance		0.528	0.835	-	1.00
	Model-averaged coefficient	-1.614	0.273	0.586	-	2.129
	Unconditional SE	0.670	0.226	0.288	-	0.671
Snake	Variable importance		0.584	1.000	0.067	0.465
	Model-averaged coefficient	-5.037	0.478	1.505	0.020	0.601
	Unconditional SE	1.604	0.364	0.579	0.058	0.521
Turtle	Variable importance		0.569	0.704	0.125	0.218
	Model-averaged coefficient	-2.690	0.370	0.461	-0.062	0.065
	Unconditional SE	1.78	0.303	0.290	0.113	0.210

Table 5 - 7. Variable importance (based on cumulative Akaike weights), model-averaged coefficients and unconditional standard errors for variables in establishment models ΔAIC < 4 and recommended for inference based on Akaike weight (w_i).

		Variable					
Taxonomic group		Constant	RECENTAVG	LOGPASTAVG	LOGDECVALUE	FINALSOURCE	ESTABELSE
Bird	Variable importance		0.284	1	0.158	0.06	0.596
	Model-averaged coefficient	-2.363	-0.002	0.811	0.057	-0.039	0.68
	Unconditional SE	0.882	0.09	0.327	0.084	0.055	0.459
Lizard	Variable importance		0.256	0.883	-	-	1
	Model-averaged coefficient	0.469	0.136	1.069	-	-	3.357
	Unconditional SE	1.753	0.187	0.54	-	-	0.197