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USING PATHWAY ANALYSIS TO INFORM PREVENTION STRATEGIES FOR ALIEN REPTILES AND AMPHIBIANS

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Abstract: Alien reptiles and amphibians are deserving of greater attention that has hitherto been bestowed upon them by managers and researchers. Eradication or control of established taxa will generally be infeasible, leaving prevention of introductions as the primary management tool for controlling herpetological invasions. I analyzed >5,700 introductions of alien reptiles and amphibians worldwide to obtain the pathway information necessary for design of informed prevention programs. Six pathways account for the large majority of introductions: accidental introductions via cargo and the nursery plant trade and intentional introductions for biocontrol, food use, the pet trade, and aesthetic purposes. Pathway importance varies taxonomically, temporally, and geographically. Unlike other taxa for which introductions have been dominated by either accidental pathways alone or intentional pathways alone, reptile and amphibian introductions involve a mix of both. Consequently, prevention programs must involve a two-pronged approach for these taxa: risk assessment of pathways for taxa introduced accidentally and risk assessment of species for taxa introduced intentionally. Because of variation in pathway importance, information on how taxonomic, temporal, and geographic variables co-vary with economic and social data may allow for predictive assessment of pathway risk for accidental introductions. In contrast, some predictive assessment of taxon risk was achieved using variables that measure climate-matching between native and introduced ranges, phylogenetic risk, and prior history of successful taxon establishment.

Key Words: alien species, amphibians, importation, invasive species, nursery trade, pet trade, reptiles, risk assessment.

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INTRODUCTION

In the past decade, invasive alien species have begun to receive (outside the Austral English-speaking countries, which have long been responsive to the problem) the increased scientific and managerial attention they merit by virtue of their ecological and economic destructiveness. For terrestrial invasive species, this attention has a marked taxonomic bias, with considerable study and management directed toward mammals, plants, and economically important insects, and less so toward other taxa. This is reasonable inasmuch as those priority taxa cause tremendous damage that is frequently apparent even to the casual observer. The concern, though, is that silence about the ignored taxa not be mistaken for a tacit admission of ecological inconsequentialness.

Among those alien taxa largely overlooked as scientific or management subjects are reptiles and amphibians, collectively referred to as “herps”. With the exceptions of brown treesnakes (*Boiga irregularis*) in Guam, bullfrogs (*Rana catesbeiana*) in the western United States (US), and cane toads

(*Bufo marinus*) in Australia, sustained efforts to assess the ecological impacts of alien populations of amphibians or reptiles are lacking. However, impacts have been reported for a number of other alien herp populations (Kraus, in prep.) and descriptive autecological data are available for a modest number of additional populations. This is a remarkable degree of inattention given that 1,034 naturalizations of 315 species of alien herps have successfully established in 287 political jurisdictions worldwide. The reasons for this negligence are likely twofold. First, most alien reptiles and amphibians do not directly affect humans, their domestic stock, or crops. Indeed, their effects are likely to be nuanced ecological impacts on other wildlife (e.g., insects, other herps) whose ecological importance is readily discounted by most humans. Hence, they are easily perceived – including by most scientists – as of little concern. Second, most species, even large ones, are cryptic. This makes them difficult for the average human to notice and difficult for any scientist to study. Their study is made more difficult by the compounding

fact of their nuanced ecological effects, which often takes careful experimental research to determine. Consequently, alien herps rarely give the impression of occurring at plague proportions, as do more visible taxa.

In this paper, I briefly review evidence suggesting that this frequent oversight of alien herps is neither warranted nor advisable. This evidence is presented in greater detail in a forthcoming book (Kraus, in prep.), and I will give only the most cursory summary of that evidence here. I then examine what mitigation measures might be feasible for alien reptiles and amphibians and how information derived from analysis of the pathways by which these animals are transported can potentially assist in the design of effective measures to prevent future invasions. That work is ongoing, so this paper largely represents a broad conceptual overview of how alien herp invasions might best be mitigated and a short status report of efforts to date to meet that goal.

MATERIALS AND METHODS

I reviewed the literature up through the end of 2005 to construct a database of alien reptile and amphibian introductions worldwide. Data collected, when available, included jurisdiction to which introduced, date(s) of introduction, pathway(s) of introduction, minimum number of introductions involved, and whether the introduction led to a currently established population. Jurisdictions were typically countries but distinct island groups were tracked separately from the remainder of the country (e.g., Galapagos separate from Ecuador, Ryukyu and Ogasawara archipelagos separate from Japan) and species were tracked by state and province within the US and Canada. From these data, analyses were conducted to assess the pathways by which herp species were being transported and to determine how those pathways have varied. The same literature was reviewed to assess what ecological and economic impacts have been reported for alien herp introductions and what control measures have been attempted to date.

DO ALIEN REPTILES AND AMPHIBIANS WARRANT BEING IGNORED?

A variety of ecological and social impacts from alien reptiles and amphibians has been documented, even though only a small pool of species has been studied rigorously. Documented ecological impacts

include predation or poisoning of native species, secondary trophic effects, competition, and vectoring of parasites; evolutionary effects include genetic contamination via hybridization, as well as changes to morphology, physiology, and behavior (Table 1). A number of these impacts directly affect endangered native species, with perhaps the most dramatic example affecting Raffone's wall lizard (*Podarcis raffonei*), which is almost extinct due to competition (and perhaps genetic swamping) from introduced Italian wall lizard (*P. sicula*; Capula et al. 2002). Direct effects on humans include economic losses to agriculture, power supplies, and property values; health impacts via envenomation, water contamination, and disease vectoring; and loss of scientific knowledge in biogeography, taxonomy, and ecology (Table 1). In short, alien reptiles and amphibians are capable of causing many of the negative impacts widely appreciated in better-known taxa. Yet, despite this broad array of documented effects, ecological impacts have been little studied in alien herps, being noted for only 23 of 315 species having established extra-limital populations. And non-epistemological effects on humans are reported for only six of these populations (Table 1). Loss of scientific knowledge has been a fairly common result and only some of the more obvious examples are provided in Table 1, although additional examples from Mediterranean, Caribbean, and Southeast Asian islands likely exist. It is to be expected that damaging impacts are far more widespread than currently evident and that examples will multiply once a broader array of taxa and populations is sampled.

Establishment of jurisdictional populations of alien reptiles and amphibians has been growing exponentially since 1850 (Figure 1), with a doubling time of 30.4 years (Kraus, in prep.). Thus, introductions are not abating, and the pool of invasive herp species is likely to grow in the foreseeable future. The wide array of impacts already documented despite sparse study, coupled with the rapidly increasing pace of alien herp naturalization, lead me to conclude that negligence of alien reptiles and amphibians is not warranted or advisable from either an ecological or purely anthropocentric viewpoint. Instead, I suggest that greater scientific and managerial attention to these taxa, their impacts, and potential tools for their management is overdue.

Table 1. Impacts reported for alien reptiles and amphibians. Only ecological impacts on natives are noted; species reported to affect other aliens are omitted. Only a few of many possible examples are given of the scientific impacts. Data taken from Kraus (in prep.), which details references for all instances.

Impact	Species
Ecological	
Predation	<i>Anolis carolinensis</i> , <i>Anolis sagrei</i> , <i>Boiga irregularis</i> , <i>Bufo marinus</i> , <i>Natrix maura</i> , <i>Osteopilus septentrionalis</i> , <i>Rana catesbeiana</i> , <i>Xenopus laevis</i>
Poisoning	<i>Bufo marinus</i>
Secondary trophic effects	<i>Anolis carolinensis</i> , <i>Boiga irregularis</i> , <i>Bufo marinus</i> , <i>Carlia ailanpilai</i> , <i>Hemidactylus frenatus</i> , <i>Rana perezii</i>
Competition	<i>Anolis carolinensis</i> , <i>Anolis sagrei</i> , <i>Bufo marinus</i> , <i>Carlia ailanpilai</i> , <i>Eleutherodactylus johnstonei</i> , <i>Hemidactylus frenatus</i> , <i>Osteopilus septentrionalis</i> , <i>Podarcis sicula</i> , <i>Rana catesbeiana</i> , <i>Trachemys scripta</i>
Disease vector	<i>Ambystom tigrinum</i> , <i>Rana catesbeiana</i> , <i>Xenopus laevis</i>
Evolutionary	
Hybridization	<i>Ambystom tigrinum</i> , <i>Anolis distichus</i> , <i>Anolis sagrei</i> , <i>Cuora flavomarginata</i> , <i>Emys orbicularis</i> , <i>Iguana iguana</i> , <i>Podarcis sicula</i> , <i>Protobothrops elegans</i> , <i>Rana esculenta</i> , <i>Rana lessonae</i> , <i>Rana ridibunda</i> , <i>Sauromalus spp.</i> , <i>Trachemys scripta</i> , <i>Triturus carnifex</i>
Changed morphology	<i>Bufo marinus</i>
Changed physiology	<i>Bufo marinus</i>
Changed behavior	<i>Bufo marinus</i> , <i>Natrix maura</i> , <i>Rana catesbeiana</i>
Economic	
Agriculture	<i>Boiga irregularis</i> , <i>Bufo marinus</i> , <i>Varanus indicus</i>
Power supplies	<i>Boiga irregularis</i>
Property values	<i>Eleutherodactylus coqui</i>
Human Health	
Envenomation	<i>Boiga irregularis</i>
Water contamination	<i>Bufo marinus</i>
Disease vector	<i>Bufo marinus</i> , <i>Eleutherodactylus johnstonei</i>
Airstrike hazard	<i>Iguana iguana</i>
Scientific	
Biogeography	<i>Cryptoblepharus poecilopleurus</i> , <i>Eleutherodactylus johnstonei</i> , <i>Eleutherodactylus martinicensis</i> , <i>Emoia cyanura</i> , <i>Emoia impar</i> , <i>Gehyra mutilata</i> , <i>Gehyra oceanica</i> , <i>Geochelone carbonaria</i> , <i>Hemidactylus garnotii</i> , <i>Hemiphyllodactylus typus</i> , <i>Iguana iguana</i> , <i>Lepidodactylus lugubris</i> , <i>Lipinia noctua</i> , <i>Nactus pelagicus</i> , <i>Rana ridibunda</i> , <i>Trachemys decussata</i>
Taxonomy	<i>Anolis distichus</i> , <i>Trachemys spp.</i>
Ecology	<i>Boiga irregularis</i>

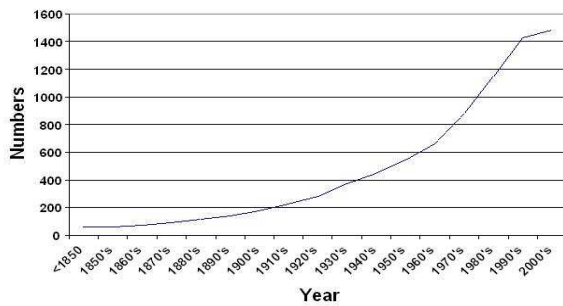


Figure 1. Cumulative growth in reptile and amphibian introductions from 1850–2005. Curve from 1850–1999 (before artifactual decline resulting from reporting time lag) is approximated by the exponential growth equation $y = 46.014e^{0.2271x}$, with $R^2 = 0.9993$ and a doubling time of 30.4 years.

HOW MIGHT ALIEN HERP INVASIONS BE FEASIBLY MANAGED?

Mitigation of impacts from invasive pests logically involves either preventing introductions in the first place, detecting and quickly eradicating new incursions, or managing entrenched populations so as to minimize their long-term impacts. I argue that the crypsis, high reproductive output, and high population densities that characterize many invasive herps make the latter two mitigation measures impossible to achieve in most circumstances. Very few examples of eradication or control have been attempted for alien herps. I will briefly review two examples that, I believe, are illustrative of the biological and social limitations that will frequently hinder such attempts.

Coqui frogs (*Eleutherodactylus coqui*) were introduced into Hawaii in the late 1980s or early 1990s in nursery plants imported from Puerto Rico. Immediately upon discovering this species in February, 1997, I repeatedly urged State officials having the responsible authorities to eradicate the species before it was irredeemably beyond control. This advice was motivated by knowledge of the high population densities the frogs achieve, recognition that their establishment would insert a novel trophic level into Hawaiian forest communities, and appreciation that their loud calls make the males readily detectable and targetable (as well as obnoxious), a necessary condition for any eradication campaign (Kraus et al. 1999).

Despite this evidence and the damage that could reasonably be predicted to follow widespread establishment, State officials resisted efforts to intervene in this invasion for years, until well after the narrow window had passed during which statewide eradication was possible (Figure 2). The reasons for this failure resulted from the intersection of the species' high intrinsic rate of increase with the social constraints that (1) officials did not believe that a tiny frog could constitute a pest problem, and (2) effective control methods were lacking and took years to identify (Kraus and Campbell 2002). The biological parameter enforced a narrow window of control opportunity before populations were irredeemably entrenched; the social limitations emasculated response options until after that window had passed.

A somewhat similar dynamic pitting high intrinsic growth rates of an alien herp against lack of human imagination characterized the recent invasion of Burmese pythons (*Python molurus*) in southern Florida. Despite having scores of captures and reliable sightings of pythons in Everglades National Park by 2002 (including 27 in that year alone), biologists consulted to assess whether a population might be established advised that all represented released pets and posed no cause for concern (R. Snow, Everglades National Park, personal communication). It was clear to everyone even two years later (and clear in 2002 to anyone with invasive reptile experience) that pythons were widespread within the park and reproducing. They are now known to occur in high population densities and to range over an extensive area, including well beyond park boundaries (Snow et al. 2007). Again, the narrow window of opportunity for effective human response passed before it was even recognized.

Both these examples illustrate the common reaction from managers and many scientists to invasive herps: disbelief that a problem exists. And both species were allowed to expand beyond the point of effective control despite the fact that certain control advantages were present in these instances that would not obtain for most alien reptiles and amphibians. In particular, the problem of crypsis, which seriously hampers detecting most herp species, did not apply in the case of the coqui because the males' loud calls make them readily targetable for control. And the extremely large size of the pythons (>7 m), which certainly makes them more conspicuous than most alien herps, provided no advantage for early recognition of their naturalization. I suggest that both of these

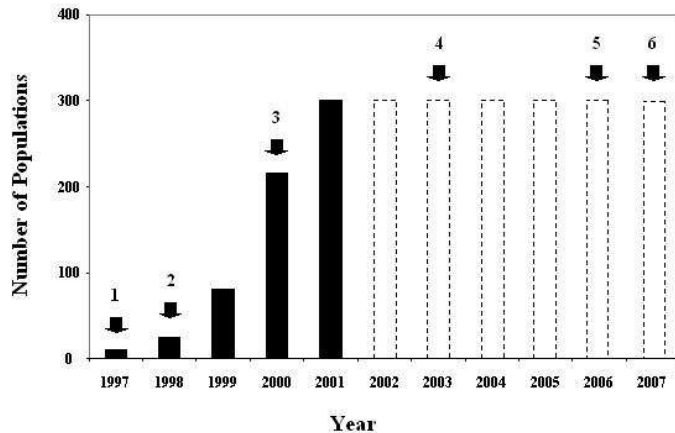


Figure 2. Contrast in growth in numbers of Hawaiian populations of coqui (*Eleutherodactylus coqui*) with milestones of State government response. Populations became too numerous to track after mid-2001 but presumably continued to grow exponentially, at least for a time. Despite that presumption, I merely outline the 2001 figures for all remaining years; estimated infestation by 2006 on Hawaii Island alone was >5000 acres (M. Wilkinson, HI Dept. Land & Nat. Res., personal communication). 1 = Alarm first raised by DLNR and USDA employees regarding threat posed by coqui, March 1997; 2 = first significant media coverage of coqui threat, November 1998; 3 = first State support to identify means of chemical control for coqui, June 2000; 4 = first Legislative action to facilitate control of coqui, indemnifying landowners to allow access for control operations, May 2003; 5 = first quarantine measures requiring treatment of inter-island shipments from infested nurseries, pending as of February 2006; Legislature declares coqui a pest, May 2006.

examples were unusual only in that biological weaknesses existed that could potentially have been exploited for effective control. However, these advantages were squandered by blinkered human responses that did not recognize the evidence of or admit the potential seriousness of the situation.

On the other hand, the coqui and python examples well exemplify the high reproductive rates (Kraus et al. 1999, Kraus and Cravalho 2001, Snow et al. 2007) that typify many other alien herp species. These high intrinsic population growth rates create very narrow windows of opportunity for implementing successful control. It is true that early detection and eradication of alien herps will sometimes be possible (cf., Whitaker and Bejakovich 2000 for Eastern banjo frog [*Limnodynastes dumerilii*] in New Zealand, and Fisher and Garner 2007 for bullfrogs in Britain). However, I suggest that most alien herp species will be even more difficult to control than coquis and pythons because (1) we will typically lack the benefit of having a readily identified biological fulcrum against which to act, (2) other species are

likely to be more cryptic, and (3) psychological unresponsiveness to alien herps is likely to persist for the foreseeable future. From these considerations, I conclude that meaningful management of alien reptiles and amphibians must largely rely on prevention of their introduction. But design and implementation of effective prevention programs requires knowledge of how and why these animals are being transported. In short, one must understand the pathways by which alien reptiles and amphibians are moved and how those pathways vary.

HOW ARE ALIEN REPTILES AND AMPHIBIANS BEING TRANSPORTED?

Only one study (Kraus 2003) has quantified how alien herps are being transported by humans and that study was preliminary to the expanded database analyzed in Kraus (in prep.) and briefly summarized here. Kraus (2003) showed, based on a dataset of 577 introduction records, that six pathways have accounted for most herp

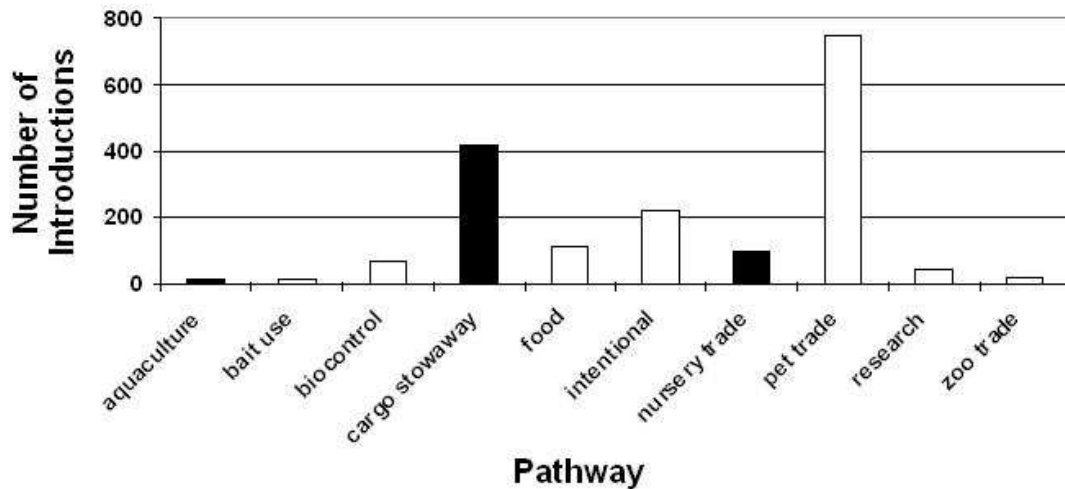


Figure 3. Numbers of introductions of alien reptiles and amphibians by pathway, 1850-2005. Open bars indicate intentional pathways; closed bars accidental pathways. “Intentional” refers to deliberate private introductions for aesthetic self-indulgence or other purpose.

introductions and that pathway importance varied taxonomically, temporally, and geographically. These major conclusions are upheld by the far more complete sampling (>5,700 introduction records) now available. Unlike most higher-level taxa, both intentional and accidental pathways have been important in the introduction of reptiles and amphibians (Figure 3). Intentional pathways include introductions for biocontrol, food use, the pet trade, and personal release of animals for aesthetic self-indulgence. Accidental pathways include transport as aquacultural contaminants, cargo stowaways, and hitch-hikers in nursery plant materials, the last a special subcategory of cargo stowaways deserving of separate tracking because of its increasing importance.

Frogs and lizards have been the most commonly transported herps and are the only major taxa to have utilized all six major pathways (Figure 4). Snakes and turtles have been introduced via a

number of pathways too, but at lower levels, and salamanders and crocodylians have been transported relatively rarely (Figure 4). Only the pet trade and personal aesthetic pathways have involved all higher-level taxa, whereas the other four pathways have been more taxonomically limited in scope (Figure 4). Relative success in leading to naturalization varies among pathways, with transport via the nursery, biocontrol, and food pathways being far more likely to lead to successful establishment than transport via the other three (Kraus 2003, in prep.).

Pathway importance has varied temporally, with the cargo pathway being of greatest importance for the second half of the 19th Century, intentional aesthetic introductions of greatest importance for the first part of the 20th Century, and the pet trade of greatest predominance since the 1970s (Figure 5). The biocontrol pathway has been largely quiescent for the past several decades, the food-use pathway has grown relatively little during that same

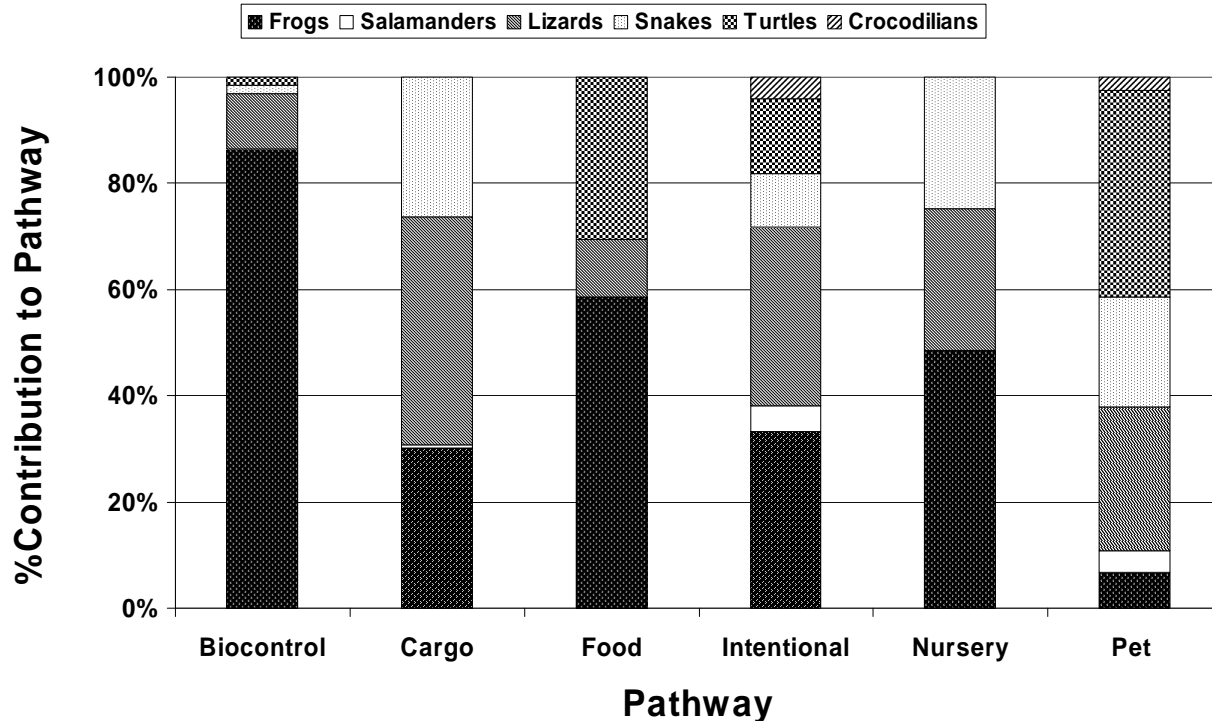


Figure 4. Relative taxonomic distribution among the six primary introduction pathways, 1850-2005. “Intentional” refers to deliberate private introductions for aesthetic self-indulgence.

period, but the nursery-trade pathway has increased considerably in importance since the 1970s (Figure 5). Introduction rates from 1980-2005 have been considerably higher for the pet-trade, nursery-trade, and cargo pathways than for the period 1850-1979 (Kraus, in prep.). Rates of introduction for biocontrol have been drastically less during that same period, while rates for food use and intentional aesthetic introductions have remained unchanged (Kraus, in prep.).

The large majority of documented introductions have involved Europe and North America (Kraus, in prep.). Kraus (2003) showed pathway importance varies among the US, Caribbean, and Pacific regions, and this pattern holds true for other regions as well. Generally speaking, the pet trade is the most important pathway for introductions into North America, Europe, and Asia, whereas cargo has predominated in the Pacific, and cargo and the nursery plant trade are co-dominant in the Caribbean (Figure 6). The upshot is that each major

geographical region has its own unique signature of pathway representation and relative importance (Kraus, in prep.).

HOW MIGHT EFFECTIVE PREVENTION PROGRAMS BE DESIGNED FOR ALIEN HERPS?

The information above has important ramifications for designing and implementing effective prevention strategies for invasive reptiles and amphibians. First, strategies to abate intentional versus accidental introductions are quite different, but both will need to be included to limit further alien herp incursions. Intentional introductions may be addressed by implementing some form of taxon-based risk-assessment system incorporating features that appear diagnostic for either naturalization or invasiveness, as is done for weeds (Pheloung et al. 1999, Walton et al. 1999, Williams et al. 2002) and some vertebrates (Bomford and Hart 1998, Kolar and Lodge 2002, Bomford 2003, Bomford and Glover 2004). Such a method requires identification of ecological or other predictors of naturalization/invasiveness for

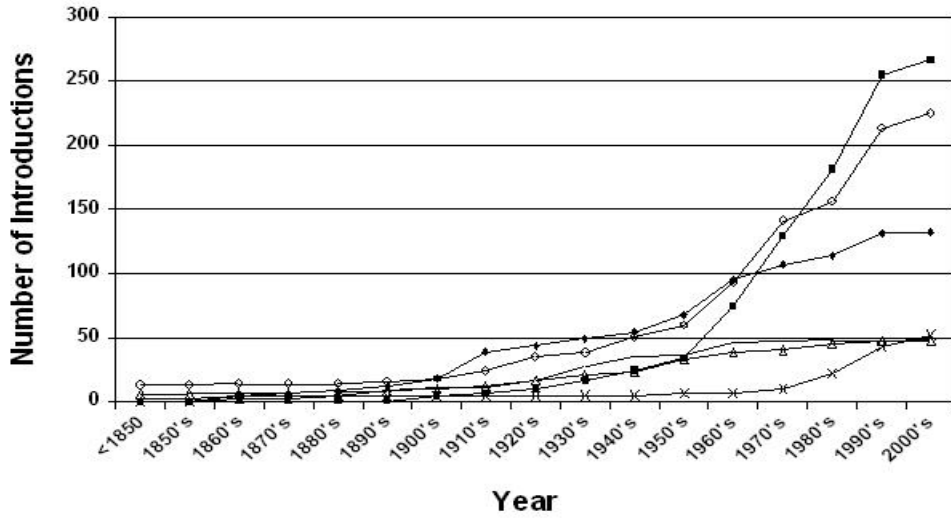


Figure 5. Changes in global pathway importance for the six major pathways, 1850-2005. Solid line, biocontrol; open circles, cargo; open triangles, food use; X's, nursery trade; filled squares, pet trade; filled diamonds, intentional aesthetic releases.

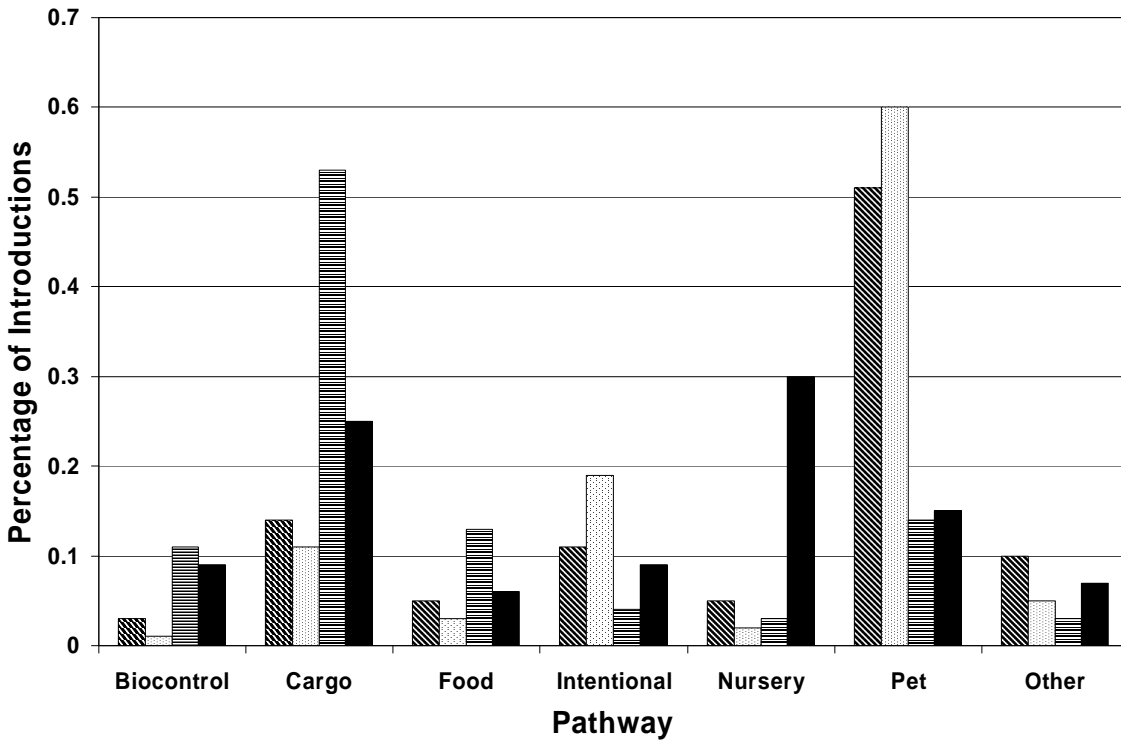


Figure 6. Variation in pathway importance by geographic region for all documented introductions, 1850-2005. Diagonal lines, North America; stippling, Europe; horizontal lines, Pacific region; and solid bars, Caribbean.

the targeted taxa. Higher numbers of predictive variables should be expected to lead to more robust results, as typifies the weed-risk-assessment systems (Pheloung et al. 1999, Daehler et al. 2004).

Bomford et al. (2005) tested the utility of four variables for their usefulness in predicting naturalization among alien reptiles and amphibians introduced to Great Britain, California, and Florida. They found that degree of climate match between native and introduced ranges, a taxonomic-risk variable, and whether a species had previously established elsewhere were useful in segregating among species that successfully established in these three jurisdictions versus those that did not. In contrast, they found that size of native range (thought to reflect breadth of ecological tolerance) had no predictive value. This study is currently being refined, and a larger number of variables needs to be included, but their results suggest that such an approach may be promising for predicting naturalization ability among reptiles and amphibians in particular regions, thereby providing a tool for screening intentionally introduced species. Efforts will also soon be made to identify additional ecological variables that may refine this approach.

Approaches toward preventing reptile and amphibian introductions via accidental pathways (primarily cargo and nursery plant trade in my study, but also including lesser numbers introduced on vehicles and as aquacultural contaminants) are more tentative. Recall that each geographical region exhibited its own characteristic signature of pathway representation and importance. It may prove possible to correlate these patterns with simple economic or legal variables for any country within each region and use those indicators to predict which pathways merit greatest attention within any particular jurisdiction. Should that prove true, one could then prioritize limited resources to those pathways so identified, thereby maximizing prevention efficiency. For example, should magnitude of nursery-trade introductions correlate with income levels, assessing the magnitude of the latter could be used to predict the risk of the former and inform decisions as to how much effort to devote to searching or treating that pathway. Assessing whether economic indicators correlate with pathway intensity is the subject of ongoing investigation by the author along with B. Kaiser and K. Burnett.

Should such economic predictors be identified, it would still leave unresolved how animals in the accidental pathways are best intercepted. All such

pathways must involve some form of port-of-entry inspection program, relying on the border quarantine programs widely in place around the world. But such programs necessarily sample only a very small portion of arriving goods and must rely on repeated sampling schemes to identify highest-risk pathways and provide quality assurance. This is where prioritization of inspection effort informed by economic predictiveness of pathway importance may prove useful. However, treatment methods to remove hitch-hiking herps, other than hand-capture, have been little investigated and we require development of methods of scale that can effectively treat entire cargo shipments. As one example of what is needed in this regard, a short hot-water drench is sufficient to kill hitch-hiking frogs in potted nursery plants (F. Kraus unpublished data), a pathway of increasing importance, but is just beginning to be scaled up to a level commensurate with industry volume in Hawaii (D. Cravalho, Hawaii Dept. Agriculture, personal communication). Similar scaled-up methods that go beyond visual inspection and hand-capture are needed to more effectively address reptile transport via this same pathway and to address all species transported in other accidental pathways.

Note that both prevention options discussed above – taxonomic risk-assessment systems for intentional introductions and identification of economic indicators to assess risk of accidental pathways – serve (ideally) only to best identify those taxa or pathways of highest risk for inadvertent importation or establishment. In many countries, having that information does not necessarily mean it will be used for interdiction, due to a variety of political, legal, and procedural hurdles discussed in detail by Simberloff (2005) for the case of the US. For intentional introductions, use is required of a comprehensive white list/black list system that explicitly adopts the precautionary principle and forbids importation until a species has been assessed as posing little risk. Such methods may have their statistical limitations (cf. Smith et al. 1999, Caley et al. 2006) but are vast improvements over the minimal, reactive programs that typify the majority of countries. In the case of the US specifically, this reactive stance is embodied in the Lacey Act, part of which includes a miniscule list of “injurious wildlife” banned from import because they have proven harmful elsewhere. A problem with that reactive approach, of course, is that only a tiny fraction of proven invasive species – those that have garnered some

level of political concern – are included on that list and high-risk species that happen not to have been imported anywhere yet are ignored entirely. Similar problems attend assessments of risk for particular pathways, which typically assess only a limited pool of likely risks and impacts (Simberloff 2005). It is worth noting that continued pursuit of such minimalist policies for preventing invasions is inconsistent with the risk-analyses outlined here, which are intended to identify high-risk taxa and pathways so that exclusionary measures might actually be implemented. As far as I am aware, a comprehensive approach based on the precautionary principle seems to have been adopted to date only by Australia and New Zealand.

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