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CHAPTER 23

INTRODUCED SPECIES THAT INVADE AND SPECIES THAT THRIVE IN TOWN: ARE THESE TWO GROUPS CUT FROM THE SAME CLOTH?

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Abstract — We review the literature to identify natural history traits hypothesized to be associated with amphibians and reptiles in each of three categories: invasive, urban, and pet. We examine the natural history traits to determine the extent to which species' traits overlap between these groups. Ecological generalists (e.g., diet, habitat) are believed to do well in all three settings, and indeed all three settings are associated with species bearing a number of common attributes (e.g., adaptability, tolerance of artificial habitats, high population density). We review the evidence for this commonality and explore the management implications, especially those germane to the prevention of biodiversity loss attributable to invasive species. Key questions are whether invasive species colonizations threaten indigenous wildlife or are capable of spreading beyond urban areas. Many introduced herpetofaunal species have not yet spread beyond urban environments, but initial spread is often a poor indicator of eventual distribution. With the increase in urbanization and expanding trade and human population, the nexus among pet, urban, and invasive species issues is set to affect a progressively larger proportion of the globe.

Key words — Ecological Generalists, Invasive Species, Native Range, Pet Trade, Urban Colonists, Urban Transport, Wildlife Management

Are urban herpetofaunas also invasive herpetofaunas? Or vice versa? Perhaps the best way to assess the degree of overlap between the subsets of herpetofaunas that are known to be successful in introduced and urban settings would be to list for each of the world's reptile and amphibian species the extent to which each has succeeded in urban areas and areas outside of their native range. If the two phenomena – urban success and invasiveness – are correlated, our hypothetical data matrix should show a statistical correspondence between the attribute scores. Unfortunately, the ecological data to create such a matrix have for the most part not yet been collected, and those few reports that are available are highly biased in the choice of species and geographic areas documented. More importantly, such an empirical analysis would not directly provide us with any basis for making predictions. We would like to develop an understanding of the factors that promote invasion or urban success. From a wildlife manager's viewpoint, the most useful associations are those that would allow us to predict whether a previously unstudied species justifies regulation or special precautions to prevent undesirable population changes (e.g., colonization by an invasive species or depletion of resident species). Ideally we would like to know not only which species exhibit correspondence between urban success and invasiveness, but why.

In the absence of comprehensive empirical data on ecological success in urban and extralimital situations, we compiled hypotheses from the literature about the natural history attributes associated with urban, pet, or invasive species. In some cases, hypotheses were stated in identical ways, but more often they were framed in similar, potentially correlated ways. For example, one author might argue that urban species are habitat generalists, and another author might argue that species

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are more likely to be invasive if their native range is very large. Might these two hypotheses be reflections of a similar underlying capability for a wide ecological niche breadth? To address possible overlap between both the conceptualizations and the attributes of the different groups we: 1) compiled all relevant hypotheses from the literature, 2) grouped hypotheses to bring similar concepts into juxtaposition, and 3) scored each invasive species concept for the degree of concordance with urban and pet species attributes as we understand them.

Materials and Methods

The first step in our analysis was to categorize concepts of natural history traits and bring related concepts together. This required a review of the various stages of species introductions (transport, establishment, and spread) and the different types of urban herpetofauna (residual natives, synanthropes). Natural history attributes of invasive species have been identified for a variety of taxa, though reptiles and amphibians have received only limited attention (see references in tables). We examined the literature derived from a wide spectrum of invasive fauna and flora to obtain a fuller review. Natural history attributes of urban herpetofauna have likewise received little attention; this volume will substantially expand the relevant literature. Bodies of literature for invasive and urban species make reference to the pet trade as an important contributor: the pet trade is both directly and indirectly a key source of invasive herpetofauna, and discarded pets often end up populating urban areas. We therefore expanded our analysis into the natural history characteristics that promote a species' popularity in the pet trade. Regrettably, there seems to be no literature explicitly generalizing natural history attributes of herpetofauna in the pet trade.

Once similar concepts of natural history traits were delineated and appropriately grouped, we scored each identified natural history trait for its relationship to pet, urban, and invasive species. In comparing these lists of traits, we focused on two potential pairwise associations: pets compared to invasives, and urban compared to invasives. A "yes" score was given for probable concordance between the traits, a "no" score for disparate attributes (e.g., if large species were favored for invasiveness, but small species favored for pets), and a zero given to those natural history traits that had no apparent bearing on success as pets or urban herpetofauna. We used invasive species traits as the primary axis for scoring simply because the literature for invasive species is more developed than that for the other two groups. Overall, the natural history attributes of each pairing (invasive cf. urban, invasives cf. pets) were judged to be concordant if the number of yes scores greatly outnumbered the number of no scores for a given category (see below for choice of categories). A more quantitative approach must await hard ecological data and rigorous separation of related ecological concepts, but we hope this preliminary compilation will contribute to defining and identifying the ecological hypotheses most worthy of testing.

Results and Discussion

Urban Herpetofaunas — Reptiles and amphibians occur in urban areas either because they were present in the natural habitats that existed prior to creation/expansion of the urban zone and have managed to persist in remnant natural habitats, or because these original occupants or new arrivals thrive in habitats created by humans (e.g., Germaine and Wakeling 2001), synanthropes in the jargon of Johnston (2001). We are interested in those species that thrive alongside humans. In the case of the Tucson, Arizona, vegetation studied by Germaine and Wakeling (2001), these would include not only the Tree Lizards (*Urosaurus ornatus*) that did well in the native and introduced residential vegetation that was studied, but also the various introduced house geckos (*Hemidactylus* sp.) that thrive in and on Tucson's buildings, and Clawed Frogs (*Xenopus* sp.) and Painted Turtles (*Chrysemys picta*) in Tucson's golf course ponds (Stebbins 2003).

What makes it possible for a species to thrive in urban environments? Koenig et al. (2001) asked this question with regard to a very large viviparous skink (*Tiliqua scincoides*). This species is relatively fecund and long-lived (so as to outlive periods of low recruitment in this environment), relatively immobile (thereby minimizes contact with urban predators such as dogs, cats, and automobiles), well adapted to the structure of urban habitats (lawns, buildings), prone to eating the food of human pets, and averse to crossing roads. DeStefano and Koenen (2003) and DeStefano and Johnson (2005) studied urban vertebrates in general and found many of the same attributes — broad habitat tolerance, dietary generalism, ability to use lawns and buildings, and r-selected — but they also reported two attributes that did not conform to the suggestions of Koenig et al. (2001): small-body size and high mobility. Small body size effectively increases the capacity of habitat patches (a 0.4 ha lot might support a viable population of hundreds or thousands of small 1 g skinks, but would not support the home range of even a single 500 g *Tiliqua scincoides*). Mobility might facilitate colonization or recolonization of isolated habitat patches and speed of range expansion, but for terrestrial species, could also lead to more frequent and unfavorable contacts with automobiles or predators. Most of the species considered by DeStefano and Koenen (2003) were avian, for which high mobility would promote rapid recolonization of patches from which they had been extirpated. A different dynamic may apply to urban amphibians and reptiles.

Missing from either of these lists of traits is an explicit recognition that to be a successful urban species, both animal and humans must be tolerant of close physical proximity to each other. Perhaps that point is too obvious to warrant explicit mention, but for large or dangerous species such as monitor lizards, snakes, and crocodilians (Nichols and Letnic 2008), any disinclination to approach or tolerate humans or intolerance of their presence by humans would be a significant deterrent to urban dwelling (Palmer 1992), especially for diurnal species.

It may be appropriate to group these attributes of urban species into three broad categories: wide niche breadth (diet, habitat, etc.), high fecundity, and ability to withstand predators that are especially common in urban areas: dogs, cats, rats, humans, and automobiles. In general, urban areas have an abundance of edificarian habitats and early successional vegetation on land, and high nutrient loads in the water. These habitats are usually tolerated and often favored by urban herpetofauna.

The remarkable success of certain urban species can be attributed not so much to *wide* niche breadth as to the ability to exploit a niche that simply does not exist in nature (e.g., house geckos that rely on capturing insects drawn to electric lights: McCoid and Hensley 1993; Petren et al. 1993; Perry et al. 2008). These geckos need not necessarily have a broad tolerance for microhabitats, but they must be able to exploit a particular unnatural habitat: the vicinity of electric lights. The ability and willingness of species such as *Bufo marinus* or *Tiliqua scincoides* to feed from dog food bowls is a manifestation of a natural ability to exploit novel food sources in unfamiliar environments. Their dietary niche breadth need not be extraordinarily wide (although for these species it is), as long as it includes dog food.

Some urban wildlife, such as Tucson's *Urosaurus ornatus*, may not be so much specially adapted to urban living as much as benefiting from the absence of competitors or predators, such as large *Sceloporus*, that avoid urban settings (Germaine and Wakeling 2001). This may be an example of mesopredator release (Soulé et al. 1988; Crooks and Soulé 1999) attributable to urban intolerance by larger predators.

Pets — There does not seem to be a literature describing natural history attributes of herpetofauna associated with the pet trade. There are papers advising prospective pet owners as to what species are readily available and which are desirable or should be avoided (e.g., Spiess 1997a,b). There are papers detailing import and export figures (e.g., Schlaepfer et al. 2005), but these do not account for species traded domestically, and international trade statistics often include some extraneous individuals traded for food, leather, and medicines. None of these pet studies addresses the natural history characters that pet dealers subconsciously or consciously use for inclusion or promotion of a herpetological species in the pet trade. We hypothesize that four key characters, in approximate order of importance, are: low cost to the dealer, exotic or colorful appearance, non-secretive habits, and docility/ease of handling. Low cost to the dealer is not, of course, a natural history trait, but probably reflects high animal population density in a part of the world (often tropical) where prevailing salaries are low (usually associated with high human population density). For example, the top amphibians and reptiles imported into the U.S. for pet purposes (Schlaepfer et al. 2005) during 1998–2002 were: *Hymenochirus curtipes, Cynops orientalis, Bombina orientalis, Hemidactylus* spp., *Python regius, Trachemys scripta, Varanus salvator,* and *Iguana iguana*. All of these species reach high population densities (at least locally) in low salary areas (mostly tropical). From the perspective of the general public, all but *Hemidactylus* have an exotic appearance. *Hemidactylus* are conspicuous at night and all others are non-secretive. All are relatively easy and safe to handle.

Do these species show the primary characteristics of urban herps: wide niche breadth, high fecundity, and ability to withstand urban predators? Compared to similar species, most show relatively broad habitat tolerances, and many show broad dietary niche width (Table 1). *Python regius* is a dietary (rodent) specialist, though rodents are relatively abundant in many urban areas. *Iguana iguana* is a dietary specialist in being a folivore, but it eats a broad spectrum of leaves and flowers and the required leaves are available in all urban areas. The association with high fecundity is much less clear (Table 1). Several species (*Hemidactylus, Python, Trachemys*) would be regarded as moderately fecund compared to similar species, although all reach high densities in a wide variety of habitats. Population density may be more of a commonality than high fecundity. Solid data on tolerance of urban predators is lacking, though urban populations of most of these species are known.

Invasive Species — A variety of widely overlapping terms has been used for species outside of their native range: alien, introduced, invasive, exotic, and so forth (Ruiz and Carlton 2003). In theory, one can make an important distinction between species that have been merely introduced (outside of their native range by virtue of anthropogenic causes) and those introduced species that have become numerous in their extralimital range and thereby created social, economic, or ecological problems (i.e., they are "invasive"). Two weaknesses of distinguishing problematic range extensions from harmless ones are that one's definition of "harmless" is somewhat subjective and the discovery of harm is often delayed by ecological time lags or lack of sufficient monitoring (Mack et al. 2000). We don't know how long it takes for the damage from an introduced reptile or amphibian species to be fully manifest; time lags for woody plants in Germany were found to average 147 yrs (range 8–388 yrs: Baskin 1996, 2002; see also Crooks and Soulé 1999) from introduction to spread. For mammals introduced between Europe and North America, Jeschke and Strayer (2005) estimated an average delay of 14 yrs between introduction and establishment, but 62 yrs between establishment and spread. Their corresponding values for birds were 52 and 60 yrs, respectively. Thirty years after the Brown Treesnake invaded Guam, no one had described this introduction as invasive or harmful, but 40 yrs after the introduction, it was widely understood to be catastrophic (Rodda et al. 1999). The harm caused by an introduced species may not be obvious until decades later when a key predator or prey is introduced. It is too early to tell whether any given herpetological introduction is truly harmless; investigators are still discovering problems caused by species introduced by the ancient Romans (Eisentraut 1950; Alcover and Mayol 1981; Moore and Griffiths 2002). We believe that the burden of proof should be on those arguing that an introduction is harmless; until

Table 1. Attributes of popular herpetofaunal species recently imported for the U.S. pet trade.

Species	Common name	Native range	Habitat niche width	Diet/diet niche width	Fecundity (cf., similar sp.)	Tolerance of urban predators	Sources
Hymenochirus curtipes	African Dwarf Frog	West Africa	Unknown	wide?	moderate?	unknown	Noble 1924; Obst et al. 1988; various herpetoculture websites
Cynops orientalis	Chinese Fire Belly Newt	China	wide?	unknown	unknown	unknown	www.livingunderworld.org/caudata/ database/salamandridae/cynops/ Accessed Sept. 2006
Bombina orientalis	Oriental Fire-bellied Toad	China	unknown	wide	moderate	unknown	www.anapsid.org/bombina.html (accessed Sept. 2006); Kaplan 1992
Hemidactylus spp.	House Geckos	Pan-tropical	wide	insects	moderate	high	Bolger and Case 1992; Petren et al. 1993; Luiselli and Capizzi 1999; Meshaka 2000
Python regius	Ball Python	West Africa	wide	rodents	low	high?	de Vosjoli et al. 1995
Trachemys scripta	Red-eared Slider	Southeast US	wide	omnivore	moderate	high?	Gibbons 1990; Vogt 1990
Varanus salvator	Water Monitor	Southeast Asia	wide	carnivore, invertebrates	high	high	Bennett 1998
Iguana iguana	Green Iguana	Neotropics	wide	diverse leaves and flowers	very high	low (breeding females)	Rand 1978; Rodda 2003

proven otherwise, all introduced species should be treated as potentially invasive and hence detrimental.

Several steps are involved in a species invasion (Williamson 1996), each of which may have its own suite of natural history attributes. We organize our discussion around three steps: *transport* (= arrival), *establishment*, and *spread/harm*. First a species must be transported to a new location: this can occur without direct human intervention, as the result of habitat alteration (e.g., Boarman 1993); accidental transport (e.g., geckos stowing away in cargo); intentional transport (e.g., release of Cane Toads for biocontrol in Australia); or accidental or intentional release of unwanted captives (e.g., boa constrictors in Miami were initially transported to south Florida intentionally, but their release may or may not have been intentional).

Establishment usually requires at least one male and one female meeting at an opportune time, although parthenogenetic species (e.g., *Ramphotyphlops braminus*) escape that requirement and females of other species may use stored sperm to circumvent it. Establishment is very closely related to transport in the sense that the greater the probability of a single transport event, the more probable is the occurrence of multiple transport events that will result in a receptive female encountering a reproductive male. For establishment to occur, there must be not only multiple transport events (or transport of a gravid female), and the transported individuals must not only remain alive at the destination, but they must also remain spatially close in order to eventually meet at an appropriate time. Individual reproductive events must be repeated often enough for the population to be sustained. Thus, establishment has several additional requirements beyond those needed for transport.

Species that fail to expand their population or to spread beyond their new location are unlikely to have measurable ecological consequences (and their small populations are highly vulnerable to stochastic extinction). Spread that does occur may be either habitat-limited or involve expansion of the population into additional habitats. A very important threshold is passed whenever a new population spreads beyond its original urban colonization. Although it is possible for a colonization to occur anywhere, most invasive herpetofauna have originally colonized an urban area, usually a port (Meshaka 2004; Powell and Henderson 2008). To date, relatively few introduced herpetofauna in the United States have spread beyond urban habitats (Meshaka 2004). If the invasive species never spreads beyond its urban origin, the species is unlikely to have strong adverse ecological impacts, though it may have significant social and economic consequences (e.g., snakes causing power outages by crawling on power lines: Fritts and Chiszar 1999). Much popular attention has been paid to the rapidity of spread (rapidly spreading species are newsworthy), but the key parameters are ultimate geographic range and severity of ecological impacts. All things being equal, the severity of ecological impacts is a function of the size of the geographic range and population density achieved.

Natural History Characters Germane to the Transport Stage of Invasion — The natural history correlates of the transport stage for species that are not moved intentionally were derived by reviewing the substantial literature on natural history correlates of invasive species and omitting those phenomena unrelated to transport. About a dozen hypotheses remain (Table 2), covering both the likelihood that a species will accidentally enter a cargo and the likelihood that it will survive the transportation. In addition to these hypotheses, several authors (e.g., Simberloff and Boecklen 1991; Kolar and Lodge 2001) have noted that success in invasions is in itself a good predictor of whether a species will invade elsewhere. This observation has merit for predicting which species are most likely to invade a novel locality, but it doesn't provide specific mechanisms for understanding the causes of success (hence it was omitted from relevant tables).

Several of the hypotheses for natural history correlates of transport (Table 2) relate to the geography of the species' native range. Brockie et al. (1988) argued on evolutionary grounds that continental species (contrasted with island species) are more likely to be successful invaders. Although not related to transport *per se*, we propose that continental species are more likely to come into contact with cargo because most cargo originates on continents (cf., islands). Likewise, a variety of authors (Table 2) have argued that species with larger native ranges would be more likely to be successful invaders, as such species would have a wider ecological niche. All things being equal, the larger a source area, the more often the species will come into contact with cargo and hence be more likely to be transported. Such correlations are also found with high vagility or high density of the focal species in its native range (Table 2), as more mobile or abundant organisms will more

Table 2. Natural history characters hypothesized to correlate with *transport* of invasive species. The "good pet?" and "good urban?" scores indicate whether the specified trait is favorable to a species' inclusion in the pet trade or survival in urban environments, respectively (y = yes, n = no, 0 = neutral or unknown).

Species attribute	Rationale	Good pet?	Good urban?	Relevant literature
Cargo contact opportunities				
continental (cf. island) native range	most cargo originates on continents	y	0	Brockie et al. 1988
geographically large native range	increased opportunities to enter cargo	0	0	Williamson and Fitter 1996
high density in native range	increased opportunities to enter cargo	y	y	Ehrlich 1989; Williamson and Fitter 1996
high vagility in native range	increased potential for contact with cargo	n	n	Ehrlich 1989; Lodge 1993
disturbed habitat preference	cargo originates from human habitats	y	y	Meshaka 2004; Stohlgren and Schnase 2006
associated w/ human habitats	cargo originates from human habitats	y	y	Ehrlich 1989; Lodge 1993; Mack et al. 2000
small propagules	reduces likelihood for detection/ rejection from cargo	n	y	Rejmánek and Richardson 1996 (pines); plant studies in Kolar and Lodge 2001
arboreality	may reduce probability of detection in cargo	0	y	Ebenhard, (mammals) 1988
insectivorous	all cargo facilities host suitable prey	y	y	Meshaka 2004
lizard (cf. other herp)	many lizards are small, ecological generalists	y	y	Meshaka 2004
Survival in transport				
tolerant of wide climatic range	can more easily tolerate climate in transport	y	y	Ehrlich 1989; Lodge 1993; Duncan 1997
associated with human habitats	transport facilities are human habitats	y	y	Ehrlich 1989; Lodge 1993
mammal (cf. other vertebrates)	mammals presumed to have evolved superior homeostatic mechanisms	0	0	Brockie et al. 1988

frequently come into contact with cargo, as will those species already present in urban environments (Meshaka 2004).

Plant ecologists have regularly associated small propagule size with invasion success (Table 2). Could this apply to reptiles and amphibians? Small size would reduce the probability that the hitchhiker would be detected and removed by cargo handlers. For example, small adherent gecko or *Eleutherodactylus* eggs easily evade detection in cargo, whereas large eggs or live animals are more likely to be noticed. Other traits such as arboreality (Ebenhard 1988) and insectivory (Meshaka 2004) have been suggested as being favorable to invasive species. An association with insectivory may be due to either the ready availability of insects (cf., plants, vertebrates) in warehouses, docks, and ports, the small average body size and hence lower rate of detection of lizards (cf., turtles, crocodilians, snakes), or lizards' tolerance for desiccation (cf., amphibians) in cargo facilities. The predilection of arboreal lizards to cling to the sides of cargo objects, especially during their inactive period, might predispose them to accidental transport. The numerous invasive geckos of south Florida and West Indies provide examples (Meshaka 2004; Powell and Henderson 2008).

Meshaka (2004) also noted a statistical association between being a lizard and being established as an invasive in Florida. Lizards are often small (< 5 g). To the extent that Meshaka's observation is a reflection of the prospects for coming into contact with cargo, the indirect correlation between being a lizard, small size, and evading detection in cargo illustrates an important point. While many natural history attributes might be of statistical value in predicting which species are likely to invade, care should be taken in distinguishing those attributes that are predictive because they are causal and those that appear to be of predictive value solely due to covariance among species attributes.

The transport stage includes not only contact with cargo but also surviving transport. Compared to other vertebrate taxa, herpetofauna, with their low energy demands, seem uniquely suited to long-term survival inside shipments. For example, a Brown Treesnake (*Boiga irregularis*) survived nine months in a sealed shipping container, a time period that would have exceeded the survival abilities of most non-herpetofaunal vertebrates (Fritts et al. 1999).

Tolerance of a wide range of climates has been mentioned by a variety of authors as a facilitator of establishment (see Table 2), but a successful transportee must also survive potentially wide variation in temperature, humidity, and pressure en route (Perry 2002), especially during air and land transport (modern sea cargos experience fairly uniform conditions). The association of certain species with humans predisposes them to survive in transport, as all cargo vessels have at least some compartments specifically conditioned to human climate tolerances.

Natural history correlates are of minimal importance for predicting survival during transport of live animals that are intentionally transported for the pet and food industries (Schlaepfer et al. 2005); the shipper purposefully places the species in a shipment and provides at minimal cost an environment that ensures that most individuals will survive the journey. The selection of a species for food uses may reflect natural history traits such as fecundity and rapid growth (which facilitate captive propagation), and large size (increased yield of meat per carcass). We will not further analyze the traits that might lead a species to be chosen for biocontrol, food, or other non-pet intentional introductions, although these would repay careful consideration in any comprehensive analysis of introduction risk factors. For example, being a game species for hunting is an important predictor of invasion success for mammals, fish and birds (Jeschke and Strayer 2006). Note that in Tables 2–5, the characterization of an attribute as being a "good pet?" implies benefits to the pet trader, not necessarily to the purchaser. The edible species in herpetofaunal trade are relatively few in number (e.g., bullfrogs, many pond turtles) and are often intentionally stocked in climatically-appropriate sites proximate to consumers. For these species, transport, establishment and spread are not accidental. For pets, biocontrol, and food species, transport is not accidental, but the later stages of establishment and spread may be (Kraus 2003; e.g., pet, food, or biocontrol tadpoles accidentally shipped with fish stock). The association between *accidental* transportation and pets is therefore less sure than that for urban species, though still dominated by positive associations. Of the eleven associations, three are neutral, two are negative, and six reflect a positive correlation (Table 2). Nonetheless, intentional placement of pet species via commerce is likely to eclipse any association based on accidental transport.

Natural History Characters Germane to the Establishment Phase of Invasion — The crux of the establishment challenge for an invader is recruitment, with factors affecting survival (Table 3), finding a mate, and producing enough offspring to offset mortality (Table 4) being of equal importance to any factor that increases the flow of conspecifics to a destination (i.e., all transport factors). The first destination after initial transport is an urban area (usually a port); thus by default the factors that facilitate a species' presence in urban landscapes will also promote subsequent establishment. For survival, all else being equal, a species with high longevity will survive longer than one with limited longevity (Table 3). All else is rarely equal, of course, and a basic requirement is that the colonist arrive in an area with a tolerable climate. Climate matching is a core activity for regulators wishing to predict a species' potential invasiveness. Some species are able to extend their climate tolerance in a new environment, but most can survive only under conditions similar to those in their native range. Destinations with a maritime climate provide a suitable environment for many prospective invaders, and islands in particular may be prone to invasion (Brockie et al. 1988; Stohlgren and Schnase 2006).

The vulnerability of islands to invasion touches not only on the matter of climate, but also on the concept that invasion is promoted where there is an empty or underutilized niche at the site of colonization. Darwin first drew attention to this phenomenon, which continues to engender heated debate

(May 2000; Baskin 2002). Less controversial is the supposition that species vary in their degree of phenotypic plasticity and that more plastic species may have better ability to adapt to a new environment. Although this hypothesis was generated with reference to plants, which habitually find themselves growing in unfavorable sites, many reptiles and amphibians are capable of limited phenotypic plasticity (e.g., tadpoles reducing their locomotion in response to predator odors in the water). High genomic heterozygosity is another tool for addressing a climate or habitat mismatch, but it starts to come into play only in subsequent generations, so the colonist first has to reproduce.

The remaining four factors in Table 3 are general ecological attributes. Meshaka (2004) and Powell and Henderson (2008) argued that insectivores are more successful invaders, perhaps because most insectivores have very broad diets. The majority of herpetofaunal species are insectivores, so this phenomenon may be difficult to test rigorously. If a species requires a symbiont for its survival or reproduction (as a plant may need an insect pollinator), it can only establish in those sites where a suitable symbiont is present. This does not seem to be a factor for most reptiles and amphibians, although some monitor lizards and crocodilians appear to be obligate termite mound nesters. Finally, species that modify their environment to suit their specific needs would seem to be more likely to survive than those that require a readymade specific environment. For example, a Desert Tortoise could potentially dig a burrow in a burrow-less place, whereas a snake dependent on rodent burrows might overheat upon arrival in a destination where pre-existing burrows were lacking.

There are seven new factors identified as facilitating reproduction during the establishment phase (Table 4). Ability to shift between r and K strategies was envisioned with relation to facultative reproductive mode switching in fish or invertebrates, but recent discoveries of facultative parthenogenesis may be an example of this phenomenon operating in snakes (Schuett et al. 1997; Groot et al. 2003). Gregariousness, while not an obvious attribute of any mature but non-breeding reptile or amphibian, was suggested as a feature that would facilitate mate finding (largely by inhibiting dispersal). Although reptiles and amphib-

Table 3. Natural history characters (exclusive of reproduction) hypothesized to correlate with the *establishment* of invasive species (y = yes, n = no, 0 = neutral or unknown).

Species attribute	Rationale	Good pet?	Good urban?	Described by
Survival				
longevity	increases chances of intergenerational overlap	y	0	Newsome and Noble 1996; Rejmánek and Richardson 1996 (plants); Duncan et al. 1999 (birds)
climate/habitat match of destination to native range	greater survival in destination	0	y	Newsome and Noble 1986; Meshaka 2004
tropical/oceanic/mild climate at destination	greater survival in destination	y	y	Brockie et al. 1988
island destination	islands have maritime climates	0	0	Brockie et al. 1988
empty niche at destination	competitive displacement unlikely	0	y	Darwin (1964)
adaptation to environmental stress (phenotypic plasticity)	can adapt to novel environment	y	y	Baker 1965 (plants); Parker et al. 2002; Sexton et al. 2002
high heterozygosity	increased chance of producing ideal genotype	0	y	Ehrlich 1989; Lodge 1993
insectivorous	presumption is that insectivorous niche is very wide and open; Meshaka (2004) specifies beetles, roaches, and ants	y	y	Meshaka 2004
broad diet	increased chance of finding suitable food	y	y	Ehrlich 1989; Lodge 1993; Sorci et al. 1998
required symbionts present at destination; parasites absent	parasites may be more important for herpetofauna	0	0	Richardson et al. 2000
species (e.g., gopher tortoise) that alter environment	can create required habitat	n	y	Lodge 1993

Table 4. Natural history characters of reproduction hypothesized to correlate with the *establishment* of invasive species (y = yes, n = no, 0 = neutral or unknown).

Species attribute	Rationale	Good pet?	Good urban?	Described by
Reproduction				
ability to shift between r and K strategies	can shift to r strategy when in incipient population	0	y	Ehrlich 1989 (fish)
early maturation	decreases inter-generational lag time	y	y	Ehrlich 1989; Rejmánek and Richardson 1996 (plants); Williamson and Fitter 1996; plant studies in Kolar and Lodge 2001; Meshaka 2004; Stohlgren and Schnase 2006
solo female: parthenogenesis	only single (female) propagule needed	0	y	Ehrlich 1989; Kolar and Lodge 2001 (vegetative reproduction); Lodge 1993
solo female: sperm storage	only single (female) propagule needed	0	y	Ehrlich 1989; Lodge 1993
gregarious	less chance of an individual dispersing away from conspecifics	y	y	Ehrlich 1989
high fecundity (large clutch size per unit time)	expedites population expansion and siblings may be potential mates	0	y	Rejmánek and Richardson 1996 (plants); Kolar and Lodge 2001; Meshaka 2004; Stohlgren and Schnase 2006
short interclutch interval	expedites population expansion	y	y	O'Connor 1986; Rejmánek and Richardson 1996 (pines); Veltman et al. 1996
sexual monomorphism (excl. dichromism, sexual size dimorphism)	mechanism not clear: often produces a larger effective population size for a given absolute N	y	0	McLain et al. 1995; Sorci et al. 1998

ians are rarely termed "gregarious," all herpetofaunal species seek out each other for mating and subtle predilections for sociality may be found in a variety of species (Burghardt 1977).

Are these correlates of invasive species establishment (survival and reproduction) relevant to the success of urban reptiles and amphibians? Longevity does not have a strong association with urban living (though Koenig et al. [2001] argued that it facilitated the urban persistence of *Tiliqua scincoides*). Island habitats and symbionts do not appear to have a strong relation to urban success, but eight of eight other factors in Table 3 are positively associated with urban success, and no factors are negatively associated. We conclude that the factors affecting urban success are closely associated with the factors that promote survival and thereby establishment of introduced species.

The association between factors affecting pets and factors affecting survival and establishment of introduced herpetofauna are slightly weaker: five of six factors are supportive, while one factor is adverse. Species that modify their environments may not make particularly good pets, although modest amounts of burrowing may be entertaining.

Reproductive traits associated with establishment of invasive species were uniformly germane to urban herps, but only mildly applicable to pets (Table 4), with four of eight traits showing a positive association and the remaining four being neutral. Reproductive traits are relatively unimportant for the vast majority of imported pets, which are taken from the wild and usually held until death. Reproductive traits are important for pets that are propagated in captivity, but the volume of trade in those species is poorly documented.

Natural History Characters Germane to Invasive Spread and Ecological Consequences — We have considered the factors that influence transport and establishment of a potential invasive. Once a viable population has been established in one small area, the key questions are whether and how far it will spread and how much damage will result. In practice, few incipient populations remain static; over time it is unlikely that a small population's average abundance change (λ) will remain exactly 1.0. The introduced population may encounter a string of adverse conditions and die out, or as is more often the case, the population remains small and geographically limited, perhaps for a very substantial period, but then grows, spreads, or irrupts. The quiescent period is often deemed a "lag phase" (Crooks and Soulé 1999) and is sometimes assumed to be a

routine event in the spread of invasives (Williamson 1996; Hastings et al. 2005).

Much of the literature on invasive species has subconsciously focused on the subsequent irruptive phase, emphasizing differences between invaders that spread little or cause little disruption and those such as the Brown Treesnake that have spread to the geographic limit of their landmass and caused ecological catastrophes. There are many factors that have been associated with the severity of ecological impacts (Table 5), and potentially all of the factors listed in all tables in this paper could influence the ecological success of a species. Nonetheless, certain factors are probably more important than others in determining how far a species spreads (both geographically and ecologically), the population density that it achieves at the peak of its irruption (generally when the species inflicts maximal damage), and the degree to which a given individual species stresses natural systems (e.g., loss or addition of keystone species may cause more distortion).

If the establishment phase emphasizes rapid reproduction (associated with r-selected species able to quickly attain sustainable population sizes), then the spread phase should emphasize competitive ability (typically associated with K-selected species). Thus, Table 5 starts with two factors related to shifting life history strategies between an "r"-like strategy and a "K"-like strategy (whether or not that posited evolutionary tradeoff is real). These are followed by nine factors associated with general ecological success. For example, a species that is abundant over its vast native range is more likely to be problematic when introduced than is a species that is rare and geographically restricted in its native range. However, a variety of authors have also hypothesized that particular natural history attributes are favorable for the ecological success of introduced species. The eight traits listed in this category in Table 5 are unlikely to all be true for invasive herpetofauna, but they are all worthy of consideration. "Fire-adapted," and "gregarious" are two that would seem to have limited application to introduced herpetofauna, but cannot be dismissed with the data available.

Finally, there are four attributes of the destination that have bearing on the success of an introduced species. These four are not inherent to the species, but rather to the match between the destination and the species.

How well do these 23 natural history attributes of particularly harmful invasive species compare to attributes favorable for urban and pet herpetofauna? With regard to urban herpetofauna the outcome is clear: of the 18 attributes of invasive species that had a recognizable bearing on urban success, 17 favored success of urban herps, the exception being large body size (Table 5).

Correspondence between pet and invasive characters is in the same direction but weaker: 13 of 17 distinguishing characters favored a species being good for the pet trade. In this case, however, the results from the first (r to K conversion), third (specialized attributes), and fourth (destination match) groups were all equivocal (Table 5). Only the natural history attributes associated with general competitiveness were clearly supportive (8 of 8).

Considering all three stages of species invasion — transport, establishment, and spread — the pattern for urban herpetofauna seems relatively clear: the traits that most likely make them good invaders may also enhance their success in urban environments. This agrees with results from Jeschke and Strayer (2006) showing that association with humans is a strong predictor of invasion success for mammals, birds and fish. The pattern for pets is a little less clear, but the traits that most likely make them good invaders largely appear to also enhance their value to the pet trade. If accidental transport of pets was the only pathway for these species' establishment as invasive species, concern about pets as potential invasives would be warranted. However, accidental transport is not the primary means of spreading herpetofaunal introductions, as most are transported by *intentional* movements of individually-owned pets or pet trade bulk shipments (Kraus 2003). Combining accidental and intentional pathways, pets become a primary source of invasive herpetofauna.

Management Implications — What does the apparent three-way overlap between invasive, pet, and urban herpetofauna imply for management policy? As long as commercial collection of amphibians and reptiles does not negatively impact wild stocks and pet owners act responsibly and do not dump unwanted animals or allow escapes, we have few ecological concerns about the pet trade per se. Similarly, the existence or success of urban wildlife is positive to the extent that it enriches the lives of urbanites with opportunities to see and interact with herpetofauna. Urbanization is not benign, but if we must exist in cities, it is better that cities support reptiles and amphibians (Johnson and Klemens 2005). However, reptiles and amphibians in the wrong places can produce permanent and irrevocable damage to global biodiversity and natural ecological processes. Therefore, our concern is the degree to which pets and urban herpetofauna may contribute to biological invasions.

Native urban herpetofauna (species that also occur naturally in the surrounding exurban matrix) are no threat to adjacent ecosystems, but may be a potential threat to distant lands via transportation links. Cities that are the source of much export material are particularly crucial. Accidental transportation of animals should be prevented whenever possible, by eliminating hitchhikers from cargos and isolating cargos from resident populations. However, future risk assessments may also show that the risk of accidental exportation is severe enough to warrant population restrictions on urban herpetofauna in the vicinity of manufacturers, cargo, or cargo handling facilities. Any localized loss of proximity to urban herpetofauna by human residents may be more than compensated for by the enhanced protection of biodiversity and natural ecosystems abroad.

The case for non-native urban herpetofauna suppression is less equivocal, in that such control measures are always justifiable. Invasive herpetofauna threaten native species and ecosys-

Table 5. Natural history characters hypothesized to be important in the *spread and ecological impacts* of invasive species (y = yes, n = no, 0 = neutral or unknown).

Species attribute	Rationale	Good pet?	Good urban?	Described by
Shift to competitiveness				
ability to shift between r and K strategies	can shift to competitiveness when colonizing occupied niche space	n	y	Ehrlich 1989 (fish)
adaptation to environmental stress (phenotypic plasticity)	enhanced ability to adapt to new location	y	y	Baker 1965 (plants) in Parker et al. 2002
Generic improved chances of finding an open niche				
broad diet	better chance of finding suitable prey	y	y	Ehrlich 1989; Lodge 1993; Sorci et al. 1998
continental native range	continental species presumed to have evolved in presence of many limiting factors (cf., islands)	y	0	Brockie et al. 1988
disturbed habitat preference	may achieve high density because natural predators are missing from much anthropogenic habitat	y	y	Mack et al. 2000; Meshaka 2004; Stohlgren and Schnase 2006
high density in native range	factors facilitating high density in native range may also act in introduced range	y	y	Ehrlich 1989; Williamson and Fitter 1996
high heterozygosity	increased chance of producing genotype better adapted to new habitat	0	y	Ehrlich 1989; Lodge 1993
wide latitudinal range of native range	species with wide latitudinal range are adapted to surviving and growing under wide range of conditions	y	y	Ehrlich 1989; Williamson and Fitter 1996
size of native range	correlated with latitudinal range	y	0	Williamson and Fitter 1996
sexual monomorphism (excl. dichromism, sexual size dichromism)	mechanism not clear: increased ability to adapt to a novel environment?	y	0	McLain et al. 1995; Sorci et al. 1998
tolerant of wide range of climates		y	y	Ehrlich 1989; Lodge 1993; Duncan 1997
Specialized attributes believed to be useful				
arboreality	Ebenhard was thinking primarily in terms of predators	0	y	Ebenhard 1988 (mammals)
fire adapted	Fire resistance could confer a greater successional advantage in fire-prone areas	0	0	Richardson et al. 1990 (plants)
gregarious	gregarious species may behaviorally displace solitary competitors	y	y	Ehrlich 1989
lizard (cf. other herp)	being a lizard may increase potential for high density, but the correlation is very weak	n	y	Meshaka 2004
predator	may have more generalized adaptations	y	y	Ebenhard 1988 (mammals); Lodge 1993, esp. on islands

Table 5. Continued

Species attribute	Rationale	Good pet?	Good urban?	Described by
species (e.g., beaver) that alter environment	can be ecosystem transformer	n	y	Lodge 1993
insectivorous	presumption is that insectivorous niche is very wide and open	y	y	Meshaka 2004
large adult size	larger species better competitors?	n	n	Ehrlich 1989; Veltman et al. 1996; Williamson and Fitter 1996 (UK plants); Meshaka 2004
favorable environment at destination				
climate/habitat match of destination and native range	competitiveness enhanced by favorable climate	0	y	Newsome and Noble 1986; Meshaka 2004;
tropical/oceanic/mild climate at destination	competitiveness enhanced by favorable climate	y	y	Brockie et al. 1988
island destination	empty niches and/or few natural predators	0	0	Brockie et al. 1988; Stohlgren and Schnase 2006
empty niche at destination	competitive displacement unlikely	0	y	Darwin (1964)

tems, and the risk of spreading the damage is especially acute in the vicinity of transportation facilities. Since 1995, for example, substantial sums of money have been spent by the U.S. government to eliminate Brown Treesnakes from the vicinities of export cargo facilities on Guam (Vice and Vice 2004). Other potential impacts of invasive species that have not been discussed here include: genetic degradation of an endemic, hybridization leading to more potent invaders, and the possibility of a single introduced individual vectoring new and devastating parasites and diseases. We predict that in the future much more non-native urban herpetofaunal control will be warranted as additional understanding is developed regarding the ecological, social, and monetary costs of invasive herpetofauna.

The challenges for regulators of the pet industry are very complex. Ideally one would seek to regulate the pet trade and pet ownership only for those species in specified geographic areas where release of designated species into the wild is predicted to be detrimental. Unfortunately, various free trade laws and constitutional or statutory privileges associated with unrestricted interstate commerce make such limited regulation impractical (Orr 2003). Furthermore, the establishment of released pets in urban areas from which they are unlikely to spread to the surrounding ecosystems is not entirely benign, as feral or naturalized pets may enter cargo in such urban areas and thereby spread to new geographic areas where they could spread into wildlands. In addition, urban pet owners may travel a significant distance away from their homes to set free inconvenient animals. An example is Burmese Pythons released at the end of the road in Everglades National Park (S. Snow, Everglades NP, pers. comm.). A partial solution is for herpetoculturalists to adopt a very strong ethic against the release of unwanted pets. It is NOT a humanitarian act to release your sick turtle into the city pond or Desert Tortoise Natural Area (Dodd and Seigel 1991). It is in the pet industry's long-term interest to energetically educate their clients about the ecological dangers of pet release, with failure at this endeavor a stimulus for future restrictions on pet ownership and criminalization of unethical pet release. As most pet owners love animals, it should be fairly easy to educate pet owners about behavior that helps preserve global biodiversity, and this should be done immediately, without waiting for governmental subsidies or regulation (e.g., www.parcplace.org/DontTurn.pdf, 17 September 2007).

But no matter how successful an educational campaign, the result will not be airtight. Sooner or later a pet snake will escape, or a herpetological supply facility will collapse in a hurricane. Mistakes, neglect, and malice are inevitable, though reducing the number of escapes and releases may so alter the risk factors that regulation may be needed for only a few particularly biohazardous species.

Many countries already bar the importation of particularly troublesome species. How do they arrive at the list of precluded species (Hayes 2003)? To date, the regulatory process in the leading countries (Australia and New Zealand) has focused on climate matching and natural history correlates of invasiveness (e.g., Bomford 1991, 2003; Hayden and Whyte 2003; Pheloung 2003; Bomford et al. 2005). Climate matching has been of relatively little use for the U.S. as a whole, as the climatic range of potential U.S. destinations covers the full gamut from tropical island rainforests to high arctic deserts. As various U.S. laws and constitutional protections generally prevent regulations that would effectively prohibit the movement of animals between states or climatic regions, regulatory opportunities to prevent release of hazardous species are forced to operate at international borders only. A species that can survive anywhere in the U.S. is a risk regardless of the

climate at the site of its importation. For the U.S. therefore, a greater priority must be put on the identification of the highest risk species independent of climate matching, and for this purpose, natural history correlates have been identified as being essential to estimating risk (Stohlgren and Schnase 2006). To the lists of natural history correlates that we have found hypothesized in the literature (Tables 2–5) we can now add success as pets and success in urban areas.

Strong statistical tests of these concepts are needed to address all prospective pets and urban herpetofauna. Adequate tests will require the acquisition of solid natural history data for many species in their original habitats. Acquiring natural history data has lost favor with many scientific granting agencies, but the prevention of herpetofaunal invasions may well depend on it. Natural history knowledge is denigrated by many mainstream biologists as passé, but for many applied herpetological problems it constitutes a core data acquisition need (Greene and Losos 1988).

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