Chapter 3
Impacts of Alien Reptiles and Amphibians

The entire motivation for concerning ourselves with invasive alien species, of course, relates to the ecological and economic damage these species cause. For many non-herpetological taxa, as noted in Chapter 1, damages have been extensive and severe, justifying the considerable attention that has been devoted to a host of invasive pests of all groups. As for these better-known taxa, when determining the degree of attention that alien reptiles and amphibians might merit as a management problem it is imperative to assess to what extent these species inflict damage. Clearly, if these animals are not affecting natural or human ecosystems, concern for their introduction will be lessened. And, indeed, it has been argued that most reptile and amphibian introductions to Florida provide no such impact, and the threat of alien herpetofauna there has been largely discounted (L.D. Wilson and Porras, 1983; Butterfield et al., 1997). Alternatively, if it be shown that alien reptiles and amphibians do cause an array of ecological or societal damages, a greater responsibility for management response would inhere. In either event, a broader awareness of these impacts or their absence would improve our assessment of the relative standing of alien reptiles and amphibians as environmental, conservation, or social problems. It would concomitantly serve to identify obvious research needs for further clarifying extent and ecological mechanisms of impact as well as control and mitigation measures.

A broad survey of ecological impacts attending invasive reptile and amphibian introductions has not previously been available. In providing one here, I confine my attention to studies that clearly demonstrate some level of impact from alien herpetofauna and that provide some evidence or compelling argument as to what the mechanism of such impact might be. In including instances that provide only reasoned argument to identify impact mechanism I hope to highlight several hypotheses that have languished in the literature for lack of further investigation. The literature occasionally contains correlational evidence that simply notes the decline or disappearance of a native species to be coincidental with expansion of a naturalized alien (e.g., Münch, 2001). However, such correlations need not result from the introduced alien per se; both species may simply be responding differently to underlying environmental changes (cf. L.D. Wilson and Porras, 1983 for herpetological examples). Such instances are generally omitted in this summary because evidence identifying the causative mechanism of replacement is not provided.

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Nonetheless, such correlational evidence points to additional potential instances of detrimental impacts that may warrant investigation. Lastly, concerns have frequently been expressed in the literature for a variety of potential impacts for which no evidence is provided whatsoever. Some of these speculations may be valid, but in the absence of documentary evidence or reasoned argument they do not approach minimal scientific standards and are ignored here.

This survey reveals that a surprisingly wide array of deleterious impacts are documented across a variety of herpetological species, even though taxonomic sampling among naturalized herpetofauna has been sparse. Indeed, research into impacts from alien reptiles and amphibians is rather recent, and it is to be expected that additional examples and further impacts will be identified as research into this area garners greater momentum. Impacts identified to date may be broadly categorized as ecological, evolutionary, or social. The first includes impacts on individual species as well as broader community-level disruptions. Ecological damages from alien herpetofauna most often derive from food-web disruptions, with impacts stemming from predation on sensitive species, poisoning of predators, competition with natives, vectoring of novel parasites, or secondary disruption of food webs. Evolutionary impacts encompass genetic contamination via hybridization with natives as well as changes in inherited morphological, physiological, or behavioral traits. Genetic impacts relate to introgression of alien genes into native gene pools, sometimes to the point of genetically swamping native forms out of existence. Under the category of evolutionary change are included both changes observed in the invasive alien as well as modifications induced in native fauna by its introduction. Social damages include direct impacts on humans or their cultural institutions. These impacts can be to human health, economies, quality of life, or scientific knowledge.

Ecological Effects

Removal of Native Prey Species

The most widely studied and commonly considered ecological effect from alien reptiles and amphibians is predation on sensitive native species resulting from the introduction of novel predators. In only a few instances has direct evidence of population-level effects on natives been demonstrated, but many anecdotal observations suggest it may be a frequent phenomenon. This is, however, difficult to document because intense, novel predation may provide only a narrow window of opportunity for observing populations during the phase of decline. More often, sudden rarity is noticed after the fact and the cause can only be inferred retrospectively by temporal correlation with a newly introduced predator.

The best-known instance of predation leading to loss of native species is the introduction of the brown treesnake (*Boiga irregularis*) to Guam in the years immediately following World War II. This snake caused the loss from Guam of ten forest bird, three seabird, 1–3 bat, and six lizard species within a span of approximately 40 years (Savidge, 1987a; Engbring and Fritts, 1988; McCoid, 1991; Rodda and Fritts, 1992; Fritts and Rodda, 1995, 1998; Rodda et al., 1997, 1999b; Rodda and Savidge, 2007). Three of the birds and one bat were endemic to Guam and are, therefore, globally extinct. Two further bird species remain only in captivity, and most of the native vertebrates remaining on Guam do so at extremely reduced abundances (Rodda and Savidge, 2007), where too they may be susceptible to predation by other introduced reptiles, such as *Varanus indicus* (McCoid and Hensley, 1993a). This introduced snake population has been the subject of scores of studies, and early ecological research clearly ruled out a variety of other hypotheses to explain the observed bird declines (Savidge, 1987a; Savidge et al., 1992). The dire effects caused by this snake have led to a 14-year control program to prevent the species colonizing additional Pacific islands, but indications are that Saipan may now be invaded as well. If true, similar ecological effects may be expected there in the coming decades (Fritts and Rodda, 1995; Rodda et al., 1999b).

The snake *Natrix maura* was introduced to the Balearic Islands approximately 2,000 years ago (Alcover and Mayol, 1981). It is credited with reducing the range of the formerly island-wide endemic frog *Alytes muletensi*s to plunge pools in a few steep-sided gorges in the uplands of Mallorca (Tonge, 1986; Moore et al., 2004a; Pleguezuelos, 2004). It is also thought to have played a role in the extinction of the endemic *Alytes talaioticus* during the Holocene (Pleguezuelos, 2004). Evidence for these claims lies in the highly ranivorous behavior of *N. maura*, its absence from fossils predating human settlement of the islands, and the persistence of *A. muletensis* at elevations where the snakes are scarce (Alcover and Mayol, 1981; Tonge, 1986; Moore et al., 2004a).

The lizard *Anolis carolinensis* was introduced to Chichijima in the Ogasawara (Bonin) Islands in the period from 1965–1968 (M. Hasegawa et al., 1988) and subsequently released on Hahajima in 1981 (Miyashita, 1991). It has expanded its range quickly (M. Hasegawa et al., 1988) and increased to tremendous population densities ranging from 600–2,570 animals/ha and averaging 1,270 animals/ha (Okochi et al., 2006). Feeding trials, direct observations, and stomach-content analyses have demonstrated this lizard to feed on a variety of native insects (Karube, 2004b, 2006; Karube and Suda, 2004; Makihara et al., 2004). Comparisons of insect faunas on Chichijima and Hahajima before and after *Anolis* invasion, as well as comparisons between these islands and nearby uninvaded islands, correlate the decline or extirpation of several formerly common species of buprestid, cerambycid, cucurlionid, and melandryid beetles; lycaenid and papilionid butterflies; bees; and odonates to that invasion (Karube, 2004a, b, 2005; Karube and Suda, 2004; Makihara et al., 2004; Takakuwa and Suda, 2004; Yoshimura and Okochi, 2005; Okochi, et al., 2006). To date, toxic, nocturnal, and large, hard-bodied species have not experienced catastrophic declines (Makihara et al., 2004; Karube, 2005). In all, at least 15 species of endemic insects appear to have vanished or strongly declined because of the lizard. Most of these are small, diurnal, non-toxic species with a fondness for resting on the sunlit vegetation favored by the lizards

(Karube, 2001, 2004a; Karube and Suda, 2004). Although preferred prey are small diurnal inhabitants of vegetation, *A. carolinensis* has also been documented foraging on large, hard-bodied cicadas, strictly ground-dwelling species, and nocturnal species sleeping in leaf axils, with the last apparently leading to declines in some nocturnal cerambycids as well (Karube and Suda, 2004; Karube, 2005). This switch from preferred prey is thought to result from declining resources (Karube and Suda, 2004; Karube, 2006), and it is anticipated that yet additional insects will disappear from Hahajima and Chichijima as more preferred prey species disappear (Karube and Suda, 2004). Persistence of some of these endangered insects on adjacent islands may be only temporary inasmuch as poor-quality habitat makes them population sinks that historically were replenished by migration from the two islands now having *Anolis* infestations (Takakuwa and Suda, 2004).

The related *Anolis sagre*i was introduced to Florida in the mid- to late-1800s (Garman, 1887; W. King and Krakauer, 1966) and has rapidly expanded across the state (Campbell, 2003a). During this expansion it has frequently been noted that the native *A. carolinensis* has either disappeared or declined in numbers in many populations (Tokarz and Beck, 1987; P.R. Brown and Echternacht, 1991; Echternacht, 1999), and rapid replacement of that native by *A. sagrei* has been experimentally demonstrated in the field (T. Campbell, 1999a). In highly disturbed habitats, it appears that *A. carolinensis* can disappear entirely, but in more structurally complex habitats it persists at lower population densities occasioned by its occupancy of fewer, elevated territories than prior to invasion by *A. sagrei* (Echternacht, 1999). Decline of the native appears largely due to predation on *A. carolinensis* hatchlings by *A. sagrei*, with preference shown by *A. sagrei* for consumption of heterospecific hatchlings over conspecific hatchlings in the laboratory (Gerber, 1991; Gerber and Echternacht, 2000), and predation on hatchlings on *A. carolinensis* documented in the field (T. Campbell and Gerber, 1996). Hatchlings of both species live near ground level, thus bringing them in frequent contact with dense populations of adult *A. sagrei* (but not *A. carolinensis*) and making them susceptible to predation by that species (Echternacht, 1999). The dense populations routinely formed by *A. sagrei* place the hatchlings of the sparser *A. carolinensis* in peril wherever insufficient ground cover is available for refugia (T. Campbell, 1999a), and occasional consumption of an *A. carolinensis* hatchling is all that is needed to severely depress recruitment in that species (Echternacht, 1999). This appears to explain the observed inability of *A. carolinensis* to persist in sympatry with *A. sagrei* in heavily modified habitats lacking structural diversity.

The rapid spread of introduced *Anolis sagrei* and observed shift in perch heights of native *A. conspersus* in the Cayman Islands (Losos et al., 1993) are likely accounted for by similar dynamics. In that case too, laboratory trials have indicated an asymmetrical preference of adult *A. sagrei* for consuming *A. conspersus* hatchlings (Gerber and Echternacht, 2000). This, combined with the dense populations again seen in *A. sagrei* and the occupation by hatchling *A. conspersus* of lower vegetational strata, would provide a similar mechanism for population declines in the native anole (Gerber and Echternacht, 2000) as seen for Floridian *A. carolinensis*.

Cane toads (*Bufo marinus*) introduced to Australia have been documented to inflict population-level effects on the ground-nesting rainbow bee-eater (*Merops ornatus*). In the absence of toads, these birds produce an average of 1.2 fledglings/nest. But toads prey upon eggs and nestlings and usurp nest burrows, thereby destroying one-third of all nests and reducing nest success rate to an average of 0.8 fledglings/nest (Boland, 2004a, b). Displaced adult birds suffer reduced average nest productivity with subsequent nesting attempts, making the effects of the toads even broader than that measurable by direct predation and nest destruction (Boland, 2004a, b). Susceptibility to nest predation by toads appears to result at least partly from lack of proper defensive behaviors in the nesting birds, which can successfully fend off attacks by much larger native predators (Boland, 2004a, b). Cane toads have been reported to prey on an array of other native vertebrates (e.g., Rabor, 1952; Pippet, 1975; Stammer, 1981; Freeland and Kerin, 1988; Caudell et al., 2000), but effects on populations have not been systematically researched. One study reported a correlation between presence of toads and reduction in beetle populations (Catling et al., 1999); another reported a similar correlation with a reduction in gecko populations (Watson and Woinarski, 2003, cited in McRae et al., 2005). Others have noted toads to have greater volumes of prey in their stomachs where recently established compared to areas where they have been longer established (Anonymous, 1968), suggesting suppressive effects on invertebrate communities by a prolonged history of predation, although temporal changes in invertebrate populations have not been measured directly. Anecdotal reports of pest and native invertebrate declines following introduction of toads (e.g., Wolcott, 1937, 1948, 1950a, b; Simmonds, 1957) suggest the same suppressive effects, but studies on most native invertebrate communities are lacking (but see Greenlees et al., 2006 for an exception).

A variety of studies has implicated alien bullfrogs (*Rana catesbeiana*) in declines of native herpetofauna across the western United States. Evidence includes anecdotal (Lardie, 1963; Dumas, 1966; Hammerson, 1982) and statistical (Moyle, 1973; Schwalbe and Rosen, 1988; Fisher and Shaffer, 1996; Kupferberg, 1997a; Rosen and Schwalbe, 2002) analyses of distributional or historical trends, partial recovery of affected populations with experimental reduction or exclosure of bullfrogs (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1996a, b), skewed size-class distributions in populations syntopic with bullfrogs (Holland, 1991, cited in Hayes et al., 1999), and experimental demonstration of increased mortality or decreased growth in laboratory or field experiments (Kieseker and Blaustein, 1997, 1998; Kupferberg, 1997a; Lawler et al., 1999; Adams, 2000; Pearl et al., 2004; Maret et al., 2006). Natives argued to be affected by bullfrogs include the frogs *Bufo boreas* (Lardie, 1963), *Pseudacris regilla* (Jameson, 1956), *Rana aurora* (Lardie, 1963; Pearl et al., 2004), *R. blairi* (Hammerson, 1982), *R. boylii* (Moyle, 1973; Kupferberg, 1997a), *R. chiricahuensis* (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995, 2002; Rosen et al., 1995), *R. draytonii* (Moyle, 1973); *R. pipiens* (Hammerson, 1982), *R. pretiosa* (Lardie, 1963; Dumas, 1966; Pearl et al., 2004), *R. yavapaiensis* (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995, 2002), the entire suite of central Californian amphibians (Fisher and Shaffer, 1996), the turtle *Actinemys marmorata* (Hays et al., 1999), and the snake *Thamnophis eques* (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995, 2002). Similar declines in native herpetofauna concurrent with introduction of bullfrogs have been noted in Germany (C.R. Boettger, 1941; Thiesmeier et al., 1994). Because of the bullfrog's catholic, opportunistic diet (Bury and Whelan, 1984) and numerous observations of predation on sensitive species (Table 3.1), declines have most often been attributed to bullfrog predation. This interpretation is bolstered by scarring and tail loss seen on affected natives and by skewed population structures consistent with predation on juveniles (Schwalbe and Rosen, 1988; Rosen and Schwalbe, 1995). Furthermore, experiments have confirmed bullfrogs to mediate their negative effects in part via direct predation (Kiesecker and Blaustein, 1997). However, bullfrogs can also induce behavioral changes in microhabitat use by natives that decrease the latter's survival and growth rates (Kiesecker and Blaustein, 1998). Further, a variety of other factors, including habitat modification or loss (Moyle, 1973; Hayes and Jennings, 1986; Jennings, 1988b; Fisher and Shaffer, 1996; Adams, 1999, 2000; Kiesecker et al., 2001; Davidson et al., 2002; Rosen and Schwalbe, 2002), presence of alien fish (Hayes and Jennings, 1986; Jennings, 1988b; Rosen et al., 1995; Kieseker and Blaustein, 1998; Adams, 1999; Adams et al., 2003; Maret et al., 2006), commercial exploitation (Hayes and Jennings, 1986; Jennings and Hayes, 1985; Jennings, 1988b), disturbance regimes (Jennings and Hayes, 1994; Doubledee et al., 2003; Maret et al., 2006), diseases (Rosen and Schwalbe, 2002), and toxicants (Hayes and Jennings, 1986; Rosen et al., 1995; Davidson et al., 2002) can also be involved in declines of native species or interact synergistically to exacerbate bullfrog effects. This complexity frequently makes parsing the exact contribution of bullfrog predation to native-species declines problematic. Despite such complications, predation by bullfrogs has likely played a central role in declines of several native reptile and amphibian species in the western United States. It has been claimed that *R. catesbeiana* has led to decline of native *Rana* in the region around Florence, Italy (Touratier, 1992b) and of native fish in the Aquitaine of southwestern France (Touratier, 1992a), and concern has been expressed about their potential effects elsewhere in Europe (e.g., Albertini and Lanza, 1987; Stumpel, 1992). But in none of these cases has any of the above-mentioned forms of evidence been provided. Concerns have also been expressed about the potential threat of bullfrogs to the endangered snake *Opisthotropis kikuzatoi*, endemic to Kumejima Island, Ryukyu Islands, Japan. The threat comes both from the frog's potential to directly prey upon these small snakes but also because it is known to eat the endangered freshwater crab, *Candidiopotamon kumejimense*, the only known food source for the snake (Ota et al., 2004a).

Three of six dissected *Xenopus laevis* in an introduced population in southern California were found to contain one or more of the endangered tidewater goby (*Eucyclogobias newberryi*) as food items (Lafferty and Page, 1997). The high frequency of occurrence of the endangered fish in this small sample of stomachs, in concert with the high densities at which *X. laevis* can occur in California, led to the supposition that the alien frog might serve as a substantial cause of mortality for the fish (Lafferty and Page, 1997). However, further work to identify population-level

Table 3.1 Reported instances of alien reptiles or amphibians preying upon endangered or sensitive native wildlife

Alien predator	Native prey	Prey status	Location	Reference
Anolis carolinensis	*Cryptoblepharus nigropunctatus*	Restricted range	Ogasawara Islands	Suzuki and Nagoshi, 1999
Anolis grahami	*Eumeces longirostris*	Endangered	Bermuda	Griffith and Wingate, 1994
Caiman crocodilus	*Crocodilus rhombifer*	Endangered	Cuba	Varona, 1980
Hemidactylus frenatus	*Nactus coindemirensis*	Endangered	Mauritius	Cole et al., 2005
Litoria aurea	*Leiopelma archeyi*	Endangered	New Zealand	Thurley and Bell, 1994
Python molurus	*Neotoma floridana smalli*	Endangered	Florida, USA	D.U. Greene et al., 2007
Python molurus	*Aramus guarauna*	Species of concern	Florida, USA	Snow et al., 2007b
Python molurus	*Endocimus albus*	Species of concern	Florida, USA	Snow et al., 2007b
Rana catesbeiana	*Ambystoma californiense*	Endangered	California, USA	Balfour and Stitt, 2003
Rana catesbeiana	*Ambystoma tigrinum stebbinsi*	Endangered	Arizona, USA	Maret et al., 2006
Rana catesbeiana	*Bufo nelsoni*	Restricted range	Nevada, USA	Jones et al., 2003
Rana catesbeiana	*Anas bahamensis*	Regionally rare	Puerto Rico	López-Flores et al., 2003
Rana catesbeiana	*Candidiopotamon kumejimense*	Endangered	Kumejima Is., Japan	Ota et al., 2004a
Rana catesbeiana	*Gallinula chloropus sandvicensis*	Endangered	Hawaii, USA	Viernes, 1995
Rana catesbeiana	*Gila purpurea*	Endangered	Arizona, USA	Schwalbe and Rosen, 1988
Rana catesbeiana	*Poeciliopsis occidentalis sonoriensis*	Endangered	Arizona, USA	Schwalbe and Rosen, 1988
Rana catesbeiana	*Thamnophis gigas*	Endangered	California, USA	Wylie et al., 2003
Rana perezi	*Alytes muletensis*	Endangered	Balearic Islands	Pleguezuelos, 2004
Rana perezi	*Gallotia galloti*	Restricted range	Canary Islands	Nogales et al., 1989
Tupinambis teguixin	*Eretmochelys imbricata*	Endangered	Fernando de Noronha	Homewood, 1995
Tupinambis teguixin	*Caretta caretta, Chelonia mydas*	Endangered	Isla de San Andrés	Rueda-Almonacid, 1999
Varanus niloticus	*Athene cunicularia floridana*	Species of concern	Florida, USA	T. Campbell, 2005
Varanus exanthematicus	*Gopherus polyphemus*	Endangered	Florida, USA	Owens et al., 2005
Xenopus laevis	*Eucyclogobias newberryi*	Endangered	California, USA	Lafferty and Page, 1997

effects of these frogs has not appeared. More compelling correlational evidence is available from France, where *X. laevis* was introduced in Deux-Sèvres in the mid-1980s (Fouquet, 2001; Fouquet and Measey, 2006). Amphibian communities in ponds containing *X. laevis* closest to the original site of introduction were found to have lower species richness and diversity than ponds lacking that frog or having it but occurring farther away (Grosselet et al., 2005). In this case, distance from introduction site is taken as a rough measure of duration of infestation with *X. laevis*; hence, long association with *X. laevis* is correlated with reduced native amphibian diversity. Numbers of eggs of native salamanders (*Triturus* sp.) were also approximately an order of magnitude lower in ponds containing *X. laevis* than in those lacking them. Finally, populations of *Triturus cristatus* from ponds containing *X. laevis* lacked the smaller size classes present in ponds without that frog (Grosselet et al., 2005).

It has been noted that populations of *Hyla squirella* and *H. cinerea* in a Florida hammock were found to decline dramatically upon colonization of the hammock by adult *Osteopilus septentrionalis* (Meshaka, 2001: 98). Although the mechanism of decline remains unidentified, it was presumed to be predation, given the known feeding habits of the alien.

Tadpoles of *Rana catesbeiana* were demonstrated to feed upon eggs and larvae of the endangered fish *Xyrauchen texanus* in laboratory conditions (Mueller et al., 2006), and their densities in artificial habitats (human-made levee ponds) can be sufficiently high that they may be depressing larval recruitment of the fish, but studies have not yet demonstrated direct impacts on fish in wild habitats. Tadpoles of *Osteopilus septentrionalis* have been demonstrated to prey upon and significantly reduce average survivorship of native *Hyla squirella* tadpoles under crowded laboratory experiments (K.G. Smith, 2005b) but not under conditions of moderate density and alternate food availability (K.G. Smith, 2005a).

Individual reports of alien reptiles or amphibians feeding on endangered or potentially sensitive native species have been reported (Table 3.1) but each of these reports is based on single or few observations, and depression of native populations has not been investigated. In other instances (Martínez-Morales and Cuarón, 1999; Enge et al., 2004c) reasonable concerns have been voiced over the potential for recent reptile introductions to impact endangered or sensitive native wildlife, but insufficient time has elapsed to validate these concerns. However, Martínez-Morales and Cuarón (1999) speculated that already-depressed populations of several endemic birds and mammals on Cozumel might be due to introduced *Boa constrictor*.

In sum, predation impacts from alien herpetofauna are frequently invoked and have been clearly demonstrated in a few instances. Anecdotal observations (Table 3.1) suggest they may be of frequent occurrence, but population-level effects are difficult to demonstrate and may be difficult to distinguish from other causes (witness bullfrogs in the western United States). There is an additional difficulty in that there is typically a narrow window of opportunity after an invasion begins during which predation impacts can clearly be demonstrated by direct observation and measurement. But this is precisely the stage of an invasion during which study is, in general, least likely, either because the invasion is not noticed or because it is not perceived to be a concern. More often, the swiftness with which native prey can disappear makes hypotheses of predation impact merely liable to ex post facto inference instead of direct demonstration. Nonetheless, the numerous suggestive or compelling examples make it likely that population suppression via predation represents one of the more common ecological impacts from alien herpetofauna.

Removal of Native Predators

A second effect involves destruction of native predators via introduction of species bearing novel defensive mechanisms. This is documented for the cane toad (*Bufo marinus*), a Neotropical anuran that attains large size, defensively secretes quantities of highly toxic bufoteneins from its skin, and attains high population densities where introduced. It appears to have had dramatic effects on many native predators in its introduced range in Australia because of the naivety of native Australian predators to that species and its toxin. There are several reports of native snakes, lizards, turtles, crocodiles, birds, and mammals dying after ingesting toads (Breeden, 1963; Rayward, 1974; Covacevich and Archer, 1975; Stammer, 1981; Ingram and Covacevich, 1990; Shine, 1991; Tyler, 1994; S. Burnett, 1997; van Dam et al., 2002; Fearn, 2003; Phillips and Fitzgerald, 2004; Doody et al., 2006a) or experiencing population crashes or community changes subsequent to arrival of toads (Pockley, 1965; Shine and Covacevich, 1983; S. Burnett, 1997; McRae et al., 2005; Doody et al., 2006a, b; Shine et al., 2006). At least 26 native Australian vertebrate species have experienced such toad-induced mortality (C. Lever, 2001). These reports tend to be anecdotal or inferential but the studies by Doody et al. (2006a, b) contained pre-invasion abundance estimates for *Varanus panoptes*, *V. mertensi*, and *V. mitchelli* and demonstrated significant population declines synchronous with arrival of toads, as did the independent study of Griffiths and McKay (2007) for *V. mertensi*. B.L. Phillips et al. (2003), using ecoclimatic, dietary, and toxin-sensitivity information, systematically assessed risk to Australia's snake species from cane toads and concluded that 43% of Australia's non-scolecophidian snake fauna (i.e., excluding the burrowing blind snakes) are potentially threatened by the toads. Identical conclusions placing much of Australia's large herpetofauna at risk derive from a similar analysis for the remaining Australian taxa of large reptiles (J.C. Smith and Phillips, 2006).

Unpublished data suggest that some *Varanus* populations can survive invasion by cane toads (van Dam et al., 2002). In the invasion area studied, most *Varanus* consumed toads and were killed by doing so; however, those few lizards that survived the invasion did not eat toads, and this allowed for long-term recovery of lizard populations. *Varanus* from populations having long exposure to toads also refuse to attack toads (van Dam et al., 2002). Both these observations argue for strong selective pressure against toad consumption by some predatory lizards, which may lead to eventual recovery of native populations. However, further data are needed to determine how general this result is across Australia's diversity of native predators, and no research has yet investigated the effect such strong selective pressure has had on genetic diversity within the varanid populations. Ecological studies at the expanding front of toad invasion in Northern Territory are underway (R. Shine, University of Sydney, personal communication, 2007), so more direct evidence of population-level effects may be forthcoming.

Bufo marinus were also introduced to Kayangel Atoll in Palau and to Ponape and Kosrae in the Federated States of Micronesia in a deliberate attempt to control *Varanus indicus*, which were considered undesirable because of their propensity to kill chickens (Gressitt, 1952; W.B. Jackson, 1962; Dryden, 1965). Introduction of *B. marinus* did result in a dramatic reduction of *Varanus* in Kosrae, with some dead monitors found with toads in their mouths (Dryden, 1965). The toads have been credited with apparent monitor declines on Guam (McCoid et al., 1994a), Ponape (W.B. Jackson, 1962), and Palau (Thyssen, 1988) as well. Similar results have been said to attend the introduction of toads to New Guinea (Pippet, 1975) and the Solomon Islands (Cain and Galbraith, 1957). Anecdotal reports of poisoning of native wildlife from ingestion of cane toads also come from Bermuda (Davenport et al., 2001) and Fiji (Gorham, 1968).

In laboratory experiments, eggs and larvae of *Bufo marinus* can be toxic to an array of native invertebrates and tadpoles (Crossland, 1998a, b; Crossland and Alford, 1998; Crossland and Azevedo-Ramos, 1999; Punzo and Lindstrom, 2001), and that toxicity can increase ontogenetically (Crossland, 1988b). In experiments carried out in artificial ponds, these results were extended to demonstrate that presence of *B. marinus* eggs and tadpoles significantly depressed survival of native *Limnodynastes ornatus* tadpoles, presumably via poisoning of the latter. This depression of *L. ornatus*, in turn, led to enhanced survival of native *Litoria rubella* tadpoles due to release from predation by the former (Crossland, 2000). Survival of *L. ornatus*, *L. tasmaniensis*, *L. terraereginae*, and *Notaden bennetti* was also sometimes depressed in independent pool and pond-enclosure experiments (Williamson, 1999). These results are suggestive of changes liable to occur in native anuran communities from introduction of *B. marinus*, but direct examination for similar effects under entirely natural circumstances has not occurred. Larval *B. marinus* can be toxic to a few native Australian fish species as well (Crossland and Alford, 1998; van Dam et al., 2002) but are typically rejected as food (Lawler and Hero, 1997; van Dam et al., 2002), so seem unlikely to exert any significant effects on native fish populations.

Wider Changes in Ecosystem Dynamics

The widespread loss of terrestrial vertebrates occasioned by the introduction of *Boiga irregularis* and other vertebrates to Guam led to ecosystem-wide trophic changes (Fritts and Rodda, 1998). The dominant vertebrate biomass on Guam now consists of alien species, there is an increased number of predatory links in the food web, five ecological guilds previously present are now absent, and other ecological guilds have become rare (Fritts and Rodda, 1998). Wholesale loss of avian and mammalian insectivores has apparently resulted in an increase of spiders (Fritts and Rodda, 1998; Rodda et al., 1999b) and changes in their web-making behaviors (Kerr, 1993). The extirpation of volant frugivores has been predicted to lead to losses of pollinator and fruit-dispersal services to native plants, leading to long-term changes in floral composition (Savidge, 1987b); extirpation of insectivores is expected to increase damaging insect populations, leading to increased rates of herbivory on native plants (McCoid, 1991; Fritts and Rodda, 1998). Observations of slowed or failed regeneration in some plant populations (Perry and Morton, 1999; Ritter and Naugle, 1999) are consistent with these predictions, but other factors (especially high ungulate densities) are also involved, so conclusive evidence of those secondary effects is not yet available.

Secondary effects have been demonstrated to attend invasion of cane toads in northern Australia. Subsequent to arrival of the toads, monitor lizards (*Varanus panoptes*) suffered dramatic decline, apparently from preying on the toxic new arrivals (Doody et al., 2006). This removed the most significant source of nest predation on the river turtle *Carettochelys insculpta*, increasing its nest-success rate by 20%. Doody et al. (2006) hypothesized that similar secondary effects would benefit sea turtles and other native species subject to heavy predation from *V. panoptes*, potentially leading to a cascade of trophic effects as yet unstudied.

The success of *Boiga irregularis* on Guam illustrates an additional secondary ecological effect of considerable importance. Early expectations were that snake abundance would abate once its food source of native birds declined. However, that did not happen because the snake population is now maintained by supremely abundant alien vertebrate species, the most important of which are the lizards *Carlia ailanpalai*, *Hemidactylus frenatus*, and *Anolis carolinensis* (E.W. Campbell, 1996; Fritts and Rodda, 1998; McCoid, 1999; Rodda et al., 1999b, c). In this instance, the secondary effect is not from the snake itself but from the alien prey organisms that allow it to maintain high densities and continue cropping native prey to extinction. This effect from the alien prey base is maintained because the reproductive rates of the alien lizards far exceed those of the snakes (Fritts and Rodda, 1998), making them a reliably available resource.

A similar alien-prey boost to an invasive snake predator has been proposed elsewhere: high population densities of the alien frog *Rana perezi* on the Balearic Islands are thought to maintain high population densities of the alien snake *Natrix maura* (Moore et al., 2004a). This snake is thought to be the primary threat to the survival of the endangered endemic frog *Alytes muletensis* (Alcover et al., 1984; Tonge, 1986), and the latter is largely limited to rugged upland areas in which both *N. maura* and *R. perezi* are scarce (Moore et al., 2004a).

This augmentation of food resources for alien predators by alien reptiles and amphibians may be of more common occurrence than currently appreciated because many species of both taxa can attain tremendous population densities and biomass (Burton and Likens, 1975; Gosz et al., 1978; Rodda et al., 2001; Rodda and Dean-Bradley, 2002; Gibbons et al., 2006), including in their introduced ranges (e.g., Greenlees et al., 2006; Woolbright et al., 2006). Thus, many reptile and amphibian species are likely candidates to facilitate subsequent alien predator establishment by serving as a dense food source. Concern has been expressed that this phenomenon could facilitate establishment of introduced snakes in Hawaii (Kraus et al., 1999; Kraus and Cravalho, 2001; Loope et al., 2001), but this form of ecological "priming" has been uninvestigated except for the *Boiga* and *Natrix* cases discussed above. As introductions of additional herpetological predators and their prey continue to increase this phenomenon may become more widely noticed.

Dense populations of alien reptiles and amphibians could potentially affect nutrient-cycling dynamics within ecosystems, but this effect has been little investigated to date. It has been proposed that two alien frogs (*Eleutherodactylus coqui* and *E. planirostris*) could serve as nutrient sinks in Hawaii by depletion of invertebrate biomass and disruption of ecological pathways (Kraus et al., 1999). This speculation was based on known high population densities of the frogs, their high invertebrate-cropping rates, and the lack of native predators (and paucity of alien predators) to feed on them. One study (Beard and Pitt, 2006) lent some support to this conjecture, finding that in a dense population of *E. coqui* frogs were consumed in very low amounts by mongoose (*Herpestes javanicus*) but not at all by rats (*Rattus rattus* and *R. exulans*) or cane toads (*Bufo marinus*). These are the only predators available to prey on these frogs in most of Hawaii. Studies in their native Puerto Rico have shown *E. coqui* to affect nutrient cycling dynamics in forest plots by reducing aerial invertebrates and leaf herbivory and by increasing primary productivity and leaf decomposition rates (Beard et al., 2002, 2003). These effects resulted from high predation rates on aerial insects and fertilization of soil by frog feces. Identical effects were found in the invaded range of *E. coqui* in Hawaii, as were reductions in numbers of herbivorous and leaf-litter invertebrates and increases in new leaf production by the invasive plant *Psidium cattleianum* in one invaded site (Sin et al., 2008).

Similar ecosystemic impacts are considered likely to result from the invasion of *Bufo marinus* in northern Australia. In this system, a four-fold increase in amphibian biomass has been documented as toads invade virgin territory (Greenlees et al., 2006). Because the toad is largely invulnerable to predation by native species, the increase in amphibian biomass is expected to serve as a nutrient sink (Greenlees et al., 2006), although possible effects on primary productivity and decomposition rates would also merit investigation.

Another change to community dynamics is attributed to colonization by *Bufo marinus*. High prevalence of a native tapeworm in the Australian anuran *Litoria pallida* declined after invasion by cane toads, apparently because the high density of toads interfered with transmission of the parasite to its definitive snake host, *Liasis childreni* (Freeland, 1994). The tapeworm's life cycle originally involved transmission of eggs from snake feces to frogs via consumption of infected food. Cyst-bearing frogs were then consumed by the snakes, completing the worm's life cycle. The creation of high-density populations of voracious toads shunted most worm eggs to that alien species, which was shunned as a food item by the snakes, breaking the life-cycle of the tapeworms and reducing their prevalence in native frog populations. The tapeworm's decline has been associated with a decline in the stability of the local frog community (Freeland, 1994).

Each of these documented or potential changes to food webs and ecosystem dynamics stems directly from the high standing biomass that some alien reptiles and amphibians are capable of achieving. Direct measurements of biomass or densities have not often been made for alien populations of reptiles and amphibians. However, there is a number of herpetological genera with naturalized populations whose densities are sufficiently high that they are likely candidates for disrupting trophic dynamics of invaded ecosystems. These include frogs of the genera *Bufo*, *Eleutherodactylus*, *Osteopilus*, *Rana*, and *Xenopus* and lizards of the genera *Anolis*, *Carlia*, *Chamaeleon*, *Hemidactylus*, *Lampropholis*, and *Podarcis*. This list is not exhaustive but merely highlights some of the more promising taxa for investigation.

Competition with Native Species

As noted above, *Bufo marinus* has depressed reproductive success of rainbow bee eaters partially through competition for burrow use (Boland, 2004a). Tadpoles of the same species also depressed growth rates among a variety of native anuran larvae in pool and pond-enclosure experiments, but inconsistency among trials leaves unanswered the extent to which competition exerts population-level effects among tadpoles in natural settings (Williamson, 1999). Other experiments indicated apparently strong competitive effects between *B. marinus* tadpoles and those of *Limnodynastes ornatus* (Crossland, 1997, cited in van Dam, 2002). No competitive effect was noted between adult toads and native frogs (Freeland and Kerin, 1988).

The expansion of *Eleutherodactylus johnstonei* across the Lesser Antilles has been correlated with the decline or replacement of native congeners on several islands (Hardy and Harris, 1979; H. Kaiser and Henderson, 1994; H. Kaiser et al., 1994; H. Kaiser, 1997). However, this replacement largely goes hand in hand with habitat destruction: *E. johnstonei* has a greater physiological tolerance for higher temperatures and drying (Pough et al., 1977) and greater use than native *Eleutherodactylus* of opened habitats (Stewart, 1977; Stewart and Martin, 1980). This tolerance seems to facilitate its use of expanding areas of vegetation disturbed by human activities (H. Kaiser, 1997), apparently at the occasional expense of resident congeners (Hardy and Harris, 1979; H. Kaiser, 1997).

Competitive effects from larval *Rana catesbeiana* can be varied. They depress growth rates and survival in larval *R. boylii* owing to exploitative competition for algal resources (Kupferberg, 1997a). They also inhibit growth rates in larval *R. aurora* by passive exclusion under conditions in which food resources are clumped (Kiesecker et al., 2001). This happens because larval *R. aurora* avoid tadpoles of *R. catesbeiana* and, hence, lose access to the clumped food resources around which the latter invariably gather (Kiesecker et al., 2001). The two mechanisms need not be exclusive: exploitative deficiencies of native *Rana* tadpoles may be worsened by also decreasing activity levels (and, hence, amount of time spent feeding) in the presence of *R. catesbeiana* (Kiesecker et al., 2001). Severity of competitive effects may vary with environmental conditions between aquatic habitats (Adams, 2000), a confounding factor that has yet received no detailed treatment. Laboratory trials have also found survival of native European *Rana* tadpoles to be considerably reduced in the presence of larval *R. catesbeiana*, even when densities of the latter were low (Laufer and Sandte, 2004). This appeared to result from direct competition for food inasmuch as larval bullfrogs displaced native tadpoles from food resources and larval predation was never observed.

Similar competitive effects have been found with *Osteopilus septentrionalis* introduced to Florida. Tadpoles of this species depressed growth rates and delayed metamorphosis in native *Bufo terrestris* and *Hyla cinerea* when raised together in a laboratory setting; they also led to reduced size at metamorphosis in *B. terrestris* (K.G. Smith, 2005a). When raised together in mesocosm experiments *O. septentrionalis* decreased survival rates, growth rates, and size at metamorphosis of *B. terrestris*, although those effects were reversed when tadpoles were raised in the presence of predatory newts (*Notophthalmus viridescens*), which preferentially preyed upon the alien tadpoles (K.G. Smith, 2006b). Although these results are suggestive, competitive impacts of *O. septentrionalis* in natural systems remain experimentally uninvestigated.

Pearl et al. (2005b) documented unexpectedly frequent rates of interspecific amplexus between *Rana catesbeiana* and native *R. aurora* and *R. pretiosa* in the Pacific Northwest of the United States. They hypothesized that, should males of the two natives be limited in breeding pools, sexual interference by frisky *R. catesbeiana* might serve as a hindrance to population recruitment, although the importance of such a mechanism remains to be demonstrated.

A variety of alien lizards has been presumed to competitively displace native species, judging from historical patterns of changes in species abundance and geographical patterns of species assortment (Case and Bolger, 1991; Case et al., 1994). Exclusion of the long-resident geckos *Lepidodactylus lugubris* by recently established *Hemidactylus frenatu*s in urban and suburban niches in several locations in the Pacific appears to result from behavioral interference (Bolger and Case, 1992) and consumption of juveniles by the newcomer (Bolger and Case, 1992; McCoid and Hensley, 1993b), but especially by enhanced ability of *H. frenatus* to exploit food resources (Petren and Case, 1996). This exploitative exclusion is dependent upon dense concentrations of insects attracted to human light sources and the structural simplicity of building surfaces (Petren et al., 1993; Petren and Case, 1998). However, *L. lugubris* also avoid *H. frenatus* (Bolger and Case, 1992; S.G. Brown et al., 2002), and this avoidance may make *L. lugubris* more susceptible to predation subsequent to invasion by *H. frenatus* (S.G. Brown et al., 2002). Although *L. lugubris* itself may be a human introduction across much of the Pacific (Moritz et al., 1993), making this an example of displacement of one alien lizard by a more recent introduction, it does illustrate the potential for competitive exclusion to result from alien lizard introductions. A similar mechanism may be occurring between two alien geckos in Texas. There, resident *H. turcicus* are being displaced by more recently arrived *Cyrtopodion scabrum*, and the displaced species exhibits a dietary shift in sympatry that is consistent with strong dietary competition (Klawinsky et al., 1994). Both displacement and dietary shift may be mediated by interference competition for perch sites, which has been demonstrated in enclosure experiments (Vaughan et al., 1996). However, in laboratory experiments, Dame and Petren (2006) demonstrated that replacement of *Hemidactylus garnotii* across the Pacific by *H. frenatus* cannot be explained by either resource competition or aggression, leaving uncertain what mechanism is responsible.

Clearer evidence attends the competitive exclusion of endemic and highly endangered *Nactus* species in the Mascarene Islands by invasive *Hemidactylus frenatus*. In this situation it is known that the endemic geckos *N. coindemirensis*, *N. durrelli*, and *N. serpensinsula* have disappeared across most of Mauritius and its satellite islets, being confined (with one exception) only to a few islets lacking *H. frenatus* (Arnold and Jones, 1994; Cole et al., 2005). Outdoor exclosure experiments have shown *H. frenatus* to aggressively interact with individuals of the smaller *Nactus* species, displacing them from daytime refugia, injuring some individuals, and preying upon others (Cole et al., 2005). Competitive exclusion from refugia presumably makes the native geckos more susceptible to predation by invasive mammals like cats and rats, and injury is likely to directly impact survival of affected individuals. The native geckos persist only in a few small areas having substrates not easily negotiated by the alien.

The skink, *Cryptoblepharus nigropunctatus*, endemic to the Ogasawara Islands, has been reported to be declining on Chichijima since the late 1970s, and by the 1990s the skink could not be found in areas having high densities of introduced *Anolis carolinensis* (Miyashita, 1991; Suzuki and Nagoshi, 1999). This appears to result from direct competition with *A. carolinensis*. Where the two occur syntopically, there have been changes in substrate use and perch height by *Cryptoblepharus*, suggesting that competition for favorable basking sites may explain some of the native lizard's displacement. Further, *Anolis* were invariably observed to attack *Cryptoblepharus* when food was experimentally presented between pairs of each species in the wild (Suzuki and Nagoshi, 1999). Both results suggest that interference competition by the larger alien lizard is causing the decline of the native.

It has been observed that *Carlia ailanpalai*, introduced to the Mariana Islands, is extremely aggressive toward the native terrestrial lizards, attacking them, stealing their food, and possibly preying on them (Rodda et al., 1991; McCoid, 1995b). It has been proposed that this aggressive behavior may serve as a competitive exclusion mechanism contributing to the decline or disappearance of several populations of native skink in the region (Rodda et al., 1991; Rodda and Fritts, 1992; McCoid, 1995b). This hypothesis is reasonable but has yet to be experimentally tested.

Podarcis wagleriana is native to Sicily and the satellite Aegadian Islands; *P. raffonei* is a close relative restricted to some of the nearby Aeolian Islands (Capula, 1994a). *Podarcis sicula* is native to mainland Italy, Sicily, and Adriatic coastal areas but has been introduced on some islands in the native ranges of *P. wagleriana* and *P. raffonei* (Capula, 1992, 1994b). In those circumstances, *P. sicula* either dominates or replaces the native lizards. This has been argued to reflect competitive superiority because the alien lizard predominates in virtually all available microhabitats (Capula, 1992). Genetic (Capula, 1993) and distributional (Capula, 1992) evidence suggest that this competition has led to extirpation of *P. raffonei* throughout most of its original range, and the species is now virtually extinct (Capula et al., 2002).

The replacement of *Anolis carolinensis* in Florida by invasive *A. sagrei* may be due in part to competitive effects on reproduction. In enclosure experiments, female *A. carolinensis* laid fewer eggs when placed in sympatry with *A. sagrei* than when housed alone or (sometimes) with conspecifics (Vincent, 1999). In contrast, *A. sagrei* females did not reduce reproductive output in sympatry with *A. carolinensis*. Whether such results also obtain in the field remains unknown but, if so, would complement the effects of hatchling predation by *A. sagrei* discussed earlier.

Concern has been raised about alien *Trachemys scripta* competing with native *Emys orbicularis* in Europe (Frisenda and Ballasina, 1990; Servan and Arvy, 1997; Arvy and Servan, 1998; Gianaroli et al., 1999), and they have been argued to act aggressively toward the native turtle and displace it from basking sites (Kaltenegger, 2006). Cadi and Joly (2004) demonstrated weight loss and reduced survival of *E. orbicularis* when confined with *T. scripta* in outdoor enclosures in southeastern France. Data from these same enclosures suggest this effect is at least partly due to superior competitiveness of *T. scripta* for basking sites, relegating *E. orbicularis* to poorer-quality sites (Cadi and Bertrand, 2003; Cadi and Joly, 2003). This effect was not due to active displacement of *E. orbicularis* by *T. scripta*, but simply resulted from its earlier occupation of basking sites during the morning and the reluctance of *E. orbicularis* to climb onto sites already occupied. Competition for basking sites has also been posited as a likely impact of *T. scripta* on native *Actinemys marmorata* in California (Spinks et al., 2003) and is consistent with earlier data showing behavioral avoidance of the alien turtle by that same population of *A. marmorata* (Holland, 1994). Impacts on wild populations of *E. orbicularis* have not been demonstrated but may be feasible, considering the rare status of that species in many localities and the densities which the alien turtle can attain (Cadi and Joly, 2003). This supposition needs to be tempered, however, with recognition that *T. scripta* exhibits low reproductive success and juvenile survival in much of Europe (Luiselli et al., 1997). If that observation holds generally, *T. scripta* populations may undergo attrition as adults die but fail to be replaced by additional pet releases because of the European Union's import ban on this species. So the practical effects of *T. scripta* for native turtle populations in Europe remain uncertain.

Enclosure experiments have also shown that female *T. scripta* gain a competitive edge over native *Chrysemys picta* females in Ohio, United States, by being more aggressive (McKenna and Tramer, 2001). Males of the two species did not exhibit such differences. Growth of *C. picta* was not affected by this behavioral difference but it seemingly led to an increased tendency of female *C. picta* to disperse away from the *T. scripta* (McKenna and Tramer, 2001).

Vectoring Novel Parasites

The pathogenic fungus *Batrachochytrium dendrobatidis* induces a recently emerged disease, chytridiomycosis, that has caused drastic declines and extinctions of many species of amphibians worldwide (Berger et al., 1998; Daszak et al., 1999, 2003; Speare and Berger, 2000; Garner, 2005; Lips et al., 2006; Skerratt et al., 2007). Earliest known presence of this fungal infection is from the frog *Xenopus laevis* in Africa, and this suggests that the fungus may have begun its global spread with the widespread export (resulting in frequent release) of *X. laevis* for laboratory and pregnancy testing in the 1930s (Weldon et al., 2004). Infection in *X. laevis* is typically asymptomatic (Weldon, 2004), as it is in the American bullfrog, *Rana catesbeiana* (Mazzoni et al., 2003; Daszak et al., 2004). This latter frog has been widely exported, farmed for food, and escaped or released into the wild in a large number of countries (Bury and Whelan, 1984); and *Batrachochytrium* has been documented in feral bullfrog populations in many parts of its introduced range (Hanselmann et al., 2004; Garner et al., 2006). Both alien frogs are, hence, efficient potential vectors of the fungus to naive, native frog faunas, and current evidence suggests their widespread transportation and release may be a contributing source to the global explosion of the disease in the past two decades. Consistent with this hypothesis is that the first documented occurrence of *Batrachochytrium* in Great Britain is at a site in Kent having the only breeding population of *R. catesbeiana* in the country, as well as a feral population of *X. laevis* (Cunningham et al., 2005; Fisher and Garner, 2007). Although movement of these two species may have been responsible for starting and abetting this amphibian pandemic, it is clear that a large number of widely traded amphibians can serve as vectors for *Batrachochytrium* and that the amphibian trade generally, whether leading to feral introductions or not, must be viewed as highly inimical to the continued persistence of uninfected amphibian faunas (Fisher and Garner, 2007).

Daszak et al. (1999) pointed out the likelihood that other amphibian disease organisms besides *Batrachochytrium* have been transported with the widespread introduction of alien bullfrogs and cane toads, but this reasonable supposition remains uninvestigated. However, iridoviruses of the genus *Ranavirus* have been implicated in numerous amphibian mortality events across North America in the past decade (Green et al., 2002; Jancovich et al., 2005), and genetic evidence suggests these viruses to have been derived from widely introduced sport fish, with subsequent spread across western North America due to the common use (and escape or release) as fish bait of alien larval *Ambystoma tigrinum* (Jancovich et al., 2004). Outbreaks of disease caused by *Ranavirus* affect a diversity of frog and salamander species, including some endangered forms (Jancovich et al., 1997).

At least one protozoan has been vectored to Australian frogs by introduction of *Bufo marinus*, and it has been able to expand to areas beyond the invasion front of the toad (Delvinquier, 1986; Delvinquier and Freeland, 1988a). Effects on native anurans are unknown. A variety of other protozoan parasites has arrived with *B. marinus* from its native range but are not yet known to infect native amphibians (Delvinquier and Freeland, 1988). Vectoring of alien helminths to new hosts via introduced lizards has been documented in Hawaii (Goldberg and Bursey, 2000a; Goldberg et al., 2004c), but effects on native taxa are non-existent because Hawaii lacks native lizards. These examples demonstrate the potential for introduced reptiles and amphibians to transport new parasites to naive herpetofaunas, but whether this potential has translated into damage to native herpetofaunas is totally uninvestigated.

Observations of epidemic mortality events caused by viral or mycoplasma agents in *Actinemys marmorata* in California and Washington states, United States, were noted to have occurred in populations into which alien species of turtles had previously been introduced (Holland, 1994). This led to the reasonable hypothesis that the alien turtles served as vectors of a new disease agent into these populations. This speculation could not be directly tested but was consistent with the frequent maintenance of pet-store turtles under crowded and unsanitary conditions, which could easily allow for rapid acquisition of novel disease agents prior to a turtle escaping or being released (Holland, 1994).

Under somewhat more controlled circumstances, a total of 29 species of alien ticks has been imported into the United States on captive reptiles (Burridge and Simons, 2003), and at least seven of these have established breeding populations at captive reptile facilities (S.A. Allan et al., 1998; Burridge et al., 2000a; Simmons and Burridge, 2000, 2002). One alien tick, *Amblyomma rotundatum*, has been found on feral *Bufo marinus* in Florida, which is presumed to have served as the vector to that new locale (Oliver et al., 1993). That tick has a broad host range in its native Central and South America but has not yet been reported from native wildlife in Florida. Another species, *A. dissimile* is also established in Florida, is thought to have arrived on imported reptiles, and has been found infecting native reptiles (Bequaert, 1932). It continues to arrive on imported reptiles from Central and South America (Burridge and Simons, 2003). Several of these alien ticks are readily capable of switching onto hosts to which they have no prior history of exposure (Burridge, 2001), suggesting a capability to infect native reptile species. The potential for this wide array of ticks to vector diseases to native reptile and amphibian populations has been largely uninvestigated, but two of these tick species can vector reptilian haemogregarines, and severe infestations of one species have led to respiratory distress and death in some reptiles (Burridge, 2001). The finding of lethal infections of the tick-vectored *Ehrlichia ruminantium* or a close relative in a phylogenetically varied array of captive snakes suggests that risks to native reptiles are potentially serious (Kiel et al., 2006); however, this potential remains unexamined in wild populations.

Community Homogenization

Little attention has yet been paid to the broader-scale effects that accumulating introductions have for homogenization of herpetological communities. One exception is a recent investigation into regional changes in herpetological communities attending alien introductions to Florida. This study found that introductions made to date have increased homogenization of communities at the small spatial scale of adjacent counties but had not yet shown a similar tendency toward homogenization across the state as a whole (K.G. Smith, 2006a). This spatial contrast probably results from two factors: the recency of many introductions has likely not yet allowed homogenization effects to spread very far, and the climatic gradient in peninsular Florida may not allow many established southern species to access more northerly latitudes. This is the only study I know to quantify regional effects of herpetological introductions.

Evolutionary Effects

Evolutionary effects from invasive reptiles and amphibians are primarily of interest in terms of how they impact native faunas. Such effects have been demonstrated in a few cases, are frequently to be expected, but have been little studied to date. Evolutionary changes have been noted for the alien invaders themselves in a few instances. With the possible exception of the last example below, all changes discussed here have or are presumed to have a genetic basis.

Genetic Changes

Hybridization with congeners is a frequent outcome of rampant transport of organisms (cf., Levin et al., 1996; Rhymer and Simberloff, 1996; Mooney and Cleland, 2001; Low, 2003: 261–272; Largiadèr, 2007), and the same consequence has been documented for a number of alien reptile and amphibian introductions. Such hybridization may lead to loss of native allelic or genomic identity, outbreeding depression (Rhymer and Simberloff, 1996), or, in the extreme case, loss of native species due to wholesale genetic swamping by the invader (e.g., Echelle and Connor, 1989). Clearly detrimental impacts on native reptiles and amphibians resulting from introgressive hybridization of alien genomes have been demonstrated for only a small set of species. Nonetheless, these effects have frequently been grave and this seems one of the more damaging impacts attending herpetological introductions.

Among amphibians, populations of the salamander *Ambystoma tigrinum* across the western United States have experienced widespread introduction of larvae of eastern forms of this species used as fishing bait (Lowe, 1955; Espinoza et al., 1970; Bury and Luckenbach, 1976; Collins, 1981). Genetic contamination of native populations has been documented in Arizona, where genetic introgression threatens the endangered *A. t. stebbinsi* (Storfer et al., 2004), and in California, where the endangered *A. californiense* is extensively threatened with the same (Riley et al., 2003). In the latter case, hybridization appears to be promoted by habitat alteration, with alien alleles preponderating in unnatural, perennial ponds. This pattern derives from differential success of hybrid genotypes and has resulted in a complex mosaic hybrid zone (Fitzpatrick and Shaffer, 2004).

The alien newt *Triturus carnifex* has introgressed with native *T. cristatus* in both Great Britain (Brede et al., 2000) and the Geneva Basin of Switzerland and France (Arntzen and Thorpe, 1999). In the former case, evidence of introgression is still limited to the introduction site. In the latter, the alien has largely replaced the native across the landscape over a period of 30–40 generations, although it is not clear whether this is due to introgression, competition, habitat degradation, or a combination of all three.

Hybridization threatens native bisexual and hybridogenic complexes of water frogs (*Rana* spp.) in Europe. *Rana* kl. *grafi* is a hybridogenic lineage that occupies northeastern Spain and southeastern France and originated from the hybridization of *R. ridibunda* with either *R. perezi* or the hybridogenic *R.* kl. *esculenta* (Pagano et al., 2001a, c). This lineage is maintained by the standard hybridogenic mechanism of destruction of one parental genome prior to meiosis followed by backcrossing to one or the other parental species to re-form either a new generation of similar hybrids or reconstituted individuals of the parental species. Several of these hybridogenic lineages (or kleptons, designated by "kl.") occur across Europe, involving a number of different parental species and their resultant hemiclonal classes (Graf and Polls Pelaz, 1989; Günther, 1990; Pagano et al., 2001a; Arnold and Ovenden, 2002). Alien *R. ridibunda*, *R. lessonae*, and *R.* kl. *esculenta* have been recently introduced to Spain, are hybridizing with the native *R. perezi*, and are introgressing foreign genes into the local complex of water frogs (Arano et al., 1995). It is thought that this poses a threat to the bisexual *R. perezi* by boosting heterozygosity values in local hybridogenic *R.* kl. *grafi*, which may then outcompete *R. perezi*. Similar fears attend the introduction of the alien *R.* kl. *esculenta* (Arano et al., 1995). Although the feared displacement mechanism, strictly speaking, is competition, the system could not be maintained without the successful introduction of the alien genomes; hence, continued hybridization is key to the threat. Similarly, in Switzerland, hybridization of alien *R. ridibunda* with native *R. lessonae* and native *R.* kl. *esculenta* has led to creation of, respectively, additional numbers of *R. ridibunda* and new genotypes of *R.* kl. *esculenta*, which themselves are capable of producing additional generations of *R. ridibunda* by backcrossing with the alien frogs (Vorburger and Reyer, 2003). These new genomic combinations have contributed to the rapid replacement of the two native water frogs by *R. ridibunda* during the past half century (Vorburger and Reyer, 2003). The standard mechanism for maintaining hybridogenesis does not involve meiotic recombination, although such does occasionally occur (Pagano and Schmeller, 1999). In southern France, introduction of alien water frogs has also led to introgression of foreign genes into local water frog gene pools (Pagano and Schmeller, 1999; Pagano et al., 2003) as well as creation of novel assemblages of water frog genomes that were previously absent (Pagano et al., 2001c). The potential for similar genetic pollution elsewhere in the ranges of these hybridogenic water frog complexes is obvious.

As mentioned earlier, *Podarcis wagleriana* is native to Sicily and the satellite Aegadian Islands and *P. raffonei* to the nearby Aeolian Islands (Capula, 1994a). On some of these islands, the introduced *P. sicula* has been documented to hybridize with the native – with *P. wagleriana* on Marettimo and with *P. raffonei* on Vulcano

(Capula, 1993). These events have led to some genetic introgression on each island, and evidence indicates there was hybridization with *P. raffonei* prior to its extinction on Lipari as well (Capula, 1993). To what extent genetic introgression has contributed to the decline of *P. raffonei* beyond that attributed to the competitive effects noted earlier remains unknown.

Hybridization between *Iguana delicatissima* and *I. iguana* is documented and is argued to be contributing to the displacement of the former in Guadeloupe and les Îles des Saintes (Day and Thorpe, 1996; Day et al., 2000; Breuil, 2000a, b, 2002). It remains uncertain that *I. iguana* is alien to this region but it highlights the potential for similar problems in nearby areas (e.g., northern Lesser Antilles) where it certainly is not native.

Some populations of *Anolis distichus* may originally have been native to Florida (L.D. Wilson and Porras, 1983, but see A. Schwartz, 1968a for a contrary opinion) and were given the designation *A. d. floridanus* (H.M. Smith and McCauley, 1948). But three other subspecies of *A. distichus* have been introduced to Florida (W. King and Krakauer, 1966; Bartlett, 1995a), and hybridization between one of these, *A. d. dominicensis*, and the presumptive native has been sufficient to largely obliterate the distinctiveness of the latter, creating instead a continuum of phenotypes having no geographic structure (Miyamoto et al., 1986). Mitochondrial DNA evidence also supports a history of extensive hybridization among three or four lineages of *A. distichus* in this region (Kolbe et al., 2007a). Thus, the original population of *A. distichus* inhabiting Florida in the 1940s is now extinct and replaced by a variable hybrid swarm of largely alien composition. Whether this represents loss of a unique lineage or not is unknown.

Hybridization between native *Anolis carolinensis* and alien *A. porcatus* has also occurred in southern Florida (Kolbe et al., 2007a), but the magnitude of any genetic impact on the native remains unknown.

Hybridization with introduced *Trachemys scripta* may be a threat to the endemic *T. stejnegeri malonei* of Great Inagua Island (Mealey et al., 2002). If one believes the argument of Lee and Ross (2001) that *T. terrapin* is native to Grand Bahama Bank and not to Jamaica, the same threat would be posed by introduced *T. scripta* and *T. stejnegeri* on the islands of that bank (Lee, 2004, 2005), where hybrid swarms have resulted from past introductions (Seidel and Adkins, 1987; Seidel, 1988). Alien *T. scripta elegans* are widely hybridizing with native *T. scripta scripta* in Florida (Bartlett and Bartlett, 1999; Aresco and Jackson, 2006) and Virginia (Mitchell, 1994), but the degree of genetic pollution in these populations is not yet quantified. Introduced *Cuora flavomarginata* interbreed with the native species *Geoemyda japonica* in the Ryukyu Islands, and hybrids are moderately frequent on the same island between native *Protobothrops flavoviridis* and the introduced *P. elegans* (Nishimura and Akamine, 2002; Ota, 2002d; Ota and Hamaguchi, 2003). In both cases, the genetic integrity of the natives may be threatened by interbreeding with closely related aliens. Alien subspecies and DNA haplotypes of *Emys orbicularis* have been widely distributed around much of Europe (Lenk et al., 1998; U. Fritz et al., 2004), posing the threat of genetic contamination or swamping of local populations (Kaltenegger, 2006).

Genetic changes can also occur in the introduced species itself. The clearest example is for *Anolis sagrei*, native to Cuba, the Bahamas, and the coast of northern Central America and introduced to a variety of other localities. In Florida, *A. sagrei* was introduced at least eight separate times. These introductions were from a variety of localities in the native range of the lizard and this resulted in genetic diversity within Florida populations greatly exceeding that available in native populations (Kolbe et al., 2004, 2007b). This increased genetic diversity has been retained to a diminished extent in further populations in Grand Cayman Island, Hawaii, Louisiana, Taiwan, and Texas founded by animals from Florida, and it is thought to be one of the reasons for the success of *A. sagrei* in these several invaded localities (Kolbe et al., 2004, 2007b). Similar admixture of native genomes by multiple introductions has been shown for a number of other *Anolis* species introduced to Florida and the Dominican Republic (Kolbe et al., 2007a). Chuckwallas (*Sauromalus* spp.) found on Alcatraz, Sonora are claimed to be a hybrid swarm involving the three introduced species *S. ater*, *S. hispidus*, and *S. varius* (Case, 1982; Petren and Case, 1997; Mellink, 2002), although evidence for this assertion has not been published. More often, a decrease in genetic diversity (the so-called "founder effect") is expected to obtain in most alien populations, reflecting their founding from very few individuals, each containing only a limited sample of the species' total genetic diversity. Such reduced genetic variation has been observed within some populations of alien reptiles (Gorman et al., 1978) and can also serve to set the introduced population on a different evolutionary track from its parental species. So are novel genetic entities created by the process of human introduction.

Morphological Changes

Morphological changes in head shape and body size have been documented in two species of ranivorous Australian snakes, *Dendrelaphis punctulatus* and *Pseudechis porphyriacus*, with degree of change correlated with duration of exposure to invasive populations of cane toads, *Bufo marinus* (Phillips and Shine, 2004). Both snakes are highly sensitive to toad toxins, and observed morphological changes are toward reduced gape size and increased body size, in accordance with predictions for minimizing size-dependent vulnerability to toads (Phillips and Shine, 2006b).

The toads themselves have also changed morphologically through time, with reduction in body size and parotoid gland size both being negatively correlated with time since establishment of different populations (Phillips and Shine, 2005, 2006c). These changes presumably result from the high costs of producing large bodies and large quantities of toxin in novel environments in which they are unnecessary (Phillips and Shine, 2005), but response to climatic and seasonal variables is also involved (Phillips and Shine, 2006c). Furthermore, toad leg lengths have increased with time, giving a colonization advantage to longer-legged individuals, and dramatically increasing the rate at which toads are expanding their range in Australia (Phillips et al., 2006).

Microevolutionary changes in morphometric and scale-count variables have occurred in Floridian populations of the alien *Anolis sagrei* (J.C. Lee, 1985, 1987), and these changes are the side-effect of novel admixing of independently introduced genomes from different parts of the species' native range (Kolbe et al., 2007b).

Physiological Changes

Australian snakes of the species *Pseudechis porphyriacus* are sensitive to toxin from introduced *Bufo marinus*. Snakes from populations exposed to toads for several decades have developed some degree of toxin resistance compared to conspecifics from toad-naive populations. This is not an individually acquired trait, and so must involve evolutionary adaptation of exposed populations to the toxin (Phillips and Shine, 2006a).

Behavioral Changes

Australian snakes of the species *Pseudechis porphyriacus* from populations exposed to toads for several decades have developed a non-learned aversion to eating the invasive *Bufo marinus* compared to conspecifics from toad-naive populations (Phillips and Shine, 2006a).

Native *Alytes muletensis* tadpoles, endemic to Mallorca, respond to chemical (and perhaps visual) cues from alien *Natrix maura* snakes by decreasing their activity levels, both in native plunge pools as well as under laboratory conditions (Griffiths et al., 1998). Post-metamorphic individuals show the same avoidance of snake chemical cues (Schley and Griffiths, 1998). Tadpole responses are specific to snake cues from the introduced population of *N. maura* on Mallorca and do not extend to conspecific snakes from the Iberian Peninsula (Griffiths et al., 1998). Use in these tests of captive-reared *A. muletensis* naive to snakes shows that behavioral responses are genetic and most likely acquired since the introduction of *N. maura* to the Balearic Islands approximately 2,000 years ago. Morphological changes in tadpole shape are also induceable by exposure to *N. maura* chemical cocktails, with exposed tadpoles developing longer tails with deeper musculature and shallower ventral fins (Moore et al., 2004b). This developmental plasticity again seems to have evolved in response to the introduction of *N. maura* (Moore et al., 2004b).

Similarly, tadpoles of native *Rana aurora* derived from ponds inhabited by alien *R. catesbeiana* show increased antipredator behavior and higher survival rates when exposed to *R. catesbeiana* in captivity than do tadpoles from evolutionarily naive populations (Kiesecker and Blaustein, 1997). Learning could be ruled out as a mechanism because tadpoles were derived from collected egg masses and, hence, were individually naive to bullfrogs. Thus, behavioral avoidance appears to have a genetic basis. Juvenile *Pseudacris regilla* from ponds inhabited by *R. catesbeiana* also showed avoidance of chemical cues from the latter species, whereas juveniles from ponds lacking the alien frog did not (Chivers et al., 2001). In this last case, although evolution of avoidance behavior may be involved, the study design did not exclude the possibility of learning.

Until the extirpation of most birds and mammals from Guam brown treesnakes were primarily nocturnal in behavior. With the loss or extreme depletion of these nocturnal food sources during the 1980s, the snakes switched to largely feeding on diurnal lizards, and that prey switch is reflected in a major change in activity patterns for the snakes, with diurnal activity approaching 50% of all snake activity in the 1990s (Fritts and Rodda, 1998). Similarly, prior to 1988 the brown treesnake was primarily arboreal in behavior; during the 1990s, ground-level activity became the mode for some populations on Guam (Rodda, 1992b; Fritts and Rodda, 1998). It is uncertain whether these changes have a genetic basis or merely represent behavioral plasticity in the species. The latter seems more likely but it does highlight the degree to which behaviors that are thought to be typical for a species (in this case arboreality and nocturnality) may change in short order as circumstances require.

Social Effects

Economic

Economic effects from alien herpetofauna have been little considered, but those of the brown treesnake in Guam have been recognized as considerable. From 1978–1997, this species caused >1,600 power outages on Guam (Fritts et al., 1987; Fritts and Chiszar, 1999), including many of island-wide scope. Incurred costs are conservatively estimated to be from US$1–4 million/year (United States Geological Survey, 2007) and include (1) damage to electrical-distribution equipment, (2) increased maintenance and emergency-repair costs, (3) damage to electrical products due to voltage surges, (4) loss of revenues during outages, (5) loss of business by consumers during outages, and (6) investment in backup generators and transformers to ensure stable power availability (Savidge, 1987b). Occasionally, power outages have resulted in loss of water to some parts of the island for periods up to one week (Savidge, 1987b). Outage durations have risen from an average of 1 hour every 3–4 days in 1997 to 1.5 hour every two days in 2003 (Burnett et al., 2006). Power outages on a very localized level have also been attributed to Cuban treefrogs (*Osteopilus septentrionalis*) taking refuge in transformers in Florida (S. Johnson, University of Florida, personal communication, 2007), but no quantification of costs is available.

Brown treesnakes are significant predators of domestic chickens and their eggs on Guam. Although the dollar value of this predation was not determined, approximately 80% of chicken farmers surveyed reported predation, and 45% of these attributed predation to snakes (Fritts and McCoid, 1991). Fritts and McCoid (1991) concluded that brown treesnakes were an apparent factor contributing to Guam's inability to produce sufficient quantities of eggs for local consumption, leading to high-cost import substitution of eggs from Australia and the United States. As well as reducing the viability of a commercial poultry industry, increases in agricultural insect pests attributed to the snake's extirpation of insectivorous birds is argued to be partly responsible for Guam's agricultural decline since 1945 (United States Geological Survey, 2007). The snake also takes a toll on pets, primarily puppies and cage birds, but the cost of this loss is unestimated (Rodda and Savidge, 2007). Total costs of brown treesnakes to the United States have been estimated at US$12 million/year (Pimentel et al., 2005), which includes damage costs on Guam and funds expended to control the species and prevent its further introduction elsewhere.

Poultry depredation has also been reported for *Varanus indicus* in Guam (Crampton, 1921; Fritts and McCoid, 1991), the Northern Mariana Islands (Crampton, 1921; R.P. Owen, 1974; Wiles et al., 1990), Marshall Islands (Fulbeck, 1947), and the Federated States of Micronesia (Uchida, 1966, 1967, 1969). The same species is reported to reduce native populations of coconut crabs in Micronesia, leading to an additional loss of protein to local villagers (Uchida, 1966, 1969). The related *Varanus niloticus* is reported to attack pets in Florida, United States (T. Campbell, 2005). In none of these instances are economic costs quantified.

The introduction of *Eleutherodactylus coqui* to Hawaii led to the prediction of potential economic effects to the nursery industry, hotel industry, and residential property values because of the noise pollution caused by the frogs' loud calls (Kraus et al., 1999; Kraus and Campbell, 2002). Some of these effects have subsequently been documented. Negative effects of *E. coqui* on residential property values on Hawaii Island alone have been estimated to be 0.16% of total value for houses within 500 m of an infestation and 0.12% for houses between 500–800 m of an infestation, leading to a potential loss of revenues of almost US$8 million/year as frogs continue to spread (B.A. Kaiser and Burnett, 2006). Total costs would increase accordingly should the frogs become well established on Maui or Oahu, with their higher property values (B.A. Kaiser and Burnett, 2006). Realtors on Hawaii Island now include declaration of coqui presence in sellers' disclosure statements (Wu, 2005). An alleged failure to make such a declaration has led to the first lawsuit generated by this pest invasion (Dayton, 2007). Since December 2004, Guam has required nursery shipments from Hawaii to be certified as having been treated prior to export with either a 16% citric-acid solution or a 42°C hot-water drench for five minutes (D. Gee, Guam Department Agriculture, personal communication, 2007), treatments known to kill *E. coqui*. As well, plants imported from Hawaii are temporarily quarantined, preference is given to bare-rooted plants, and public education programs have been launched on Guam (Christy et al., 2007a). Some additional cost to Hawaiian nursery growers must follow from these restrictions, but they have not yet been calculated.

Introduced *Bufo marinus* became a significant predator of honey bees (*Apis mellifera*) in Australia and led to economic losses for apiarists and reduction in crop-pollination services (Goodacre, 1947; Hewitt, 1956; Tyler, 1994). Consequently, the government of Queensland recommended placing hives on collapsible wooden stands to remove them from the reach of toads. C. Lever (2001) estimated the cost of doing this to be AUS$1 million for stand procurement and replacement every five years; this excludes labor and transportation costs, which are expected to be heavy (Tyler, 1994). Upon advent of the cane toad in their region, aboriginal communities in the Borroloola area changed their ceremonies to request the spirits to return the local food and totem species lost subsequent to the toad invasion (van Dam et al., 2002). This bespeaks a significant, though unquantified, effect of the toads on the local subsistence economy. Similar impacts were predicted to occur to native communities in the Kakadu region subsequent to toad invasion (van Dam et al., 2002). Cane toads also consume large numbers of dung beetles, which were introduced to Australia to rid the continent of accumulating waste from non-native ungulates introduced for ranching (Waterhouse, 1974). Although the costs of this consumption of beetles do not appear to have been calculated, the threat of an upsurge in cattle dung was serious enough to prompt the search for additional dung beetles that would be immune to toad predation (Waterhouse, 1974). These toads have repeatedly been noted to poison naive domesticated pets (e.g., Rabor, 1952; Gebhardt, 1967; Krakauer, 1968; Otani et al., 1969; Roberts et al., 2000), leading to some unmeasured degree of veterinary and replacement costs. Research costs to Australia in an effort to identify a means of controlling cane toads have been estimated at AUS$500,000/year (Bomford and Hart, 2002) and have totalled more than AUS$9.5 million as of 2006 (Shine et al., 2006). As well, the Northern Territory has pledged AUS$100,000/year for a three-year program of research to identify long-term control methods for the species, and Western Australia invested AUS$600,000 to develop a strategy to prevent toads from entering that state (R. Taylor and Edwards, 2005). Far higher research and mitigation costs are proposed for the future (T. Robinson, 2006).

Green iguanas (*Iguana iguana*) and black spiny-tailed iguanas (*Ctenosaura similis*) have become nuisance problems in southern Florida, eating residential and commercial landscape plantings and digging burrows that can undermine human structures (Krysko et al., 2003a, 2007a). Costs of these activities are unestimated but likely to be significant in aggregate, though widely dispersed.

Information on control and prevention costs for invasive species, including reptiles and amphibians, are rarely made public and are often difficult to obtain. Nonetheless, these costs can be illustrated in a few cases. Control costs (including research and public-outreach expenses) for *Eleutherdactylus coqui* in Hawaii for Fiscal Year (FY) 2007 are in excess of US$4.2 million, increasing dramatically from approximately US$1 million in FY 2005 (M. Wilkinson, Hawaii Department of Land & Natural Resources, personal communication, 2007). Costs to control *Rana catesbeiana* in five ponds in Germany has been estimated at € 270,000 annually (Reinhardt et al., 2003). Costs to control the same species for three years in two ponds in England summed to £20,000, excluding personnel time and in-kind costs (Inskipp, 2003); costs across seven ponds managed since 1999 have now summed (as of early 2008) to £100,000 (J. Foster, Natural England, personal communication, 2008). Since 1994, there has been a control program on Guam to prevent brown treesnakes from accidentally being shipped to other localities. Direct programmatic costs for FY 2006 were US$5.76 million and do not include additional expenses provided by in-kind services (E.W. Campbell, United States Fish & Wildlife Service, personal communication, 2007). During that same fiscal year, the State of Hawaii spent US$210,000 to inspect vehicles and cargo arriving from Guam to ensure they were free of brown treesnakes (D. Cravalho, Hawaii Department of Agriculture, personal communication, 2007). Total federal funding for the brown treesnake program in FY2007 was US$6.26 million; this included costs of both operations and research (E.W. Campbell, United States Fish & Wildlife Service, personal communication, 2007).

Control costs for future protection of human health from the alien viper *Protobothrops mucrosquamatus* on Okinawa have been estimated to vary from 430 million to 10.8 billion yen (US$3.7–93 million) in the first year of operations, depending on how densely traps might be employed for snake control (Nishimura, 2005). To this cost are added depreciation costs varying from 130 million to 2.3 billion yen (US$1.17–20.6 million) each year. These costs do not include direct economic harm caused by the snakes, such as hospitalization costs, lost agricultural productivity, or lost tourism revenue (Nishimura, 2005).

Health

Brown treesnakes are rear-fanged and venomous and have been responsible for many instances of snakebite on Guam, 80% of which have involved individuals sleeping in their homes (Fritts et al., 1990, 1994; Rodda et al., 1997). A majority of victims seeking or requiring medical treatment have been children less than six years of age (Fritts et al., 1994), and several infants exhibited signs of serious envenomation, including respiratory distress or temporary neurological impairment (Fritts et al., 1990, 1994). The potential of this snake to generate medically serious envenomation in infants is well established. Although fatalities have not been documented, doctors have privately related that they believe some early unexplained child fatalities exhibited the same symptoms later recognized in sublethal envenomations by brown treesnakes (G. Rodda, United States Geological Survey, personal communication, 2008). Thus, it may be that a few human fatalities have occurred from this snake. The odd pattern of biting predominately sleeping humans, biting predominantly small children, and frequent coiling around victims suggests that many bites represent attempted feeding behavior by the snake (Fritts et al., 1994; Rodda et al., 1997; Fritts and McCoid, 1999). Recent figures indicate that approximately 150 brown treesnake bites require emergency-room treatment each year (S. Shwiff, United States Department of Agriculture, personal communication, 2007).

Rear-fanged snakes, such as *B. irregularis*, are generally not as dangerous to humans as the highly venomous front-fanged snakes of the families Elapidae and Viperidae, many of which easily kill adults. The fact that members of these families (*Naja kaouthia*, *Protobothrops elegans*, *P. mucrosquamatus*) have successfully established alien populations on Okinawa raises a potentially more serious health issue than is presented by *B. irregularis* in Guam. The two alien vipers of the genus *Protobothrops* are more aggressive than the native *P. flavoviridis*, and *P. elegans* has already been calculated to have a nine-fold greater rate of human envenomations than the native species (Nishimura, 2005). It has been estimated that once the related *P. mucrosquamatus* expands over much of Okinawa in the next century it will cause between 112–258 bite cases annually, much higher than the approximately 60 annual cases caused by its native congener (Nishimura, 2005). Variance in these estimates depends on how far and how fast the alien viper spreads as well as how aggressive it truly proves to be as human-contact frequency increases. Other dangerously venomous snakes have been introduced intentionally or accidentally through the pet trade to numerous other jurisdictions (Appendix A), and their potential to create grave health risks should be obvious.

A similar threat is posed, but not yet realized, by alien populations of large constricting snakes. Pythons (*Python molurus*) are now established in southernmost Florida, and population densities are high and increasing. This species attains a length of at least 7 m, is known to eat leopards in its native range (C.H. Pope, 1935), and can be exceedingly cryptic. Several instances of pythons killing and eating alligators (*Alligator mississippiensis*) in the Everglades are already documented. Although it is unlikely to be a frequent occurrence, it seems fairly likely that a visitor to Everglades National Park or surrounding area will eventually be killed by one. Similar concerns would pertain to other massive snakes (*Python reticulatus*, *P. sebae*, *Eunectes* species) should they become established in Florida or other localities.

Flinders Island spotted fever is a recently recognized human rickettsiosis (R.S. Stewart, 1991). Endemic reptile ticks (*Aponomma hydrosauri*) have been identified as a reservoir, and possibly a vector, of the disease (Stenos et al., 2003; Whitworth et al., 2003). Although the rickettsia, ticks, and reptile hosts are all native to the system studied, the potential for a reptile-borne tick to vector a human disease is newly recognized and raises the possibility that other, currently unrecognized, human diseases may accompany the widespread dispersal of reptile ticks via the pet trade. This may be particularly obvious in the case of the African tick *Amblyomma variegatum*, sometimes vectored by *Varanus* lizards, and known to carry the human disease agent *Rickettsia africae* (Burridge, 2001). An outbreak of human Q fever was associated with the handling and removal of alien ticks from imported reptiles and is suggestive of a possible connection between the two, but direct evidence for a causal relationship remains lacking (Burridge et al., 2000a; Burridge, 2001).

Alien frogs (*Eleutherodactylus johnstonei*) and toads (*Bufo marinus*) in Barbados have been reported to host serovars of *Leptospira interrogans* that are pathogenic in humans, livestock, and domestic dogs (Everard et al., 1988, 1990). Everard et al. (1990) argued that amphibians may be more involved in human leptospirosis epidemiology than currently appreciated, but this supposition remains uninvestigated. Similarly, it has been noted that cane toads can carry extremely high levels of pathogenic *Salmonella* and related bacteria (O'Shea et al., 1990; Thomas et al., 2001), as well as pathogenic *Leptospirosis* (Babudieri et al., 1973; Everard et al., 1980, 1983, 1988), but it is unknown whether wild populations of this species have a practical role in causing disease for humans. In Guam, it has been determined that *Bufo marinus*, *Anolis carolinensis*, and *Carlia ailanpalai* have high infection rates for *Salmonella* species, including *S. waycross*, a serotype that contributes significantly to high human salmonellosis rates in Guam but is rare in other countries (Haddock et al., 1990). High prevalence of *Salmonella* in fenced yards that exclude feral mammals has led to the inference that these lizards and toad are significant contributors to the high prevalence of salmonellosis in Guam (Haddock et al., 1993). In the United States, 6% of all *Salmonella* infections (and 11% of those in patients <21 years of age) are related to contact with amphibians or reptiles, which equates to approximately 74,000 cases/year (Mermin et al., 2004). Exposure in these cases is attributable to keeping reptiles and amphibians as pets and not to established populations of alien species per se. However, this finding does show the potential for similar transmission via close contact with alien species – such as house geckos and Cuban treefrogs – that are commensal with humans in the tropics and commonly reside and defecate in homes or cisterns. As far as I know, disease transmission via these routes has not been examined; however, health officials in the British Virgin Islands attempt some control of Cuban treefrogs because of their propensity to occupy cisterns used for collecting residential water (Owen et al., 2006).

Cane toads serve as a mechanical vector for human helminths in its native range (Marinkelle and Willems, 1964) and in Puerto Rico (Hoffman and Janer, 1941) because of its coprophagous habits. Hence, they have been conjectured to serve as vectors for human diseases or helminth parasites in areas lacking proper sanitation (Hoffman and Janer, 1941; Freeland, 1985; van Dam et al., 2002). However, the epidemiological importance of these conjectures in any portion of its introduced range remains unexamined.

There is one documented case of human death following ingestion of three cane toads that were mistaken for an edible species (Rabor, 1952). This species has also been reported to cause illness in humans after handling (Allen and Neill, 1956; Gebhardt, 1967) and after toxin entered open scratches (Gebhardt, 1967; Otani et al., 1969). Contamination of water sources by dead *Bufo marinus* has been reported for Palau (Gressitt, 1952) and Australia (van Dam et al., 2002). In at least the former instance, contamination threatened scarce water resources on an atoll. The threat is created by the sometimes large numbers of toads that may die and rot in a water source, as well as their released toxins, which may possibly be stable in such an environment for several days (van Dam et al., 2002).

Tadpoles of *Bufo marinus* have been shown to have a depressive effect upon growth rates in four species of mosquito and on survival rate in one species when reared together in small containers of water (Hagman and Shine, 2007). Although many variables remain unresolved (e.g., cane toad effects on native anurans and native mosquito predators, fitness of different size classes of mosquitoes), this has led to the speculation that cane toads might potentially have a suppressive effect on mosquito populations in the wild and lead to reduced transmission rates of mosquito-vectored diseases for humans (Hagman and Shine, 2007).

Green iguanas (*Iguana iguana*) have become abundant on Puerto Rico, where they now pose an airstrike hazard at San Juan's international airport (Engeman et al., 2005b). There have been five collisions of airplanes with iguanas at this location, and flight operations were temporarily halted six times during a two-month period in 2001 because of iguana incursions on the runways (Engeman et al., 2005b). The size and abundance of these lizards make them an important airstrike hazard in San Juan and of potential importance at airports in other parts of their introduced range (Engeman et al., 2005b).

Scientific Loss

The irreversible damage that alien invasions can cause is not limited to ecological and economic impacts but includes epistemological loss as well. Information lost can include knowledge of original range for a species, evolutionary status of populations, and ecological relationships within invaded regions. Such knowledge loss can have practical importance for conservation efforts.

Rampant introduction of reptile and amphibian species has resulted in many species being cryptogenic; that is, the distinction between their native vs. introduced ranges is obscure or totally unknown (Carlton, 1996). The term was originally coined in the context of marine species, many of which have presumably hitchhiked on the bottoms of ships for thousands of years, resulting in complete uncertainty about the extent of their original ranges. However, among reptiles and amphibians many examples exist too, and most are derived from introductions made prior to the historically recent period of scientific documentation. It is almost certain that the set of lizards (*Gehyra mutilata*, *G. oceanica*, *Hemidactylus garnotii*, *Hemiphyllodactylus typus*, *Lepidodactylus lugubris*, *Nactus pelagicus*, *Cryptoblepharus poecilopleurus*, *Emoia cyanura*, *E. impar*, *Lipinia noctua*) that occurs throughout most of the Pacific islands has been introduced by humans through at least part of this region during the past two millennia. However, we do not yet know in most cases exactly where they were introduced; we know in none of these cases where exactly their native ranges lie. To discriminate among the two, detailed molecular studies using a variety of sensitive markers and comprehensive geographical sampling need to be done; to date, these are lacking. So, it remains virtually certain that much of the currently occupied ranges of these species are due to human introductions (e.g., Moritz, 1987; Beckon, 1992; Moritiz et al., 1993; Fisher, 1997; Austin, 1999; Ineich, 1999), but details are opaque.

Identical problems hold in many other regions. In the Caribbean, which islands were occupied by *Eleutherodactylus johnstonei*, *E. martinicensis*, *Geochelone carbonaria*, and *Iguana iguana* prior to human activities are variously argued about but not known with confidence (Underwood, 1962; Lazell, 1973; Lescure, 1983; Censky, 1988; Corke, 1992; H. Kaiser, 1992, 1997; Breuil, 2002; Powell, 2004). It is uncertain whether the population of *Trachemys decussata* on Grand Cayman is native or introduced by Amerindians (Seidel, 1996). In France, the native range of

Rana ridibunda is obfuscated by recent introductions of allochthonous frogs (Pagano et al., 2003). Paleontological (Alcover and Mayol, 1981) and some biochemical evidence (Hemmer and Kadel, 1980; Hemmer et al., 1981) suggests that few species of reptiles and amphibians occurred on the Balearic Islands until human occupancy and that most of the current herpetofauna there is introduced. Similar results may obtain elsewhere on Mediterranean islands (e.g., Böhme and Wiedl, 1994; Corti et al., 1999; Pascal et al., 2006; but see Vigne et al., 1997 for a counter-example) but have not yet been conclusively demonstrated. In Madagascar, the few species shared with mainland Africa have sometimes been suspected to be introductions; for example, *Kinixys belliana* is argued to be an ancient introduction (Bour, 1978, 1987, 2006). However, Madagascan *Ptychadena mascareniensis* – another species shared with mainland Africa – has recently been shown to be native (Vences et al., 2004a), and *Kinixys* merits similar testing. The lizard *Zonosaurus madagascariensis* on Aldabra and Curieuse in the Seychelles is variously argued to be introduced (Henkel and Schmidt, 1995) or native (Matyot, 2003). The parthenogenic blind snake *Ramphotyphlops braminus* now has a virtually pan-tropical distribution, most likely having travelled with humans for millenia. It's origin is unknown but is likely to be southern Asia, where its presumed closest relatives live (A. Wynn, United States National Museum, personal communication, 2006).

Conversely, the obvious fact that herpetological species are transported by humans has led to a number of uncritical claims for human introduction that have no direct or compelling inferential evidence. For example, C. Lever (2003) asserted without evidence that a variety of lizards native to islands of the central Pacific are alien (see Appendix B). Brown and Alcala (1970) provided a list of 23 reptiles and amphibians that they asserted were non-native to the Philippines, and Iskandar and Tjan (1996) did the same for 19 species of reptiles and amphibians on Sulawesi, an assertion repeated by Inger and Voris (2001). But these claims were based solely on distributional evidence and ability to thrive in human-disturbed habitats (Brown and Alcala) or distributional impressions on an imperfectly studied island (Iskandar and Tjan). In the latter case, the authors acknowledged that some of their records could be nothing more than cases of mistaken provenance. Prior belief that the endemic *Indotestudo forstenii* of Sulawesi was also a human introduction (Pritchard, 1979; Groombridge, 1982; Hoogmoed and Crumly, 1984; Iskandar, 2000) has been shown to be false (Iverson et al., 2001), so such assertions should be viewed (and made) with caution. Nonetheless, these claims, though not yet compelling, do highlight the potentially significant complement of cryptogenic species within a wide array of insular herpetofaunas. Some of these hypotheses of human-mediated origins are potentially testable by investigation of patterns of genetic variation, but that need not always be the case, and some cryptogenic species will undoubtedly remain lost to scientific understanding.

Taxonomic clarity too can suffer from alien reptile introductions, as indicated by the case of *Anolis distichus* in Florida discussed earlier. In that instance, taxonomic distinctiveness of a possibly native lineage was obliterated by genetic introgression of foreign genomes, and it is now likely impossible to determine whether *A. d. floridanus* was truly a native Floridian element or an older introduction. Turtles provide equally instructive examples. Bahaman turtles of the genus *Trachemys* have apparently not been native members of the fauna of the Great Bahama Bank in recent times but may have been in the Pleistocene (Seidel, 1988, 1996). Until recently, turtles from Cat Island and Eleuthera on this bank have been treated as an endemic species and considered highly endangered (Groombridge, 1982). More recently, they have been shown to be conspecific with the Jamaican species *T. terrapin* and are presumed to be introduced (Seidel and Adkins, 1987; Seidel, 1988). However, Lee and Ross (2001) argue alternatively that *T. terrapin* is native to the Great Bahama Bank and prehistorically introduced to Jamaica. Taxonomic confusion about Caribbean *Trachemys* persisted for many years because morphological variability within the genus had been difficult to assess. This was worsened in the Bahamas by introduced *Trachemys* species creating hybrid swarms, resulting in additional phenotypic confusion (D.G. Campbell, 1978; Groombridge, 1982; Seidel and Adkins, 1987; Seidel, 1988). Foreign *Trachemys* species introduced to the Bahamas include *T. stejnegeri* (Seidel, 1988), *T. terrapin* (Seidel, 1988), *T. decussata* (Lee, 2004), and *T. scripta* (Lee and Ross, 2001; Mealey et al., 2002; Lee, 2004), and some of these introductions continue to be made (Mealey et al., 2002; Lee, 2004). Because of this history of human intervention, taxonomic resolution of Bahaman *Trachemys* was delayed until populations on the Great Bahama Bank were very small. The result is that, without clearer historical resolution of directionality of movement for *T. terrapin*, it remains uncertain whether Bahaman populations are endangered native elements or foreign interlopers, although the latter presently seems more likely.

Similar problems plague understanding of the giant tortoises of the granitic Seychelles. It is clear that one or more species of tortoise was native to these islands inasmuch as they were noted to be common when the islands were discovered (Stoddart and Peake, 1979). However, these original populations were exterminated, and tortoises from Aldabra were later imported in large numbers. Modern giant tortoises from the granitic Seychelles can have a diversity of shapes (Bour, 1984c), which has led some to treat them as separate species (Gerlach and Canning, 1998), but molecular evidence shows them to be identical or virtually identical to each other and to Aldabran tortoises (Austin et al., 2003; Palkovacs et al., 2003; Karanth et al., 2005). In the absence of DNA evidence from subfossil specimens that unequivocally pre-date human settlement, it remains unknown whether the species that is now restricted to Aldabra naturally occupied the granitic islands or whether those islands contained only extinct endemic species. So, it remains uncertain whether the numerous introductions of Aldabran tortoises to the granitic Seychelles represent instances of reintroduction of a native species or introduction of an alien, although I have conservatively treated them herein as the latter.

It is clear from these examples that loss or muddling of taxonomic or distributional knowledge can have practical ramifications for conservation above and beyond merely reducing the total fund of human knowledge. Another example is provided by the pool frog, *Rana lessonae*, known to be introduced into Great Britain several times since the mid-1700s. It has long been thought that all populations within Great Britain originated from such introductions, but recent evidence has confirmed that a few populations (now all extinct) were native and unrelated to the lineages from which introduced animals were descended (Gleed-Owen, 2000; Zeisset and Beebee, 2001; Wycherly et al., 2002; Beebee et al., 2005; Snell et al., 2005). Without the introductions, the species would likely have been recognized as a native element of the British fauna sooner, perhaps in time to prevent its extirpation there. Similar problems hold in the case of *Iguana iguana* and *I. delicatissima*. The former is widespread across tropical America and parts of the Lesser Antilles; the latter is endemic to some of the Lesser Antilles. The native range of *I. iguana* in the Antilles is uncertain, but some populations are certainly introduced (Lazell, 1973; Lescure, 1983; Breuil, 2002). On Guadeloupe and the adjacent Îles des Saintes, the two species have been hybridizing, with *I. delicatissima* populations disappearing in the process (Day and Thorpe, 1996; Day et al., 2000; Breuil, 2000a, b, 2002). Clearer knowledge of the native range of *I. iguana* might have generated concern for a possible introduction and instigated mitigative measures to avert this loss, but such data were and remain lacking.

Other scientific losses occasioned by herpetological introductions are widely recognized, even as they remain largely undiscussed. Primary among these is that the original ecological dynamics in unique regions or habitats heavily invaded by alien reptiles and amphibians are likely to never be understood. The cascade of effects attendant upon introduction of *Boiga irregularis* to Guam (Fritts and Rodda, 1998) well illustrates the loss of understanding of original ecological dynamics that can occur subsequent to an invasion. Similar epistemological effects certainly apply to regions already heavily invaded by alien reptiles and amphibians, such as southern Florida, Hawaii, and Okinawa, and they likely occur even in areas having only a single significant herpetological introduction, such as the Ogasawara Islands. It is reasonable to expect this loss of scientific knowledge to be common even though it typically goes unremarked. In a broader sense, because much of ecology involves understanding spatial and temporal scales of disturbance regimes and the ecological patterns thereby derived, when an area becomes overwhelmed by alien introductions, the ecological dynamics and patterns due to other disturbance regimes are liable to be masked and less accessible to understanding. These problems, of course, are compounded in places like Hawaii or the Mascarene Islands where massive introduction regimes are superimposed upon large numbers of native-species extinctions.

One final epistemological loss extends far beyond the realm of science and its application. It is widely noted that modern humans are becoming increasingly alienated from nature, concomitant with increased concentration of human populations in urban areas far from any sustained contact with nature. This alienation can make it difficult to gain public acceptance for biologically sensible conservation-management decisions because large segments of society are cognitively divorced from the biological realities upon which their lives are based. One way in which this problem is worsened is by introduction of alien species, which, because of their frequent abundance, will often be unthinkingly accepted by most people as "normal", implicitly interpreted to mean "native". This has practical implications for native plants and wildlife by making needed control of invasive aliens harder for an uninformed public to accept, sometimes leading to unnecessary opposition to alien-species control programs needed to prevent extinctions of native species. I am unaware of any studies to quantify the effects of this particular form of social ignorance upon policy or managerial decisions, but the impression for many actively involved in management of invasive species is that it often leads to significant problems.

Conclusions

As the survey above indicates, a wide variety of negative impacts has been shown to attend the introduction of alien reptiles and amphibians – impacts that mirror many of those seen in better-studied groups like mammals. Despite this diversity, it is important to note that only a small subset of naturalized species or populations has received any form of impact study. Hence, while at least 322 species of reptiles and amphibians have been naturalized across the globe, only 14 species have had ecological impacts demonstrated or reasonably inferred (Table 3.2). Of these, only three species (*Boiga irregularis*, *Bufo marinus*, and *Rana catesbeiana*) could be said to be even moderately well studied; most of the remainder have had impacts demonstrated in only one or a few studies of limited scope. Similarly, evolutionary impacts have been demonstrated or implied for 17 species. Most of these involve instances of hybridization with native relatives. Although not all instances of hybridization have been demonstrated to have importance at the population level, several clearly do. Lastly, economic or health impacts on humans have been demonstrated (n = 4) or implied but not compellingly proven (n = 2) for six species. In total, excluding instances of epistemological loss of knowledge, which are currently too numerous and uncertain to quantify, 26 species of reptiles and amphibians are demonstrated to have caused or are credibly implicated in ecological, evolutionary, economic, or health effects on native wildlife or humans (Table 3.2).

It could be argued that this small number reflects the fact that alien reptiles and amphibians are largely innocuous and warrant ignoring. That is possible, but it is neither a scientifically cautious nor compelling interpretation. More likely, this modest number reflects widespread inattention to impact phenomena among reptiles and amphibians and the difficulty of convincingly demonstrating them. Consistent with that interpretation is that the large majority of articles cited above have been published in the past 20 years and that such studies are dramatically increasing in frequency (Fig. 3.1). Most of the earlier studies recorded in Fig. 3.1 are merely anecdotal references; experimental studies didn’t begin until the 1970s. Further, the species demonstrably or likely causing impacts for which dates of introduction can be estimated (this excludes several more ancient introductions of undetermined age) were introduced from 20–175 years ago, with an average introduction date of 62 years ago. Since approximately two-thirds of all herpetofaunal introductions have occurred in the past 60 years, the lag in scientific study alone suggests that a considerably larger pool of impacts will eventually emerge. This

Table 3.2 Impacts reported for alien reptiles and amphibians, excluding species reported to affect only other aliens. Only a few examples of taxa involved in loss of scientific understanding are listed because of the large and uncertain size of this cohort

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

will be even truer if lag phenomena among the naturalized populations themselves should prove common. So it seems likely that instances of ecological, evolutionary, health, and economic impacts from herpetological introductions will multiply as additional alien populations expand and become studied. This is further suggested

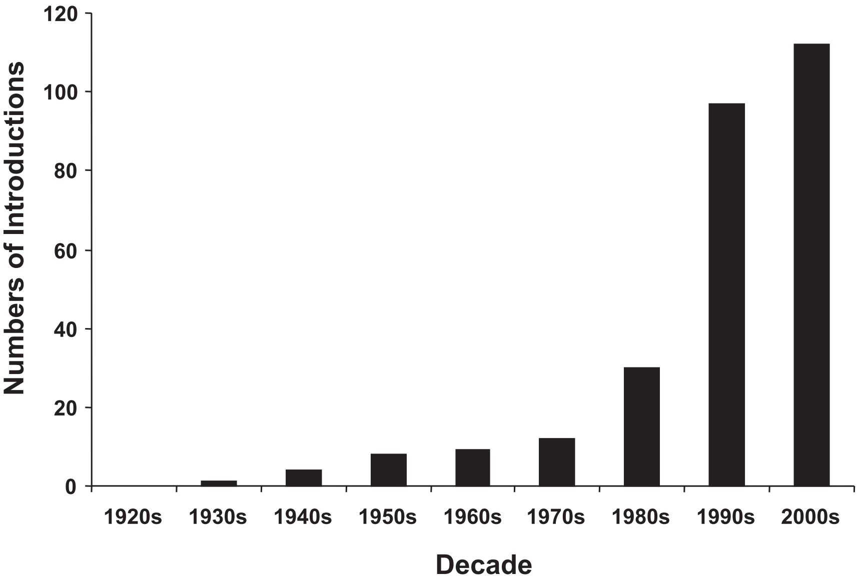

Fig. 3.1 Growth in number of scientific studies that treat the ecological and evolutionary impacts of alien reptiles and amphibians

by the large number of literature claims not surveyed here that purport, but do not document, the decline of native species of herpetofauna coincident with the advent of alien forms.

The late genesis of these impact studies is problematic in another way. The absence of such studies seems sometimes to have been interpreted as demonstrating the absence of impacts, especially when combined with the absence of obvious effects upon casual inspection – effects that we've grown to expect to be obvious because they are apparent for many plant, mammal, insect, or forest-pathogen invasions. The problem is that impacts caused by invasive herpetofauna are usually not obvious, even to trained biologists. Instead, they have proven to be subtle and difficult to discern without careful study. This form of denial was perhaps most apparent in the case of the brown treesnake – a species now widely viewed as the poster child for invasive herpetofauna, but which was vehemently denied as having any role in Guam's bird declines until years of careful research (Savidge, 1987a; Savidge et al., 1992) demonstrated that position to be baseless. But earlier claims for the neutral effect of Florida's alien herpetofauna (L.D. Wilson and Porras, 1983; Butterfield et al., 1997) – claims repeated for other jurisdictions too (e.g., McKeown, 1996) – also seem to reflect this pattern of reasoning. In raising this issue, I in no way intend to argue that most herpetological introductions do or will impose damaging impacts. I simply don't know whether that's true or not; insufficient data have been gathered to allow for generalizations. But I will argue that the diversity of evidence provided above shows herpetological invasions cause or are likely to cause far more damage than they have hitherto been credited with. Moreover, I suggest this evidence is sufficient to justify a precautionary approach with respect to further herpetological introductions, thereby meriting the devotion of greater management attention to this phenomenon. I proceed from this conclusion to now inquire what management actions have been taken in response to these invasions.