Chapter 1
Background to Invasive Reptiles and Amphibians

Concern about invasive alien species is a relatively new phenomenon that can be dated to the work of Charles Elton, the ecologist who provided the first thorough scrutiny of the topic. Elton (1958) demonstrated the severe ecological and human-health impacts that invasive alien species can cause. Since then, the number of introduced species has skyrocketed, and examples are now available to illustrate a much larger array of resulting damages. The spatial scale of ecological harm resulting from alien invasions also continues to grow because virtually all environments heavily impacted by humans are now dominated by alien species. Many "natural" areas are also increasingly subject to alien invasion.

Scientific interest began to gather momentum in the 1980s, spurred by the publication of several edited books on this topic (Groves and Burdon, 1986; Mooney and Drake, 1986; Drake et al., 1989). Many scientific (e.g., M. Williamson, 1996; Mooney and Hobbs, 2000; Perrings et al., 2000; McNeely, 2001; Mooney et al., 2005; Nentwig, 2007) and popular (e.g., Bright, 1998; Devine, 1998; G.W. Cox, 1999; Low, 1999; Van Driesche and Van Driesche, 2000; Baskin, 2002) books on the issue have appeared as concern with the impacts of alien species became more widespread. A journal specifically devoted to the topic of biological invasions was founded in 1999, and the field is increasingly replete with scientific studies addressing the dynamics and ecological processes of invasion. There is also a recent spate of books treating either specific aspects of the invasive-species problem or summarizing the status of the topic in particular geographic regions. In short, the topic is now well established in the scientific mainstream, is attracting concerned attention among a wider public, and is increasingly recognized as one of the premier environmental challenges of the new century.

In order to provide context and background information for considering the phenomenon of invasiveness in reptiles and amphibians, this chapter presents a brief introduction to invasive-species biology.

What Is an Invasive Species?

Terminology regarding invasive species has proliferated and changed through the years, and a potentially confusing array of descriptors is available (Davis and Thompson, 2000; Richardson et al., 2000a; Daehler, 2001). I use the term "alien

F. Kraus, *Alien Reptiles and Amphibians*,

species" to refer to those species transported and released outside their native ranges by the activities of humans, whether done intentionally or not. The movement of such a species by humans is referred to as an "introduction". Not all introduced species become established, but many do. Such established populations are often referred to as "alien", "naturalized", "non-native", "non-indigenous", "feral", or "exotic", but I will confine myself to the first two terms.

Human-mediated dispersal of species is not necessarily a *qualitatively* different phenomenon than dispersal by other means, such as attaching to a bear's fur or a waterbird's foot. However, the temporal and spatial scales at which humans are homogenizing the world's biota are of a far greater magnitude than previously seen in Earth's history. As one example, Loope (1998) estimated that prior to human arrival, the rate of new species establishment in the Hawaiian Islands was approximately 1 species/35,000 years. Now it is on the order of 20–30 species/year (Beardsley, 1962, 1979; Miller and Holt, 1992), an approximately million-fold rate increase. Similar changes have occurred on other oceanic islands and in marine and freshwater systems (Ricciardi, 2007), although with perhaps not so extreme a rate increase as in Hawaii. Establishment rates on continents seem to be lower but are already far above historical rates and appear to be increasing. From a spatial perspective, species are now being mixed among continents that have not been connected for 250 million years. As well, species having limited mobility – such that they would not previously travel even to locations a short distance away – are now spread around the world by human activity. This overwhelming increase in rate and areal extent of alien-species introductions has had profound effects on native species and ecosystems throughout the globe. Hence, restricting use of the term "alien" to those species introduced by humans provides a very practical distinction for scientific and management purposes.

Invasive species are that subset of alien species having a demonstrated negative effect on native ecosystems, species, or human values and concerns. Invasive species are often referred to as either "weeds" or "pests" as well, and if impacts are largely incurred by natural ecosystems the species may be termed an "environmental pest". The distinction between alien and invasive species may be made clearer by a few examples. Corn (*Zea mays*) is an alien species everywhere on Earth outside of southern Mexico, but it is invasive nowhere because it fails to establish outside the artificial ecological conditions imposed by agriculture. Many alien species – including most important crop species – are like this, growing only where deliberately planted, or living in sparse numbers in the wild, to all appearances having no deleterious effects on native or human ecosystems. But invasive aliens – such as brown treesnakes, gypsy moths, cheatgrass, or bubonic plague – are another matter entirely. They spread throughout areas to which they are introduced and cause tremendous harm to wildlife, agriculture, or human health. Escaping one or more forms of ecological constraint allows them to achieve unregulated population growth, forming the ecological equivalent to cancerous cell proliferation within an organism. The process by which an alien species establishes, expands its geographic range and numbers, and exerts ecological or economic impacts in a new locality is referred to as "invasion".

Invasive species are usually thought to comprise a relatively modest subset of all alien species (Williamson and Fitter, 1996), but this conclusion bears two important caveats. First, this view may partly reflect our limited anthropocentric perspective, and it is certainly a function of the degree to which we have attempted to identify invasives. When investigated from the standpoint of impacts on other species, such as native insects, it may turn out that far more alien species have negative ecological effects than we currently appreciate and should be viewed as invasive pests. Hence, our impression of the percentage of alien species formed by invasive pests may rise with passing time and increased research effort, as suggested by recent findings indicating higher rates of establishment (Kraus, 2003c) and spread (Jeschke and Strayer, 2005) among animals than earlier predicted (Williamson and Fitter, 1996). Second, although most pests prove invasive in many or most areas where introduced, some species prove invasive or pestiferous in only one a few localities but appear harmless in most areas where introduced. There are a number of examples of this phenomenon, such as the traveller's palm, *Ravenala madagascariensis*, that is widely and benignly planted throughout the tropics but has become an invasive pest in the Mascarene Islands (Cronk and Fuller, 1995). Consequently, one must be careful in extrapolating from an observation of non-invasiveness in one locality to infer safety in other areas. Because of our imperfect knowledge of the ecological consequences of mixing biotas, caution is required in asserting that any alien species poses no hazard. Prudence and expanding scientific understanding both dictate that the burden of proof lies on those who would argue than an introduction is harmless. This has practical consequences for designing effective management responses for invasive species, a point that will be discussed at greater length in the final chapter.

Two Misconceptions

One sometimes hears claims that the introduction of alien species is a normal, if not always positive, phenomenon that does not merit concern. One such argument is that introducing alien species serves to increase biological diversity (or "biodiversity") within a region. Because establishment of an alien species increases the total number of species – naively thought to equate to biodiversity – alien species are good, the argument goes. This argument is fallacious for two reasons. First, biodiversity is not measured as just the summary number of species in an area but also includes some measure of the relative abundances of the assembled species. Diversity is not enhanced when one species dominates over everyone else. If many (native) species are present but rare and one (invasive) is supremely common, biodiversity is relatively low, even if the number of species is one greater than it was prior to the invasion. This is exactly how invasive species tend to behave, so they frequently decrease biodiversity. Secondly, the scale at which biodiversity is measured is crucial. In particular, one must carefully distinguish among diversity measures at different geographical scales. Obviously, increasingly larger regions contain greater biodiversity than do any of their smaller, constituent subregions. My backyard in Honolulu is not very diverse; Honolulu is somewhat more diverse; the island of Oahu is yet more diverse; the entire chain of Hawaiian Islands is still more diverse; the Pacific Basin is yet more diverse; and the entire world is the most diverse. Different processes are involved in generating diversity at different geographic scales (Sax and Gaines, 2003), and this can potentially confuse discussion of biodiversity. In speaking of recent concerns for biodiversity protection, we are speaking of preserving diversity at the largest scale – that is, ensuring that the sum total of diversity on the entire planet is not diminished. Conceptually, this is a simple matter of ensuring that species extinction does not occur. Hawaii has many species unique to that archipelago. If we artificially inflate species numbers by importing alien species that cause the extinction of Hawaii's unique species, we may have boosted species numbers within Hawaii but at the cost of the global total. Replacement of globally unique elements by artificial inflation of regional species numbers with widespread aliens is not a service to biodiversity, but rather the converse: it decreases biological diversity. And indeed, introduced species are among the major drivers of biotic homogenization, the process by which formerly distinct biotas are beginning to look more and more alike (McKinney and Lockwood, 1999).

One also frequently hears the argument that species movements are "natural" and that concern about alien species is, therefore, unjustified. This claim too is specious. For the term "natural" to apply in any scientifically meaningful way it must refer to a phenomenon occurring at background ecological temporal (the rate at which a phenomenon occurs) and spatial (geographic) scales. As I have mentioned earlier, introduction rates in Hawaii are now approximately one million times as frequent as the natural, background rate. Similar high rate increases have been measured for other regions too (Ricciardi, 2007). The geographical reach of species transport by humans also extends far beyond what the organisms could have achieved under natural processes. To give just one example, there is no way that chameleons – ponderous arboreal lizards native to Africa and western Asia – could possibly have colonized places as remote as Hawaii or California under their own power. The geographical barriers that helped give rise to the tremendous and regionally unique biological diversity across Earth are proving ineffectual in the face of human modes of transport such as ships and planes. Moreover, the number of species and individuals moved during each introduction event is often now much larger than could have occurred under natural conditions (Ricciardi, 2007). For example, a single load of ballast water may dump millions of individuals of hundreds of species, a form of dispersal unparalleled in pre-human history. In short, there is nothing remotely natural about the tempo and extent of modern biological mixing by human action.

Another variant of this argument is to posit that because humans are a part of the natural world, anything we do is also natural and, hence, no cause for worry. Under this reasoning, our transport of alien species is natural and we shouldn't be overly concerned with it. Of course, by that same logic, genocide, torture, and slavery are natural too. I doubt that most readers would find these other human actions compellingly justified by so cavalier an argument. So it is with alien species. There is nothing remotely natural about the Homogocene, and arguments that pretend that this is the case are contrary to the evidence. Consequently, this book is written from the viewpoint that alien invasions – including those by reptiles and amphibians – are a serious ecological threat that demands attention and remediation.

The Invasion Process

In the past 20 years or so considerable scientific attention has been directed to understanding invasive species biology and how a species becomes invasive. Conceptually, the invasion process involves three stages: transport and release of the organism to a novel geographic area, establishment of a population in the new area, and expansion of the original population to fill ecological space beyond its point of entry. The biological and social factors that favor success in any one of these steps may not be the same as those favoring success in others (cf. Duncan et al., 2003). For example, successful transport may rely on the ability of a species to survive food deprivation for long periods or to tolerate harsh environmental conditions. Some perceived human benefit from the species, of course, also weighs heavily in the choice of those species that are deliberately introduced. Once arrived in the new habitat, population establishment requires that the climate be survivable, that appropriate food be available, and that reproduction be possible. Once established, rapid expansion may rely on access to food sources underutilized by native species, ability to avoid resident predators, or absence of debilitating disease organisms. As a consequence of these varied requirements, many organisms may fail to survive transport, those that do may fail to establish populations, and many that initially establish populations may fail to persist or to expand their ranges. To understand invasions, then, requires knowledge of how all three stages in the process are successfully negotiated by the invading species.

Transport

A host of pathways serves to introduce alien species to new environments. Unintentional introductions largely result from species hitch-hiking rides in cargo or on the vehicles used in transport. Examples include brown treesnakes (*Boiga irregularis*) being transported in wheel wells of aircraft, geckos stowing away in a variety of cargo shipments or the containers used to package cargo, plankton moved in the ballast water of ships, sessile marine invertebrates riding on the hulls of ships, and insects infesting grain shipments. Also included in this category are disease-causing agents moving about on infected humans (e.g., AIDS, malaria), their domesticated animals (e.g., rinderpest, avian influenza), or other vectors (e.g., dengue in mosquitoes travelling in used tires, cholera travelling in ballast water).

Intentional introductions occur primarily because a species is perceived to provide an amenity or use value to humans. Under this category fall introductions for use as pet animals, furs, human or livestock food, horticulture, and biocontrol of pests. Included as well are introductions and releases undertaken by individuals simply because they like a particular species and wish to be able to see it in their surroundings. As a rule, some taxonomic groups, such as marine invertebrates, insects, and landsnails are largely dispersed via unintentional pathways. Others, primarily plants, fish, birds, and mammals have largely been intentionally dispersed by humans. As I will demonstrate later, reptiles and amphibians are somewhat unusual in that they are transported via a diversity of intentional and unintentional pathways.

In considering intentional introductions, human selectivity ensures that those species introduced do not represent a random selection of all available species. Instead, species chosen for introduction can be biased taxonomically, geographically, and in having particular characteristics such as large body size, tasty flesh, or large population sizes (Blackburn and Duncan, 2001a; Duncan et al., 2003). In addition, they are often especially hardy, an attribute of obvious importance if a species is to be used for a purpose. Although this is intuitively obvious, the phenomenon has been quantified for few taxa. Recipient areas can also vary in being primarily islands (Blackburn and Duncan, 2001a; Kraus, 2003c) or continents (Kraus, 2003c), depending on the taxon in question.

Establishment

The naturalization process – the means by which a species establishes a reproducing population once transported to a new region – is not yet understood in great detail. Ideally, we would like to be able to learn enough to predict with reasonable certainty how likely a particular alien species is to naturalize in a particular area should it be introduced. But the particularities of both species and location that may be involved in any given introduction make generalization across all introductions difficult. This is because establishment success results from the interaction of the singular combination of biotic and abiotic needs of a species with the particular set of environmental conditions at the receiving location. Ideally, ability to predict naturalization success would allow us to prohibit importation of species deemed at high risk of establishment. Although we have not yet reached that point, several important generalities are becoming apparent.

First, it is important that the newly attained region provide a favorable environment. Logically, the climate must be sufficiently similar to that in the native range that a species' physiological tolerance is not exceeded. Consequently, climate matching has repeatedly been found to be an important predictor of establishment success (Blackburn and Duncan, 2001b; Duncan et al., 2001, 2003; Bomford and Glover, 2004; Forsyth et al., 2004; Hayes and Barry, 2008). The importance of climate is sufficiently uncontroversial that modeling an alien species' anticipated potential range based on matching climatic variables from its native range is increasingly common (e.g., Peterson and Vieglais, 2001; Thuiller et al., 2005; Ficetola et al., 2007a). Second, the alien must have sufficient resources available to complete its life cycle. At a minimum, this means sufficient food, living space, habitat for growth and reproduction, and whatever other biotic factors, such as pollinators, may be required. This is thought to be made easier if the intruder possesses adaptive features lacking in the biota of its newly inhabited range, thus allowing it to pursue its way of life unhindered by close competition. Third, favorability of the introduced range may also be increased by the absence of predators, parasites, and disease organisms from the alien's native range. Leaving these enemies behind often gives an alien species a considerable competitive advantage over the natives it meets in its new home.

It is also clear that propagule pressure – the number of individuals released into a new area – is an important determinant of successful establishment. Those species that have been released more often, at more sites, or in greater numbers tend to establish more successfully than those that do not (M. Williamson, 1996, 1999; Duncan et al., 2001, 2003; Forsyth and Duncan, 2001; Kolar and Lodge, 2001; Bomford and Glover, 2004; Forsyth et al., 2004; Lockwood et al., 2005; Rejmánek et al., 2005; Caley and Kuhnert, 2006; Jeschke and Strayer, 2006; Hayes and Barry, 2008), although it can take many introductions to make this pattern statistically apparent (e.g., Ruesink, 2005; Bomford et al., in press). The larger the number of individuals released at a given site, the lower the chance of stochastic extinction (extinction due to bad luck randomly happening to strike all released individuals). Similarly, releases at more sites increase the odds that at least one population will survive by effectively sampling the environment for habitat most suitable to the introduced alien. Finally, a larger number of independent releases will likely sample a greater representation of genetic diversity from within the introduced species, providing greater genetic and (potentially) phenotypic variation with which to meet the ecological and evolutionary challenges of the new environment (Lockwood et al., 2005).

Unsurprisingly, life-history and behavioral characteristics of the introduced species can be important in determining establishing success (Reichard and Hamilton, 1997; Sol and Lefebvre, 2000; Duncan et al., 2001; Kolar and Lodge, 2001, 2002; Cassey, 2002; Cassey et al., 2004; Forsyth et al., 2004; Rejmánek et al., 2005; Ruesink, 2005; Jeschke and Strayer, 2006; Thuiller et al., 2006; Hayes and Barry, 2008). Such attributes vary among taxa and may even vary within the same taxon, either because different genotypic samples are involved or because different environments may induce different phenotypic effects. This idiosyncrasy again limits the taxonomic scope across which we may identify biological traits predictive of establishment success. This makes attaining useful generalizations for a broad array of taxa a laborious undertaking.

One of the most useful predictors of establishment success is whether a species has already successfully established somewhere else (Reichard and Hamilton, 1997; M. Williamson, 1999; Duncan et al., 2001; Forsyth et al., 2004; Caley and Kuhnert, 2006; Hayes and Barry, 2008). This is obviously not a very refined tool for predictive use. It doesn't carefully discriminate among introductions to different habitats, and it is useless for all those species not yet transported by humans. One consequence of our limited predictive abilities is that practical governmental efforts to assess risk from alien species may focus on the hazards a species poses, rather than the likelihood of its establishment or spread (e.g., Bomford, 2003).

Interestingly, the extent to which the recipient location has already been invaded by other species can impinge on establishment success of new arrivals. Earlier invasions may synergistically facilitate the success of later invasions – and thereby magnify impacts on native ecosystems – in a process referred to as "invasional meltdown" (Simberloff and Von Holle, 1999). This occurs when earlier invaders provide resources – in the form of food, nutrients, pollination services, mycorrhizal associations, seed dispersal, or habitat – critical to the successful survival of later-arriving aliens. For example, the blind snake, *Ramphotyphlops braminus*, could not have survived introduction to Hawaii without its alien food sources (ants, termites) being introduced first. In this instance, the snake is ecologically benign, but many facilitated introductions are not. Facilitation frequently takes the form of acquisition of novel mutualisms among species (Simberloff and Von Holle, 1999; Richardson et al., 2000b), but it may also be effected by alterations of habitats, resource-supply rates, or disturbance regimes (Simberloff and Von Holle, 1999; Richardson et al., 2000b; Ricciardi, 2005) or by protection from predators or competitors (O'Dowd et al., 2003; Grosholz, 2005). These mutualisms may re-unite species that co-evolved together and were independently transported to the new location, but more often they involve generalists that can successfully form mutualistic pairings with a wide array of potential partners (Richardson et al., 2000b). Moreover, an alien may successfully establish but not become invasive until a facilitator species is later introduced (cf. Grosholz, 2005). The importance of invasional meltdown is that it provides a positive-feedback loop that makes recipient habitats more prone to additional invasions, accelerates the accumulation rate of alien species, and magnifies impacts. This phenomenon makes invasion and ecological disturbance more likely to occur over time, raising the concern that the rate of establishment, as well as the magnitude of impacts, may be increasing. It also makes predicting the impacts of any particular introduction more difficult.

We may also assess establishment success from a broader, community-level perspective. In this case, alien species richness (number of naturalized alien species) has been correlated with a variety of factors in an attempt to identify whether particular areas or habitat types are more prone to alien invasion. Regional richness in alien species has been correlated with human population numbers, land area, disturbance, and native-species richness, and these may vary in importance across spatial scales (Lonsdale, 1999; McKinney, 2001; Sax, 2002). With respect to human population, temporal growth in numbers of naturalized aliens has been correlated with increasing human population (Mauchamp, 1997; K.G. Smith, 2006a), and spatial variation in species richness has been correlated with variation in human population numbers (McKinney, 2001, 2002; Espinosa-Garcia et al., 2004; Gido et al., 2004). Many of these correlations are not ecologically surprising. Increasing land area should generally lead to increased species numbers because larger areas tend to hold greater habitat diversity, which will itself be correlated with increased numbers of native species. Disturbance is well known to facilitate establishment and spread of many alien species, and it too is correlated with human numbers. While these correlations can often allow us to roughly predict which areas are likely to host increased alien species richness, they are silent with respect to establishment mechanisms and, hence, are not predictive in a manner that can readily be used to prevent individual future naturalizations.

Spread

Naturalized populations can vary tremendously in their ecological dominance, ranging along a continuum from those that barely hang on in small numbers at a single locality to those that spread like wildfire over a large range and become numerically dominant. Obviously, those at the latter end of the spectrum are clearly invasive, those at the former end are not, and opinions would differ about where along the continuum one might divide "invasive" from "non-invasive". We would like to have an understanding of why these differences occur, as that would allow us to predict both the likelihood that any particular species would prove invasive as well as the relative susceptibility of particular locations to invasion.

A variety of hypotheses has been advanced to explain invasion success (reviewed in Hufbauer and Torchin, 2007). Ecological hypotheses include the notions that invaders are preadapted to the new environment, are inherently superior competitors, have novel adaptive mechanisms giving them a competitive edge over natives, have escaped from enemies that limit their population sizes in their native ranges, or interact with other introduced organisms in a positive-feedback loop that promotes population expansion. As well, ecological attributes of the invaded environment may serve to promote or to limit introduced species. In particular, the empty-niche hypothesis suggests that invasive species may use resources ignored or underutilized by natives. Conversely, the biotic-resistance hypothesis posits that natives that are close relatives of introduced species may serve to limit the expansion of the latter via competition or increased likelihood of parasite transferral. As well, invasion may be promoted by genetic changes within the introduced species. Hybridization, either with closely related natives or among populations of the introduced species from disparate parts of its native range, may increase genetic variation and allow for rapid creation of novel genotypes that are better suited to exploiting the new environment. Founder events may create new genotypes with similar ecological effect. Alternatively, the novel environment may impose a novel selective regime that promotes improved competitive ability among the invaders. In particular, release from enemies may allow energy resources that would otherwise be expended on defense to be used instead to promote growth and reproduction. Empirical support for each of these hypotheses is available for one invasion or another, although examinations of the genetic and evolutionary consequences of introductions have barely begun. Compellingly testing the empty-niche and biotic-resistance hypotheses has proven difficult because of the complexity of biotic interactions involved in assessing predictions based on community-level parameters. Unsurprisingly, mechanism importance will vary with the biological particularities of each invading species, so generalizations have been difficult to clearly identify. It is important to recognize too that some of these hypotheses are not mutually exclusive, and the proposed mechanisms may interact with each other synergistically (Blumenthal, 2005; C.E. Mitchell et al., 2006). Attempts to integrate several of these specific hypotheses into more general theoretical frameworks have recently been made (Shea and Chesson, 2002; Facon et al., 2006). These synthetic perspectives provide a variety of specific predictions (C.E. Mitchell et al., 2006; Hufbauer and Torchin, 2007) whose future testing may better explain the diversity of outcomes of species introductions, potentially making identification of high-risk invaders more successful.

The difficulty of testing these ecological and genetic hypotheses has resulted in more attention being directed toward identifying characteristics of the introduced species themselves that might prove predictive of invasiveness. Unsurprisingly, many of the same features important in favoring establishment of species also tend to explain invasiveness, in particular, degree of climate-matching between native and introduced ranges (Duncan et al., 2001; Forsyth et al., 2004; Thuiller et al., 2005), and an assortment of life-history or other biological variables (Pheloung et al., 1999; Duncan et al., 2001; Kolar and Lodge, 2001, 2002; Williams et al., 2002; Daehler et al., 2004; Forsyth et al., 2004; Rejmánek et al., 2005; Pyšek and Richardson, 2007). As with predicting establishment, however, it is clear that generalities will not obtain across all taxa (Hayes and Barry, 2008).

It is easy to misinterpret the status of an alien population in its early stages of spread. A species ultimately recognized as invasive can often appear non-invasive at that time. Few individuals are encountered, and population growth and spread can be difficult to detect during this “lag-phase”, when population sizes are doubling but appear quiescent because of low total numbers. Slow doubling rates, which are typically associated with slow maturation rates and long life spans, can make a species appear non-invasive for one or more human lifetimes. Because it is difficult to perceive the growth pattern without explicit measurement and quantification, complacency about such a species can be easy. Consequently, management responses are frequently delayed until the invasion is logistically difficult or impossible to stop. This has the practical effect that many alien invasions become managerially dichotomized into two stages: (1) “it’s not a problem”, and (2) “it’s too late to do anything”. The middle ground of the lag phase, when human control activities could prove most effective, is often squandered because we are maladept at recognizing it. This seriously undermines efforts to meaningfully control many invasive species and has been a frequent problem for herpetological invasions (see Chapter 4).

An invasion will progress more rapidly if it involves many separate populations rather than only a single one (Moody and Mack, 1988; Mack and Moody, 1992). This can occur either because a species is introduced independently to multiple localities or because a single invasive population further expands to multiple sites with human help. As multiple populations become established, each expands at (relatively) the same rate, making total rate of new range expansion proportional to the number of populations. This has tremendous practical implications for controlling invasive species. When tackling an invasion, managers often deem it best to attack the largest population(s) first. Instead, modelling indicates that limiting the number of new localities infested and eliminating small satellite populations should be higher priorities (Moody and Mack, 1988).

Impacts

It would probably be fair to say that greatest research progress in the past 20 years has been had in a broader elucidation of the numerous impacts that invasive alien species can impose. These impacts are remarkably variable and include extinctions of species, biotic homogenization, disruptions to food-webs, changes to primary productivity of ecosystems, changes in soil formation, alterations of community structure, wholesale conversion or replacement of ecosystems, changes in nutrient-cycling dynamics, collapse of fisheries, degradation of watersheds, promotion of increased fire frequency and extent, increases in erosion and flooding rates, losses to agriculture, damage to human structures, disease epidemics, and degradation of human quality of life (Greenway, 1967; Ebenhard, 1988; van Wilgen et al., 1996; Wilcove et al., 1998; Mack et al., 2000; Pimentel et al., 2000, 2005; Mooney and Cleland, 2001; Pimentel, 2002; Mooney, 2005; Towns et al., 2006; Binimelis et al., 2007; Charles and Dukes, 2007; Reaser et al., 2007). Examples of these impacts are too many to enumerate but can be found by the score in the articles just cited or in the scientific and popular books cited at the beginning of this chapter. Hence, I will not discuss this issue in detail but will merely give one brief example from the non-herpetological literature to illustrate both the novelty, unpredictability, and damage that are so frequently wedded in invasion biology.

The comb jelly, *Mnemiopsis leidyi*, a zooplankton feeder native to western Atlantic estuaries, was introduced to the Black Sea around 1982. It quickly formed extremely dense (1.5–2 kg/m^2) biomass, and zooplankton communities declined 15–40 fold (Kideys, 1994). As a result of jelly predation on their food and fry, anchovies (*Engraulis encrasicolus*) and other planktivorous fish species declined dramatically, with fisheries collapsing by 4–40 fold, depending on the fish species and country (Kideys, 1994, 2002; M. Williamson, 1996). Anchovies and other fisheries had been an important source of human protein for communities around the Black Sea, so it is not difficult to imagine the economic hardship and decline in quality of life occasioned by this introduction. It is estimated that fisheries profits declined from US$17 million/year before the invasion to US$0.3 million afterwards (Knowler and Barbier, 2000). This cost does not include the estimated several thousand lost jobs as well as secondary effects on economically linked enterprises (Knowler and Barbier, 2000). The jelly population happened to be brought under control a few years later by the inadvertent but fortuitous introduction of a second comb jelly, *Beroe*, which feeds on *Mnemiopsis*. This led to recovery of some ecosystem values and of the anchovy fishery (Kideys, 2002). *Mnemiopsis leidyi* has subsequently been introduced into the Caspian Sea as well, and can be found there in plague proportions at densities >2,000/m^2. Similar ecological and economic damage followed: fisheries losses to Iran alone have exceeded US$125 million (Kideys, 2002; Stone, 2005). Unfortunately, the salinity of the Caspian Sea is insufficient to support healthy populations of *Beroe*, thus the control of *M. leidyi* happily effected in the Black Sea looks unlikely to succeed in the second case.

It is hard to decide with this example which has a stronger grip on the imagination: the novelty or the horror of an obscure invertebrate decimating the Black Sea and Caspian Sea ecosystems. This example is especially instructive because at the time of ballast-water discharge, no one would have predicted that the "mere" comb jelly thus released would lead to such devastating impacts within a few years. A similar unpredictable scenario applied to the introduction of brown treesnakes, *Boiga irregularis*, to Guam. The literature is replete with similar examples where the ecological damage attending an introduction would have been equally impossible to predict. In other cases, negative impacts were perfectly predictable but ignored until too late, such as with the introduction of coqui frogs (*Eleutherodactylus coqui*) to Hawaii or predatory snails (*Euglandina rosea*) and flatworms (*Platydemus manokwari*) around the islands of the Pacific.

Despite an abundance of impacts on humans and their economic activities, economic costs from invasive species have only infrequently been measured, except for some agricultural pests. Economic costs include those resulting from damage, control, research, defensive prevention, and foregone economic opportunities that attend the irreversibility of pest invasions, which is especially difficult to measure (Perrings et al., 2005). Even when economic impacts are recognized, monetary estimates are usually lacking. However, this is beginning to change, and even conservative estimates have found the monetary costs of invasive species to be staggering. As one example, Pimentel et al. (2005) conservatively estimated the total cost of invasive species to the economy of the United States to exceed US$120 billion/year. Proportionately similar costs no doubt apply to many other economies. Such estimates (see Pimentel, 2002; McNeely, 2005; Perrings et al., 2000, 2005; Pimentel et al., 2000, 2005) rarely involve reptiles or amphibians, but what data are available for those taxa are presented in Chapter 3.

The impacts discussed above and emphasized in the literature are all of practical concern to one degree or another, affecting humans directly or affecting the ecosystems that support us and innumerable other species. There is one more impact that I wish to mention that is of less obvious practical import and is virtually ignored in the literature on alien species. This is loss of beauty. That such an aesthetic impact exists might seem counterintuitive inasmuch as introductions via the pet trade and deliberate introductions due to personal fondness for an animal's appearance are so frequent (see Chapter 2). After all, an assortment of lizards, birds, and many other species are lovely, widely kept as pets, and sometimes released for that reason. How could introductions motivated by an appreciation for these animals' beauty lead to loss of beauty? Does this not present us with a paradox?

No. The seeming paradox appears merely by forgetting that the biological world is hierarchically arranged into different levels of organization and that the beauty of individual animals is not the threatened beauty that I am discussing. The introduced animals themselves retain their individual beauty but by wrenching them out of their evolutionary contexts and arbitrarily placing them in a strange land the beauty of that recipient land, its native fauna, and the evolutionary history of the transported species become compromised. It is this beauty of higher organizational levels – particularly that of unique species, communities, and ecosystems – that is threatened or lost. This may sound odd to those accustomed to thinking of beauty as inherent in sensory-accessible structures, such as particular plants, animals, or human artifacts. In what does this more abstract form of beauty consist? How can one speak of the beauty of species, communities, and ecosystems? They do not have color, pleasing shapes, symmetry. If not, then what is threatened with loss by the movement of non-native species?

That which is lost is the beauty inherent in the biological systems and relationships evolved under unique historical regimes of migration, competition, and evolutionary accommodation. These unique histories have led to the evolutionary development of unique floras and faunas in different parts of the world. These evolved biotas include species, each with a unique combination of adaptive features allowing it to survive in its own particular slice of the world; communities of co-evolved and co-accommodating species creating geographically unique assemblages of life forms; and the ecosystems whose mix of unique communities, climatic regimes, and topography impart to landscapes their specific distinctiveness and appeal. I suggest that the distinctive co-evolved, unique beauty of each of these systems is besmirched by the introduction of alien species – much as a beautiful beach or coastline may be impaired by an oil spill. Or perhaps more aptly, the facile pollution of these self-generated biotas by human introductions is equivalent to splattering the canvases in the Louvre with day-glo paint: the structural integrity of the canvases may not be marred, the added colors may be beautiful, but the aesthetic integrity of the artworks is thoroughly violated. The difference, of course, is that the impact of an oil spill lasts for mere years, vandalization of a painting may be rectified by careful restoration, but alien invasions are most usually irreversible and irreparable.

I recognize that arguing loss of beauty due to alien introductions may leave many readers unimpressed. Beauty is frequently thought of as an interpretation or response to a sensory perception, and we have gained some understanding of human judgement of nature's beauty as measured by perceptive factors such as vegetative color, shape, and structure (Lohr, 2007). But recognition of common themes to sensory evocation of beauty is a far cry from arguing on behalf of the beauty of ecological relationships, evolutionary consequences, and biological uniqueness, all of which comprise a far more derivative, conceptual, and abstract aesthetic. Yet, that this form of beauty should be abstract or invisible to many people hardly serves as a compelling argument against its existence – any more than the failure of most humans to perceive abstract mathematical beauty argues against its existence. Lack of a broad appreciation for this ecological/evolutionary aesthetic may simply signify that its appreciation requires a degree of knowledge and/or training that most people have, to date, proven uninterested or maladroit at acquiring. Or such appreciation may be more widely felt but rarely articulated. In either case, lack of human interest, talent, or clear articulation do not prove such beauty to be absent or unattainable. They merely show its appreciation (or articulation) to be rare among members of our current societies – much as appreciation of literature was rare during the Middle Ages or the Renaissance and appreciation of Fourier transformations, Hamiltonian geometry, and fractals non-existent. Our current cultural status may be such that most people can do no better than respond to the sensory impact of an individual plant, animal, or landscape. This is not an ideal situation, of course, inasmuch as many people will rave about the "beauty" of highly invaded landscapes that are nothing but ecological kitsch – such as typify, say, most of lowland Hawaii. However, even this aesthetic appreciation is a tremendous advance over that available in the West in, say, the Middle Ages, when wild landscapes were viewed with fear (Oelschlaeger, 1991) and a relatively small contingent of plants and animals were valued for strictly utilitarian purposes. It is ironic, of course, that many educated people today consider knowledge of art or literature a de rigueur sign of sophistication while at the same time so many of them are the equivalent of ignorant hayseeds when it comes to appreciating the beauty of the evolved biosphere upon which their lives depend. But, then, irony is hardly a novel discovery in the human condition, and one presumes this situation will improve as human understanding and aesthetics continue to develop and be better expressed.

It will occur to many readers that concern for loss of beauty will sound a pretty trivial concern compared to more "practical" issues such as ecological degradation and economic loss. And at some level that may be true. But I would caution against unthinking recourse to the philosophy of economism, which attempts to reduce so much of human life to mere economic concerns and to ignore or dismiss those facets of experience that are not so readily reduced. We humans inveterately view ourselves as exceptional beings, often to the point of denying our creaturehood and evolutionary history, while clinging to some inchoate notion of semi-divinity. While most of this exceptionalist thinking is misguided, I would suggest that two features that truly are remarkable human attributes – possibly, but not necessarily, unique in our evolved biosphere – are our predilection for ethics and our strong response to beauty. It is these features – not language, tool-making, opposable thumbs, or bipedal gait – that so clearly demarcate human life from that of our fellow animals and which have historically served to remove us from Thomas Hobbes' pessimistic vision. They provide meaning to our lives and serve to lift them from the realm of mere selfish, resource-grubbing existence. Under those circumstances, I think that loss of beauty is not a concern we can afford to lightly dismiss, even if the rather abstract beauty under attack should not yet be widely appreciated across our species. Hence, I suggest that in allowing our native ecosystems to be carelessly vandalized by alien introductions we ensure the aesthetic and spiritual impoverishment of ourselves and future generations.

I explain this impact in some detail because even in those cases in which an established alien population does not cause economic or ecological damage, it will always incur an aesthetic cost. So far as I know, no consideration of aesthetic damage from alien introductions appears in the invasive-species literature, whether for reptiles, amphibians, or any other taxon. This probably reflects the discomfort that many biologists would have in discussing such an unquantifiable concept, as well as the fact that social scientists have barely become involved in research on alien species. Nonetheless, I suggest that this is a topic deserving of consideration and future research.

Two remaining points about alien invasions deserve emphasis. First, the effects of invasions are frequently impossible to predict, although ecological mechanisms of impact can often be identified and explained retrospectively. This situation may well remain unchanged: prediction difficulty is a direct result of the inherent complexity of ecosystems formed of the myriad interactions of hundreds or thousands of species with each other and with their changing physical environments. Our knowledge of more than a handful of these interactions in any particular ecosystem is usually rudimentary or lacking entirely, and the large number of possible relationships involved means that an inordinately large number of direct and indirect effects may attend the insertion of any particular novel species into such a system. This complexity has led to invasive-species biology often being a very reactive science – a post-mortem detailing idiosyncratic consequences of invasions that were not or could not have been foreseen. These unpredictable consequences make biotic invasions particularly fascinating and challenging from a scientific perspective, while simultaneously being disconcerting and difficult to address from a management perspective.

A second generality of extremely practical importance is that alien-species naturalizations are usually irreversible. In most instances, once introductions have been allowed to establish, no amount of money or effort can change the situation – much as is widely recognized for other lamentable and irreversible developments such as death, amputation, or the invention of disco music. This irreversibility stems from a variety of biological and social reasons whose applicability to reptile and amphibian invasions will be examined in Chapter 4, but largely reflects the fact that biological entities are self-motivated and not readily susceptible to control. Irreversibility of invasions imposes tremendous economic costs in terms of perpetual damage, control, and foregone economic opportunities (Perrings et al., 2005), a fact not yet widely appreciated by the general public or its political representatives. In those relatively rare instances when it is feasible to reduce or remove damaging alien species, doing so typically involves a rapid response to a new incursion and enormous expenditures of time and money (examples provided in Mack, 2000; Wittenberg and Cock, 2005). High expense is incurred because invasive species will frequently occur in high numbers, be difficult to locate, or both.

Already, thousands of damaging alien species have been introduced worldwide. The number of recognized plant pests alone exceeds 22,000, of which at least 2,000 are environmental pests (Randall, 2002; updated to >28,000 species at http://www.hear.org/gcw/). Hundreds of thousands of potential pests could make the future incomparably worse. This is not merely a reflection of the inherent biological attributes of each potentially invasive species. The invasive-species problem is at its most fundamental level a consequence of varied human values, decisions, and actions (Andow, 2005; McNeeley, 2005), including the commonly taken choice of doing nothing. Adding to scientific knowledge of invasion biology without acting on that information, however, is a sterile exercise. How, then, is our information being used to manage these problems? What prospects are there for improving our responses?

Solutions

A variety of actions may be taken to lessen the frequency of invasion or to reduce the negative impacts of particular invasions. Strategically, one may respond to invasive species at any or all of three stages: by preventing their arrival and establishment, by eradicating newly established populations before they expand, or by mitigating the costs of widespread invasions. Best protection against invasions is had by employing actions (or "screens") at all three stages because each screen acts independently of the others, and their combined protective effect is multiplicative (Fig. 1.1). Tactical methods useful at each stage should exploit the biological weaknesses of each species; hence, they will vary with species and with the particular environment in which control is being exercised. As a matter of observation and logic it is cheaper, more effective, and therefore more efficient to control alien species earlier in the invasion process than later (see, e.g., Naylor, 2000; Touza et al., 2007). A logical consequence of this is that prevention of introductions is far superior in terms of effectiveness, efficiency, and resource use than is reacting to invasions after they occur. Hence, comprehensive quarantine and screening systems to exclude species entry to new areas should form the foundation for any alien-species mitigation program. This paradigm has been applied to some agricultural pests, but the approach is still new and little applied to environmental pests, except in New Zealand and Australia. Should alien pests breach the quarantine barrier, the most cost-effective means of mitigation is to discover and eradicate newly established aliens while populations remain small. If successful, this avoids the large costs of perpetual control for widespread species. For environmental pests, long-term control is usually applied only in relatively small areas of especial ecological significance, making it an inherently limited solution. Important economic pests may elicit broader treatment. Clearly, avoidance of perpetual management and its attendant costs is to be preferred, so prevention of species incursions or their rapid identification and eradication prior to spread are strategically the most sensible tools of choice. Their competent application avoids the difficulty and cost of long-term control operations and the unpredictable hazards attendant upon allowing alien species to become established. Nonetheless, no single prevention screen will be 100% effective, and sensible invasive-species mitigation programs utilize all three

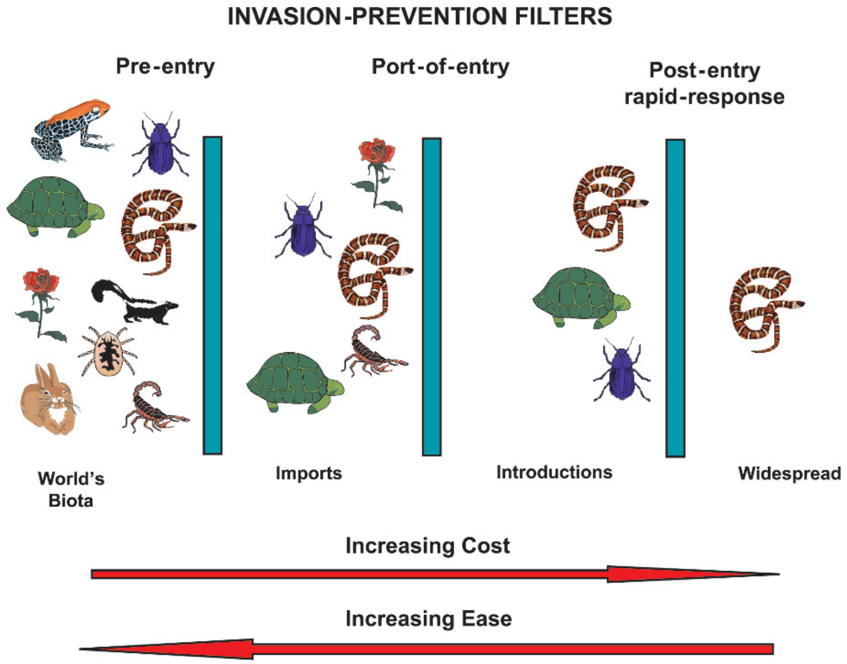

Fig. 1.1 Illustration of the multiplicative protection provided by erecting programmatic barriers to the spread of invasive alien species at the three stages of pre-entry (preventing transportation), port-of-entry (preventing introduction), and immediately post-entry (rapidly eradicating new incursions). The cost of control is less to intercept aliens early in the invasion process, and the ease of control and effectiveness are also higher. Costs increase and probability of successful prevention decrease as a species wends its way through the invasion process

approaches. I will briefly consider topics relevant to each stage of response activity, including certain limitations of each, because these highlight the need for comprehensive response programs that do not overly rely on one method alone.

Strategic Considerations

Before considering different response screens, a few cross-cutting strategic considerations merit consideration first. Although the probability that a particular species becomes an invasive pest is low, the costs if it does so can be very high. This combination of low risk of invasion with high potential hazard can easily skew human perception of risk (Perrings et al., 2005), making sensible assessment of management options problematic. The history of alien-species invasions serves as testimony to the ease with which this skewed judgment operates. The need for the future is to minimize the risk of additional introductions and effectively manage the numerous pests that have already invaded. For reasons given above, risk of future invasions is difficult to quantify. Government agencies have instead often taken a qualitative approach in which risk probabilities at each step (introduction, establishment, and spread) are qualitatively categorized by a panel of experts as "high", "medium", and "low". The product of the constituent probabilities for invasion is then scored as that of the lowest component (Simberloff, 2005). A similar assessment may be done for species hazard, and the value of the hazard risk is then multiplied by that for invasion risk to produce an overall assessment value (Simberloff, 2005).

There are many problems with the approach just outlined, including its vulnerability to political tampering, narrowly circumscribed taxonomic ambit, practical inability to assess every taxon of interest or concern, presumption of safety for species whose biology is poorly known, and inability to predict consequences for species not yet introduced anywhere (Simberloff, 2005). Hence, one must be cautious in placing too much confidence in the results of such assessment, and different means of assessing invasion impacts may sometimes be preferred (Binimelis et al., 2007). However, such qualitative assessments still have value. The important point about consideration of risk is the conceptual framework that it provides in thinking about how to reduce the future burden of species invasions. Dividing the invasion process into separate steps allows for clearer thinking about the biological and human factors operating at each stage and how those factors might be altered to best reduce invasion probability. This can allow for better decision-making about when and how to respond to alien species. For example, increased international trade increases the risk of introduction of unwanted aliens in a cumulative fashion. This trend is not likely to change in the near future, so responsible governments need to recognize the looming future risk and respond with prevention systems commensurate to the task.

One means of managing the high uncertainties involved in predicting invasiveness and costs is the adoption of a precautionary approach. This principle, as concisely put by Perrings et al. (2005), holds that "where the effects of some activity are uncertain but are potentially both costly and irreversible, society should take action to limit those effects before the uncertainty is resolved." The justification for such an approach is both that the costs of foregoing preventive action are likely to outweigh the costs of doing so and that the burden of proof for potentially damaging activities, such as importing alien species, lies with those benefiting from the activities. Fundamentally, it is a statement that scientific uncertainty should not be allowed to prevent society from taking action to avoid potential risks (Andow, 2005). It will come as no surprise, however, that the uncertainties involved in understanding species invasions allow for plenty of political bickering over relative costs and benefits. Consequently, although invasion biologists and managers have long argued for the application of a precautionary approach to alien-species management, presumptions about what constitutes precaution, safety, and risk vary tremendously among countries, government agencies, and international treaties (Andow, 2005). In at least one instance, New Zealand's Hazardous Substances and New Organisms Act of 1996, the precautionary principle has been codified into law and is discharged by that nation's Environmental Risk Management Authority (see http://www.biosecurity.govt.nz/). Elements of that approach are applied in other jurisdictions as well (e.g., Australia, South Africa). Most countries, however, have avoided addressing the issue and lack any formal process for systematically responding to invasive alien species that goes beyond ad hoc reaction.

Prevention

Successful prevention requires a clear understanding of how the organisms in question are transported and what parameters determine pathway success rates. For species that are introduced unintentionally as hitch-hikers on commercial goods – such as many insects, other invertebrates, and agricultural weeds – inspection and quarantine of arriving goods, containers, baggage, and vessels to ensure they are pest-free will theoretically suffice to keep these pests out. For organisms that are deliberately introduced – such as pets, biocontrol agents, and food species – development of screening systems to assess the likelihood of the species becoming established or becoming invasive are more appropriate. Species deemed of high risk are prohibited from import; species of uncertain hazard are also typically banned pending further assessment to clarify probability of pestiferousness.

Quarantine inspection is typically directed to those articles considered at high risk of harboring unwanted pests because the huge volume of traded material makes it impossible to search all arriving items. Risk can be assigned to particular commercial goods, types of packing material, types of vessels, or to arrivals from particular source areas; it may be estimated using analysis of past interception records, random searches of selected goods and baggage, or from "blitz" inspections that comprehensively search an entire shipment of goods or passengers. Most high-risk materials will receive an inspection at the port-of-entry that may vary in thoroughness depending on the resources available. High-risk commodities may be held in isolated quarantine facilities to determine whether they are free of pests; this is most often done for living commodities, such as pets and horticultural plants. As personnel and resources are available, effort may be directed to articles of lesser risk. For governments having the resources, certifying the pest-free status of commodities by examining them prior to export from the country of origin can be a means of improving cleanliness of imported materials. But this option is typically limited to inspection of agricultural commodities for known, high-risk pests. Practical control methods at this stage typically involve inspection for pests, treatment of articles suspected of harboring pests, and exclusion of particular commodities via trade prohibition (Wittenberg and Cock, 2005). Treatment methods for contaminated plant produce are briefly reviewed by Hallman (2007); several of these methods are useful as well for invasives that do not target plants.

Two weaknesses characterize most inspection programs: (1) only a handful of alien species are targeted quarantine pests, with the remainder ignored or allowed entry even if detected, and (2) resources are inadequate to provide comprehensive inspection, even were a larger array of alien species targeted for quarantine. In most jurisdictions, the large volume of arriving goods, passengers, baggage, and vessels often precludes meaningful quarantine for more than a handful of unintentionally arriving species. So, current quarantine inspection programs are generally far from ideal. A more promising approach would be wider application of vector science – understanding and managing the motives that create the pathways of introduction and the specific physical means of introduction (or vectors) that transport species (Carlton and Ruiz, 2005). The benefits of a vector-analytic approach are that it can simultaneously work to prevent the introduction of multiple species carried by the same vector and it is likely to be economically efficient by prioritizing those pathways and vectors accounting for the greatest numbers of introductions or invasions. Its intent is to reduce viable transport of all alien species associated with particular vectors or pathways instead of just a limited list of already-identified invasives. This approach requires identification and quantification of pathways and vectors as well as the development of tactical means to limit successful transport by those means. Vector science is relatively new but its recent application includes treatment of ballast water and placement of some restrictions on the import of raw logs for timber. Detailed studies of pathways and vectors are not available for most taxa or commodities, and much of what commodity data are available sit unpublished in government files. But much of what understanding is recently available is summarized in Carlton et al. (2003).

Currently, most countries adopt a short list of known invasives that they attempt to keep from their shores, and most of these are species liable to accidental introduction. These species are almost always pests of agricultural concern and are a very small subset of all known or potential invasives. Ideally, one would like to be able to screen any alien species for potential invasiveness and use that information to decide whether to allow or ban its deliberate importation. Such screening systems would require a methodology that can reliably identify and exclude most invasive species, approve most useful or non-threatening species, and limit the number of instances of uncertain status that require further assessment. Australia has developed screening protocols to meet these goals for plant and animal introductions (Bomford and Hart, 1998; Pheloung et al., 1999; Walton et al., 1999; Bomford, 2003; Bomford and Glover, 2004), and the plant protocol has been adopted for use in New Zealand with minor modifications (Williams et al., 2002) and found applicable to a variety of other locations (Gordon et al., 2008). These protocols are based on assigning numerical scores to a variety of biological traits for a species, summing the scores across all assessed variables, and using this summary score to decide whether to allow importation (low scores), prohibition (high scores), or further assessment (intermediate scores). By use of such a simple system, it has been determined in New Zealand that most invasive species of plants can be kept from entry, most useful non-threatening plants can be allowed safe entry, and a small proportion of species fall into a narrow numerical zone of uncertainty that requires further study prior to making a definitive decision. The system is conceptually simple, evidentiarily explicit, and objective, making it transparent to affected stakeholders. It has also been shown in Australia to be easily and cheaply implemented. The advantages of such a system over the current, widespread use of limited "black" lists prohibiting known pests is that a far larger pool of species can be explicitly evaluated for invasiveness and that a "white" list of safe species is simultaneously generated, providing a measure of regulatory stability and predictability useful when making economic decisions involving importation. The system has also been shown to not only protect natural resources but also to generate net economic benefits by exclusion of harmful pests (R.P. Keller et al., 2007).

Eradication/Control

When aliens slip through these prevention screens, the next-best means of avoiding damage is to identify a new incursion as rapidly as possible and target it for eradication. For eradication to be successful requires that several conditions be met: proper planning, socio-political commitment, a removal rate exceeding replacement rate, that all individuals be placed at risk, and prevention of reinvasion (Bomford and O'Brien, 1995; Clout and Russell, 2006). Systematic targeting of new incursions requires having in place a systematic survey program and dedicated, permanently funded staff to respond to new escapees. The former better guarantees identifying new incursions before they have proliferated too far. Doing this successfully requires sensitivity to the lag-phase phenomenon. Permanent staff are needed to ensure that eradication measures continue for the length of time required to ensure success, which can vary tremendously, depending on the species: large conspicuous animals may often be eradicated in relatively short order; plants will produce a seed bank that requires repeated control operations to remove all newly germinated plants to prevent additional reproduction. Small and secretive animals, such as most reptiles and amphibians, may be virtually impossible to eradicate once established because they are difficult to detect and because feasible control methods are frequently lacking.

Explicit use of eradication measures against incipiently established aliens is of relatively recent occurrence and is currently limited, though expanding, in scope. This method has proven successful against environmental pests in New Zealand, Australia, and Hawaii and is becoming common procedure in those jurisdictions. Invasions successfully prevented in this manner are varied, but I will give one example to show what is achievable with rapid, competent response to new incursions. Perhaps the most impressive instance is the eradication of the mussel *Mytilopsis* sp. from Darwin Harbor, which was completed within one month of its detection in three marinas, even though it occurred at densities as high as 23,650 individuals/m^2. This carefully planned and orchestrated operation involved immediate legislative action to authorize control activities, surveys of hundreds of ships and man-made structures to delimit the range of the infestation, quarantine of three infested marinas, laboratory trials of control methods, chemical treatment of the infested areas totalling approximately 20 ha of harbor, chemical treatment of interior plumbing on all quarantined vessels, public education to gain community and stakeholder support, and monitoring of the treated areas for one year (Bax et al., 2002). As noted, successful eradication was achieved within one month of first detection of the incursion, but success was not declared until mussels had remained undetected for one year. Most eradication operations neither proceed this quickly nor have a need to because most invasive species lack this mussel's capabilities for explosive growth. But this example demonstrates what may be achieved by rapid response against difficult odds when such an operation is approached with commitment and competence. In marking that achievement, Australia's Northern Territory has set a useful standard against which other jurisdictions may measure their own response efforts.

Should an invasive alien species be allowed to spread widely, it is usually impossible – or at best very expensive – to eradicate it. Under these circumstances, one is faced with the prospect of perpetual control to mitigate the worst effects of the alien invader. The means of effecting control and mitigating damage will vary depending on the taxon, habitat, and management goals, but all such efforts need to be carefully defined, planned, and executed in order to meet those goals. Mechanical and chemical control methods are the most widely utilized tactical tools, and numerous options are available, their application and effectiveness depending on the target (examples given in Kraus, 2002a; Wittenberg and Cock, 2005). Although these tactical methods form the backbone of most control operations, more biologically sophisticated techniques, such as removal of disturbance regimes that promote proliferation of the pest, or alteration of habitat to remove refugia for invasives or to provide a competitive edge to natives, can also be used against some invasive pests.

Introduction of natural enemies – either predators or parasites – from a pest's native range has been a frequently used control option and is termed "classical biocontrol". Biocontrol has most often been applied against plant or invertebrate pests, and these efforts have frequently met with some degree of success in controlling the invasive pest. When properly applied, biocontrol is often the only hope for effecting large-scale control against many wide-ranging plants and invertebrates, and some programs have reduced the target species to such low numbers that it no longer acts as a pest. However, biocontrol programs have also led to unintended disastrous consequences for non-targeted native wildlife (Howarth, 1990, 1999; Louda et al., 2002). This has occurred primarily because some released control species proved to have wide dietary ranges that went unrecognized because of poor (or no) host-specificity testing prior to their release. Attempts to use biocontrol against vertebrates have almost always been ineffective because of lack of host specificity in vertebrate predators and parasites. Use of vertebrates themselves as biocontrol agents has often been disastrous because most vertebrate predators have broad diets and do not restrict their dining to the target species. Because early biocontrol efforts often created unintended impacts on non-target species these programs are now often conducted with extensive testing prior to release so as to ensure that such collateral impacts do not occur. Nonetheless, monitoring of post-release outcomes remains insufficient (Simberloff and Stiling, 1996), and there is still scope for improving the application of this important control tool.

Because control actions taken against invasive pests can themselves have potentially broad ecological impacts, due deliberation and care must be exercised to ensure that such impacts are minimized or avoided. For example, unintended damage to native wildlife may occur because some natives may now use invasive species – such as using invasive plants for food or refugia – for lack of other options. Such conflicts arise as a direct result of the tremendous degree to which human activities have modified the world. This is not to say that large control operations against invasive species should be abjured, merely that they need to be thoughtfully planned and implemented so as to avoid creating additional problems for the biotas or resources they are intended to protect.

Long-term management and control of ineradicable pests thus can be a complex undertaking with diverse ramifications. Typically, benefits are believed to outweigh costs where the goals of the control effort are clearly defined and lead to protection of high-value resources, e.g., biodiversity or agricultural sites of high value. These issues and the complexities involved are treated in greater depth by Wittenberg and Cock (2001) and Courchamp et al. (2003), which should be consulted for more thorough treatments of management topics. De Wit et al. (2002) provide an excellent example of how to conduct an explicit cost/benefit analysis identifying best control options for a widespread invasive. It is worth emphasizing, however, that although range-wide eradication of widespread invasive pests is typically unachievable, discrete geographical units, such as islands, may be liable to removal of invasives and sustained as pest-free. For these instances, considerable progress has been made in developing tactical methods and operational strategies for the eradication of invasive pests from increasingly large areas. A recent sampling of such work can be found in Veitch and Clout (2002), and comprehensive summaries of operations against certain pests (Nogales et al., 2004; K. Campbell and Donlan, 2005; Howald et al., 2007) or for certain geographic areas (B.D. Bell, 2002; Burbridge and Morris, 2002; Ebbert and Byrd, 2002; Merton et al., 2002; Tershy et al., 2002; Clout and Russell, 2006) are also available. With respect to reptiles and amphibians in particular, however, tactical control methods are poorly developed, although mechanical, chemical, and habitat-modification tools have all been attempted. These examples will be discussed in Chapter 4.

History of Research on Alien Reptiles and Amphibians

Although impacts from some alien invasions have been recognized since the late 1800s (cf. Elton, 1958), it wasn't until rather recently that problems associated with reptile and amphibian invasions began to be noticed or documented. Hence, while Ebenhard (1988) could devote a 107-page monograph to the ecological impacts of alien birds and mammals, mention of reptiles and amphibians is absent from Elton (1958) and Mooney and Drake (1986). Similarly, the cane toad (*Bufo marinus*) is the only herpetological species to appear in Groves and Burdon (1986), and it merits only passing mention. This delayed concern for alien reptiles and amphibians probably stems from the interaction of two factors. First, most of these species are cryptic and insectivorous, making their true densities difficult to perceive and obviating any direct impact on humans or their economically important domesticated animals. Hence, alien reptile and amphibian populations are easy for most people – including most scientists interested in invasive species – to overlook or ignore. Second, much of the literature on these introductions is widely scattered in obscure sources and has previously been unsynthesized (but see Lever, 2003, for a partial, though fairly comprehensive, summary), making it difficult to develop an overall appreciation for the magnitude of reshuffling that has occurred or how it has developed.

This situation has begun to change over the past 25 years. The rapid spread of cane toads across Queensland by the 1970s, combined with anecdotal reports of their poisoning of native wildlife (Breeden, 1963; Rayward, 1974; Covacevich and Archer, 1975), led to considerable government funding to elucidate these effects, understand the biology of the toad, and identify means by which to control it (Tyler, 2006; T. Robinson et al., 2006). The results of this work were a fairly broad understanding of toad expansion, genetics, and parasites within Australia (cf. Appendix A). However, these efforts failed to identify practical control mechanisms, and the toad continues to expand its range rapidly. More effective in bringing attention to herpetological introductions was recognition that the brown treesnake (*Boiga irregularis*) was responsible for the spectacular decimation of Guam's native forest bird fauna (Savidge, 1987a; Savidge et al., 1992), which largely disappeared by the mid-1980s. Lost from Guam were ten species of forest birds, three seabirds, two bats, and six lizards within approximately 40 years (Savidge, 1987a; McCoid, 1991; Rodda and Fritts, 1992; Fritts and Rodda, 1995, 1998; Rodda et al., 1997, 1999a). Three of the birds and one bat were endemic to Guam and are now globally extinct. Two more birds – a rail and a kingfisher – remain only in captivity for the time being. Most of the few native vertebrates that remain on Guam do so at extremely reduced numbers. This was an unanticipated effect from a "mere snake" (J.T. Marshall, 1985), and most ornithologists at the time blamed pesticides or disease for the bird declines (Jaffe, 1994). Consequently, Savidge's evidence and arguments laying responsibility (dare I say) at the feet of the snake were initially dismissed as impossible. The effect of these losses has been a wholesale change in food webs on Guam, with broader ecosystem effects – such as loss of pollinators and changes in vegetation communities – anticipated (Fritts and Rodda, 1998), supported by some data (Perry and Morton, 1999; Ritter and Naugle, 1999), but not yet rigorously tested. Similarly, beginning in the late 1980s, evidence began to accumulate indicating that the bullfrog (*Rana catesbeiana*) is at least partly responsible for the decline of a diversity of native frogs and snakes across the western United States (see Chapter 3). It has also recently been shown to be a likely vector in the spread of chytrid fungus, which has decimated native frog populations around the globe in the past 20 years (Hanselmann et al., 2004; Garner et al., 2006).

The approximately simultaneous acquisition of evidence linking brown treesnakes, cane toads, and bullfrogs to damage to native species has helped foster a growing awareness of the potential ecological importance of invasive reptiles and amphibians and has provided an impetus for research on additional species. But this awareness and action still lag well behind that accorded other taxa. Most of this increased activity has merely recorded new introductions, documented range expansions, or provided descriptive autecological information on some populations of naturalized reptiles and amphibians. A growing number of studies, however, has documented additional negative impacts to native biota or to human activities resulting from a variety of invasive herpetofauna (see Chapter 3). Scientists occasionally model predicted range expansions of select taxa based on matching climatic parameters between native and invaded ranges (e.g., van Beurden, 1981; Sutherst et al., 1996; Adrados, 2002; Ficetola et al., 2007a; Urban et al., 2007). There have been regional summaries of herpetological introductions for a few areas (e.g., King and Krakauer, 1966; Bury and Luckenbach, 1976; Smith and Kohler, 1978; L.D. Wilson and Porras, 1983; McCoid, 1995a, 1999; Ota, 1999; Meshaka et al., 2004a; Ota et al., 2004a), and a recent book summarizes some of what is known about particular established species of alien reptiles and amphibians (C. Lever, 2003). A brief overview of some common pathways and impacts of alien herpetofauna has recently appeared (Scalera, 2007a) but is focused on those species associated with aquatic habitats. There have been, however, virtually no studies that test explicit scientific hypotheses about herpetological invasions – most work to date has been simply descriptive.

Little knowledge, too, has been added that would be practically useful for stemming the rising tide of naturalized populations of alien reptiles and amphibians. For example, a couple of brief assessments of introduction pathways for the alien herpetofauna of Florida exist (L.D. Wilson and Porras, 1983; Butterfield et al., 1997), but only one prior study (Kraus, 2003c) has attempted a broad-scale quantitative assessment of this topic, and that was merely an early precursor to the expanded analysis of the next chapter. As for damage from invasive herpetofauna, no rigorous summary of ecological or social impacts from alien reptiles and amphibians has previously been published. Some useful information on impacts may be gleaned from C. Lever (2003), but that book mixes evidence and speculation with little distinction, and there has been much untested speculation about impacts promulgated in the herpetological literature. If informed decisions are to be made on designing prevention systems for alien reptiles and amphibians we need better data on both introduction pathways and ecological, economic, and social impacts. Attempts to predict invasion success have just begun to be investigated for reptiles and amphibians. Rolan (2003) provided an assessment of risk to native amphibians of the United States posed by 24 species of alien amphibians, and Reed (2005) did likewise for an assortment of pythons and boids. Bomford et al. (2005, in press) provided evidence that history of prior establishment, climate match, and phylogenetic relatedness were correlated with establishment success for alien reptiles and amphibians. Rodda and Tyrrell (in press) assessed likely ecological attributes that would favor urban, pet-trade, and invasive herpetofauna, and they concluded that overlap in attributes between these three sets is high. But testing those predictions with empirical data remains to be done. Clearly, efforts to obtain the information necessary to predict invasiveness of alien herpetofauna have just begun.

In short, despite a recent increase in awareness and interest in invasive herpetofauna obtained from damaging experiences in Guam, Australia, and the western United States, the systematic compilation of information needed to make progress in scientific understanding of these invasions or to make informed, practical management decisions about alien reptiles and amphibians has been lacking. It is this information to which we now turn.