



## Now you see them, now you don't! – population crashes of established introduced species

Daniel Simberloff\* & Leah Gibbons

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville,  
TN 37996, USA; \*Author for correspondence (e-mail: dsimberloff@utk.edu; fax: +1-865-974-3067)

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### Abstract

Substantial populations of invasive non-indigenous species occasionally collapse dramatically. Although disease is often invoked, the causes are rarely studied experimentally and/or quantitatively, and some collapses remain quite mysterious. The widespread invasive snail *Achatina fulica* and pondweed *Elodea canadensis* appear to be characterized by rapid expansion followed by rapid decline. For the former species, disease may be the proximal cause of the collapse, while repeated collapse of the latter species is unexplained. Several other widely cited collapses of introduced species may simply be temporary lows during a more or less regular boom-and-bust cycle. However, on a restricted site (such as a small island), a boom-or-bust cycle may be impossible and recovery may never ensue; local extinction may even occur. In several instances, apparently spontaneous crashes were in fact probably caused by subsequently introduced competitors. Except for the few species in which spontaneous collapse has been repeatedly observed, the possibility of such an event is unwarranted as a potential rationale for a do-nothing approach to management. For such species, even if a crash ultimately occurs, the species may already have caused persistent ecological damage.

'For a short period weasels overran like fire the east coast between Tutira and Poverty Bay, and then like fire died out'.

– Guthrie-Smith 1921 [1999], p. 355

### Introduction

The phenomenon of a lag-time is well documented for some invasions (Kowarik 1995; Crooks and Soulé 1996, 1999). For instance, Brazilian pepper (*Schinus terebinthifolius*) currently infests ca. 300,000 ha of south Florida, often forming dense, monospecific stands (Schmitz et al. 1997). However, it was present as a restricted ornamental in the 19th century and did not begin its rapid regional expansion for at least 50 years (Ewel 1986). The fact that some ultimately troublesome introduced species undergo a lag, during which their populations remain small and geographically restricted, has great management significance. It gives grounds for concern even about currently harmless introductions, and it is a prime reason for the desire

to establish a good early warning and rapid response system.

Less well known is the phenomenon of a spontaneous collapse, in which a non-indigenous species is well into the increase phase of an invasion, or even fairly widely established, but then, without management actions, undergoes an apparently spontaneous decline, sometimes all the way to local extinction. If such collapses were fairly common, or if they characterized specific species or invasions with certain characteristics, then an appropriate management decision might be the 'do-nothing' option, even if the introduced species, were it to persist in great number, would have a high probability of causing a problem. If, on the other hand, spontaneous collapses are rare, idiosyncratic events, inaction might be a recipe for disaster.

We first sought examples of such collapses in exhaustive literature searches. These yielded few examples; for instance, a search of Biological Abstracts after 1997 for 'introduced species' in titles and/or abstracts yielded 952 articles, of which 52 included the word 'decline' in the abstract. Only one of these referred to decline of an introduced species, and this particular case was not relevant, as it cited a very gradual population decline over a short period. We then turned to more focused literature plus many queries to experts on invasions by particular taxa. Often, invasion biologists recalled instances, from personal experience or hearsay, in which formerly common and/or widespread invaders appeared to have declined rapidly and substantially. For most of these cases, no explanation was suggested. These examples spurred further literature searches and queries, in an attempt to generate enough of a casebook to seek patterns and possibly conduct statistical analyses. Unfortunately, even quantitative data documenting perceived declines were exceedingly scarce, while the great majority of proposed explanations were simply more or less reasonable *ad hoc* suggestions with no supporting evidence. Thus we confine ourselves to descriptions of the most thoroughly documented cases, plus an attempt to seek preliminary commonalities.

Although 'population crash' and 'population collapse' are variously defined and used loosely in the literature, for the purposes of this survey we sought cases in which population numbers or densities were believed to have fallen by at least 90% in less than 30 years.

### Regional declines

Some crashes are quite dramatic and occur over a large area. Consider the common North American waterweed *Elodea canadensis*, introduced to Great Britain. First detected in 1842 in a pond in Berwickshire in southern Scotland, it spread quickly to rivers, canals, ditches, and ponds in much of Great Britain (Simpson 1984). At its peak in the 1860s, it so clogged the Cam River that it interfered with rowing, and extra horses were needed to tow barges. It fouled fishing nets, and at least one swimmer drowned after being caught in it. Parts of the Thames were impassable. By 1900, it was considered to be abundant and occurring in all suitable waters. Then it suddenly declined to minor or even lower status throughout its entire British range, for no

obvious reason and with no human intervention. Closer examination of specific records throughout England (Simpson 1984) showed a typical cycle of colonization, whereby the plant would become established in a locality, then rapidly increase for 3–4 years, reaching pest proportions and excluding most other macrophytes. Maximum numbers would be maintained for another 3–10 years, after which there would be a decline over 7–15 years. Either it would disappear entirely in a locality, or a much smaller population would remain. By the early 20th century it had ceased to be a problem throughout Great Britain and was rare in most places.

Even more interesting is the fact that exactly the same sort of pattern has arisen with introduced *E. canadensis* in Sweden (Andersson and Willén 1999), Germany (Scherer-Lorenzen et al. 2000), and the Czech Republic (Pysek et al. 2002). Further, there were even very early accounts of its being present in Great Britain, then collapsing (Simpson 1984). Even in lakes in its native range, there are reports of *E. canadensis* typically increasing slowly, then crashing nearly to local extinction (e.g., Rysavy et al. 1999).

The cane toad, *Bufo marinus*, was introduced to Australia in 1935 (Lever 2001). Freeland (1986) and Freeland et al. (1986) studied its expansion into northern Australia. They examined 20 populations ranging in age from 1 to ca. 47 years in sites chosen because they were all within 2° of latitude and had a severe dry season. Within just 2 years of founding, population density rose as high as 1155 toads/ha, higher than any population recorded locally in Panama, in the native range, where the maximum recorded density is 84–184 toads/ha. Populations remained very high in northern Australia through 19 years. In fact, one 19-year population had 2138 toads/ha. However, by 47 years, all had crashed down to at most 284/ha, and three of the five had fewer than 20 toads/ha. Similar declines occurred in other long-established Australian populations.

Further, the older the northern Australian populations, the smaller the individual females (Freeland 1986), so that in the youngest population, 13 out of 67 were less than 100 mm snout–urostyle length and 27 out of 67 exceeded 120 mm in snout length, whereas in the oldest population, 8 out of 29 were less than 100 mm snout length and 3 out of 29 exceeded 120 mm snout length. The latter figures are very similar to those in the two native populations in Panama. Also, for any body length, toads in the oldest population weighed less than those in the other populations.

This progression seems typical of *B. marinus*. Good quantitative data show that, following its introduction to Puerto Rico in 1920 and 1924, it established substantial populations throughout the coastal lowlands by 1932–1933. Between 1935 and 1937 populations inexplicably fell and have remained low ever since (Freeland 1986). There are similar but anecdotal accounts of rapid rise, then drastic decline for the Philippines, New Guinea, Bermuda, and Barbados (Freeland 1986). A recent account (Quesnel 1998) describes a great decline in Trinidad between 1990 and 1995, followed by recovery in 1996–1997.

Various of these declines have been ascribed to food shortage or a parasite or pathogen (Wolcott 1937; Pippet 1975; Van Beurden 1980). Wolcott (1950) attributes the Puerto Rican decline primarily to the toad's having exhausted a native beetle pest of sugar cane. However, in the only major empirical study of the decline, in northern Australia, Freeland et al. (1986) ruled out both food shortage and helminth or protozoan parasitism as the cause of poor body condition, which they believe causes the population decline. They did not rule out microbial pathogens.

Least weasels (*Mustela nivalis*) were introduced by the hundreds from Great Britain to New Zealand in 1885 and again in 1886 to control rabbits; other, unrecorded releases probably occurred around that time (King 1990). On both the North and the South Islands, there were irruptions, with rapid population increase and range expansion. Then there was a severe decline in numbers, accompanied by a range contraction, so that by 1950 they were rare, as they remain today. Locally, the explosion and crash were dramatic, as witness the account in our epigraph, from a sheep station at Tutira on the North Island (Guthrie-Smith 1999).

Least weasels are well known in their native range for drastically fluctuating densities correlated with numbers and distribution of mice and voles (King 1990). The NERC Global Population Dynamics Database (NERC 1999) has three sequences of native least weasel populations; all three have declines of over four-fold, and one goes below the threshold of detectability (Korpimäki et al. 1991). King (1990) attributes the decline in New Zealand to the fact that the weasel is restricted to small prey, and to competition and perhaps predation by the larger stoat (*Mustela erminea*), released at the same time in New Zealand. In this scenario, the weasel, introduced in greater numbers and breeding faster, took advantage of whatever small prey

were available (including insects and lizards), but eventually the stoat, with a more catholic diet and now much larger populations, overtook it, caused it to decline, and continues to suppress it.

The European browntail moth (*Euproctis chrysorrhoea*) was first found in North America in Somerville, Massachusetts, in 1897 (McGuggan and Coppel 1962). It spread quite rapidly through New England and reached New Brunswick in 1902 and Nova Scotia in 1905. Populations increased quickly as it fed on many deciduous tree species (McGuggan and Coppel 1962). There was great worry that its impact would equal or surpass that of the gypsy moth, as it not only defoliated many tree species but caused skin rashes from larval urticating hairs. However, populations peaked in both New England and Canada in 1913–1914, and both numbers and range declined drastically, so that it disappeared from Canada by 1927 (McGuggan and Coppel 1962). By the 1970s it was found only on a few islands in Casco Bay, Maine, and a few coastal sites near the tip of Cape Cod (USDA 1993; Elkinton et al. 2001).

Some researchers have attributed the decline to regular spray programs plus intensive collection and destruction of overwintering webs (Clausen 1978), but Elkinton et al. (2001) argue that a main cause of the decline was parasitism by the generalist tachinid parasitoid *Compsilura concinnata*, introduced to North America in 1906 to control gypsy moths, and that another introduced tachinid, *Carcelia laxifrons*, helps restrict the browntail moth to sparsely vegetated dunes. This crash is not typical of the one native population of the browntail moth that has been extensively monitored, in the United Kingdom (NERC 1999). If Elkinton et al. (2001) are correct, the crash is not mysterious except by virtue of the fact that it happened long ago and adequate data on mortality were not gathered while it happened. It would be one of several instances in which an introduced biological control agent rapidly and permanently caused the decline of a formerly widespread and numerous host. The collapse of alligatorweed (*Alternanthera phyloxeroide*s) populations in Florida upon the introduction of the alligatorweed flea beetle (*Agasicles hygrophila*) is an excellent example (Center et al. 1997). However, the fact that the remaining remnant populations are currently devastated by these tachinids need not mean the tachinids caused the crash.

The Mediterranean fruit fly (medfly), *Ceratitis capitata*, was introduced to the Sydney area at least

as early as 1898 (May 1963), if not earlier (Maelzer 1990), and quickly spread through citrus orchards of New South Wales in the early 20th century to become a widespread major agricultural pest (May 1963). However, rather quickly the population began to decline and the last medfly in New South Wales was recorded in 1941 (May 1963; Bateman 1977). This decline is linked to the spread to New South Wales of the Queensland fruit fly (*Dacus tryoni*) in the 1920s and 1930s (Bateman 1977; Maelzer 1990), although the mechanism of the interaction has not been elucidated, and May (1963) believes that *D. tryoni* was present in New South Wales well before *C. capitata* invaded. The medfly was largely replaced in the lowland Hawaiian islands after the arrival of the Oriental fruit fly (*Bactrocera dorsalis*), apparently by a larval interaction (Keiser et al. 1974) of somewhat mysterious mechanism; Bateman (1977) suggests that a similar mechanism may operate between *D. tryoni* and the medfly.

The yellow fever mosquito, *Aedes aegypti*, native to west Africa, was introduced to Europe by maritime shipping and caused major outbreaks of yellow fever in Spain in the 18th and 19th centuries (Eritja et al. 2003). It achieved large populations in parts of Spain, possibly aided by further introductions, but it dwindled during the last half of the 20th century so that it has not been found in Spain for 20 years (R. Eritja, pers. comm.). Although there is no direct evidence of an interaction with the subsequently introduced Asian tiger mosquito (*Aedes albopictus*), the decline of *Ae. aegypti* was roughly synchronous with the arrival of *Ae. albopictus*, and the latter is better able to tolerate occasional cold spells (Eritja et al. 2003). In Florida, *Ae. albopictus* has also displaced *Ae. aegypti* from many sites, with larval resource competition strongly implicated as at least one mechanism (Juliano 1998), but with egg survival also important and climatic factors playing a role (Juliano et al. 2002). Preliminary results in Brazil point to a similar displacement (Braks et al. 2003). However, in the New World this interaction, though it has led to rapid local declines, does not appear to be leading to a regional extinction as in Spain.

The sea-rocket *Cakile edentula* from the east coast of North America was introduced to the west coast in the 1880s and spread rapidly, becoming patchy but widespread and locally abundant by the time its European congener, *Cakile maritima*, arrived in 1935 (Barbour and Rodman 1970; Boyd and Barbour 1993). As *C. maritima* spread, *C. edentula*

declined in abundance, becoming locally extinct in many Californian sites by 1969 but remaining common from northern Oregon through British Columbia. Boyd and Barbour (1993) present data that provide a cogent explanation of how *C. maritima* outcompeted *C. edentula* through a substantial reproductive advantage in foredune habitats combined with wave dispersal of fruits to other habitats. An almost identical replacement of *C. edentula* by *C. maritima* occurred in Australia (Boyd and Barbour 1993).

### Crashes of more restricted populations

The crested mynah (*Acridotheres cristatellus*), from southern China and northern Indochina, was introduced to the city of Vancouver in 1897, possibly as only one or two pairs (Johnson and Campbell 1995). Scarce until 1904, it then increased rapidly throughout southwestern mainland British Columbia through the early 1930s. By then it was estimated to number ca. 6000–7000 birds in Vancouver alone and ca. 20,000 total in British Columbia and the adjacent United States. Individual birds ranged as far south as Oregon. The population then crashed rapidly, so that by 1959, 2000–3000 individuals remained, and their range had contracted to encompass just greater Vancouver. The population remained about that size through 1980, but by the mid-1990s probably numbered fewer than 100 individuals. The last two known individuals died in 2003 (Self 2003). Reasons for the decline suggested by Johnson and Campbell (1995) include maladaptation to the Vancouver climate in recent decades, increased competition with starlings (*Sturnus vulgaris*) (which invaded British Columbia in the early 1950s), changes in building structures (fewer ledges and crevices), and loss of agricultural land to urban development.

Budgerigars (*Melopsittacus undulatus*) were imported by the thousands into the United States in the first half of the 20th century, and many aviculturists reared them in Florida (Pranty 2001). Some escaped, and large numbers were deliberately released beginning in the 1950s. Wild birds bred in natural and artificial cavities, and, as nestboxes became more popular, in wooden nestboxes. By the early 1970s, they ranged on the Gulf Coast from Pasco to Sarasota counties (160 km), though established populations were largely or wholly near the coast. At their peak, in the late 1970s, at least 20,000 budgerigars occupied the central

Gulf Coast of Florida. Elsewhere in Florida, though they were frequently reported, breeding was at best inconsistent and never extensive. By the early 1980s, range and numbers of budgerigars declined along the Gulf Coast, and breeding was confirmed in only five counties. By the mid-1990s, they were completely gone from Florida except for small numbers along part of the coast of Hernando and Pasco counties (ca. 30 km). Pranty (2001) believes that possibly 200 individuals remain, a greater than 99% decline in numbers since the late 1970s, and he feels the bird will eventually disappear from Florida entirely.

As for what caused this precipitous decline, Pranty (2001) concedes that it is mysterious, and although he rules out arguments that disease or some winter freezes were crucial, the other suggestions are all very tentative and none is strongly supported by existing data (which are often scant). He feels competition over nesting sites is a possibility. Starlings, with increased breeding populations in Florida from 1969 through 1983, probably outcompete them for natural cavities. Budgerigars therefore probably depended heavily on nestboxes, for which they competed with introduced house sparrows (*Passer domesticus*). However, nest boxes are believed to have declined in much of the Gulf Coast region, as tourism tended to replace retirement communities. The hypothesis of competition with sparrows for nestboxes is weakened by the fact that house sparrows in Florida actually declined between 1966 and 2000, significantly so between 1966 and 1979 (Sauer et al. 2001; USGS 2002).

Trexler et al. (2000) document several local crashes of introduced fish species in the Everglades. Probably the most dramatic is the crash of the Mayan cichlid (*Cichlasoma urophthalmus*). This Central American fish was first detected in 1983 in Everglades National Park. It spread rapidly throughout the region, probably aided by fishermen. Courtenay (1997) painted a drastic picture of its potential impact. However, the population peaked in 1993, when it was so numerous that, at one continuously censused site, it comprised more than 40% of all fishes trapped. Then it crashed so that by 1996 it comprised only 3% of all fishes trapped, and its numbers were less than a fourth of peak numbers. Since then its populations have fluctuated around this low number, but they have not recovered to anywhere near the previous peak. Whether this is a permanent decline or part of a long-term boom-and-bust cycle, no one knows. The crash is unexplained, but it is correlated with annual temperature minima (Trexler et al. 2000).

### **Collapse of island and other very restricted populations**

Another prominent, widespread invader seems typically to undergo a characteristically rapid population expansion followed by a crash: the giant African snail, *Achatina fulica*, introduced to many Pacific islands (Mead 1979; Pointier and Blanc 1985). Initially there is an explosive build-up, with large, vigorous individuals of healthy mien. The population remains at this plateau for an indefinite period, and then there is a general decline, often rapid. Not only do numbers fall, but large specimens become rare or disappear entirely, and many shells are distorted. Locally there is even extinction. Mead (1979) describes a disease syndrome in these populations, with a high frequency of leukodermic lesions associated with the bacterium *Aeromonas hydrophila*, but exactly what triggers the epizootic is mysterious because the bacterium is omnipresent. Waterhouse and Norris (1987) suggest that peak populations may exhaust their food and induce starvation, whereas Mead (1979) says that any stress may make the population more susceptible to the bacterium. He also points to evidence that introduced giant African snail populations typically are genetically depauperate, which might make them more susceptible to a disease. Of course, any pathogenic disease is more likely to become epidemic as a population becomes denser. From the standpoint of the pathogen, there is a threshold host density, or breakpoint, necessary to maintain a rate of transmission high enough to allow the pathogen to persist (McKendrick 1940; Macdonald 1965; Anderson 1982). Below this breakpoint, the pathogen population crashes; above it, the host population may crash. It is possible that these *Achatina* populations crashed once they surpassed the breakpoint.

The tragedy here is that the predatory rosy wolf snail (*Euglandina rosea*) from Florida and Central America was widely introduced to control the giant African snail, which it did not do, because the giant African snail is too large (Mead 1979; Civeyrel and Simberloff 1996). But the rosy wolf snail is now considered one of the worst invasive pests in the world (Stein and Flack 1996; ISSG 2001), and it has caused at least 30 global species extinctions of endemic island snails (Civeyrel and Simberloff 1996; Cowie 2001). Giant African snail populations collapsed on islands to which the rosy wolf snail was never introduced, such as Huahine-nui, as on islands to which it was

introduced (Tillier and Clarke 1983; Pointier and Blanc 1985). And now a predatory flatworm, *Platydemus manokwari*, has been introduced in several places, and may constitute a worse threat to native snails than the rosy wolf snail does (McNeely 2000).

In 1952, a hotelier near San Felice Circeo, south of Rome, purchased several individuals of the Indian grey mongoose (*Herpestes edwardsii*) to control rodents and vipers in his garden (Carpaneto 1989). They quickly escaped and through the 1960s and 1970s spread to nearby areas, including the Circeo National Park. Between 1978 and 1980 they reached their maximum range and were often observed on the shore of Sabaudia Lake in an area of over 10 km<sup>2</sup>. They were frequently seen in picnic areas in the park, feeding on tourist leftovers or handouts. Rangers reported that the polecat (*Mustela putorius*) became rare in that area, and park authorities became alarmed. However, in the early 1980s, without any human intervention, the whole population suddenly disappeared; it was extinct by 1984. No explanation has been given.

Introduced ungulates are famous for rapid irruption upon introduction to islands, without an obvious lag-time, followed by dramatic crashes (Leader-Williams 1988). Typically there is a leveling off as the population exceeds its carrying capacity by overusing vegetation. Physical condition declines, juvenile death rate increases, and there is a crash, especially in many cases when a spell of extreme weather sets in. On a large island, such as the major islands of New Zealand, animals disperse in response to the declining food, so this irruption, leveling off, and crash are seen locally at site after site. But those islands are large enough that, island-wide, some stabilization occurs, albeit at a much lower mean density than at irruptive local peaks.

However, on smaller islands, the crash may be more severe and there is little recovery. On St. Matthew Island (Klein 1968), 332 km<sup>2</sup>, an original propagule of 29 reindeer (*Rangifer tarandus*) was introduced in 1944 and increased very quickly, reaching 1350 in 1957 and 6000 by 1963. There was then a dramatic crash down to 42 individuals in 1966. The problem was that the reindeer depended on lichens as their winter forage, and these were severely overgrazed as the population increased. The reindeer were thus in poor condition, and a particularly severe winter killed most of them. Because lichens recover very slowly from grazing and trampling even when reindeer are absent, and there was no other suitable winter forage, the reindeer population has not recovered. A very similar trajectory was

followed on St. Paul Island (107 km<sup>2</sup>) (Scheffer 1951). Originally 25 reindeer were introduced in 1911. The population increased steadily to 2000 individuals in 1938, then declined to only 8 in 1950, after which it stabilized at ca. 250.

Even among native continental populations, reindeer undergo more dramatic population fluctuations than other ungulates (Couturier et al. 1990). For example, the George River herd of Quebec and Labrador declined by 81% from 1977 to 1979, then irrupted with a 1863% increase 1 year later (Couturier et al. 1990).

Sometimes an island decline is gradual rather than abrupt. In the Hawaiian islands, the Java sparrow (*Lonchura oryzivora*) may have been introduced once or twice in the 19th century but did not persist. However, in 1964 they established on Oahu and began an explosive increase in range and numbers (Berger 1981), to the point where they are now on all the major Hawaiian islands and were the most numerous seed-eating birds in the 2000/2001 Christmas counts on Oahu and Kauai (Pratt 2001/2002). However, in the Mascarenes, there was a very different trajectory. They survived, established, and spread on both Mauritius and Île de la Réunion, and then, after long residences, underwent a puzzling decline to extinction (after 133 years on Mauritius) (Simberloff 1992). Meinhertzhagen (1912), Staub (1976), and Cheke (1987) have argued that these declines and extinctions were caused by replacement of cereal crops by sugarcane, while Rountree et al. (1952) ascribe it to a large cyclone in 1892, but this bird has thrived on other islands where sugarcane is dominant, and surely a cyclone could not have eliminated it if its population and range had not already been drastically lowered.

The extinction on Mauritius of the yellow-crowned or cape canary (*Serinus canicollis*) is similarly mysterious (Simberloff 1992; Jones 1996). This species was widespread and common on the island for more than a century. Then it rather quickly dwindled at the end of the 19th century and disappeared entirely in the 1920s. Efforts to reintroduce it have failed. A disease has been proposed as the reason for this decline and extinction (Cheke 1987), but none was ever identified. Several authors suggested the same cyclone mentioned in the previous paragraph (references in Cheke 1987), but this species was present long after that event. Jones (1996) observes that the decline of this canary began around the time the village weaver (*Ploceus cucullatus*) was introduced, in 1886, but the weaver is rare in upland areas; both birds continue to coexist on

Île de la Réunion, with no overlap of their elevational ranges (Barré and Barau 1982; Jones 1996).

The red-billed leiothrix (*Leiothrix lutea*) has undergone a similarly unexplained and more abrupt decline in the Hawaiian islands. It was released on Kauai at least by 1918 and on all the other major islands in 1928–1929. Its populations grew rapidly, and it spread on all the islands (Berger 1981). By 1967 it was one of the most common birds in the Audubon Christmas counts on Oahu. However, it then crashed, and in 1968 only 18 were counted there, and none in 1969. The crash on Oahu persisted through 1987 (Williams 1987), but the leiothrix has undergone somewhat of a resurgence there beginning in the mid-1980s, with the last 3 Christmas counts at Honolulu showing 75, 151, and 87 individuals (Pyle 1999/2000, 2001; Pratt 2001/2002). It has also crashed on Kauai (Berger 1981; Male and Snetsinger 1998). However, it never recovered, and the red-billed leiothrix has apparently disappeared from Kauai (Male and Snetsinger 1998).

Lakes are habitat islands and in North America have been invaded by Eurasian watermilfoil (*Myriophyllum spicatum*), one of the worst aquatic weeds of the United States (Cox 1999). Arriving in 1942 near Washington DC (Engel 1995), this species spread throughout the east and midwest, as well as to many sites in the west, often forming dense masses that transform the habitat, especially in small, shallow lakes (Cox 1999). Collapses of populations have been documented in many lakes across the northern United States (see, e.g., Nichols 1994; Creed and Sheldon 1995; Newman and Biesboer 2000). Some of these declines have been very rapid and without substantial recovery. Many explanations had been proposed (e.g., nutrient depletion, pathogens, competition with native macrophytes, overgrowth by epiphytes), but none were consistent with all the data. Creed (1998, 2000; cf. Creed and Sheldon 1995) suggests that these crashes are associated with a native weevil, *Euhrychiopsis lecontei*, and they occurred typically 10–15 years after watermilfoil invaded the range of the weevil because it takes the weevil this long to switch from its native host and to build substantial populations.

## Discussion

A striking feature of many of these crashes is that they are mysterious. Of the 17 crashes for which we have presented detailed information, for 10 there is no strong

Table 1. Proposed causes of population crashes of 17 introduced species.

Cause	Species
Competition with other introduced species	<i>Mustela nivalis</i> , <i>Ceratitis capitata</i> , <i>Aedes aegypti</i> , <i>Cakile edentula</i>
Exhaustion of resource	<i>Rangifer tarandus</i>
Parasitism by subsequently introduced species	<i>Euproctis chrysorrhoea</i>
Adaptation by native herbivore	<i>Myriophyllum spicatum</i>
Unknown	<i>Elodea canadensis</i> , <i>Bufo marinus</i> , <i>Acridotheres cristatellus</i> , <i>Melospiza undulatus</i> , <i>Cichlasoma urophthalmus</i> , <i>Achatina fulica</i> , <i>Herpestes edwardsii</i> , <i>Lonchura oryzivora</i> , <i>Serinus canicollis</i> , <i>Leiothrix lutea</i>

evidence suggesting a cause (Table 1). Probably the most dramatic of all the large regional crashes is that of *E. canadensis* in Great Britain, and the cause of this decline is perplexing. The original infestation was clonal, and Arber (1920), drawing on the conventional wisdom of the time, suggested a sort of clonal senescence. However, aside from the fact that no such senescent mechanism is now known, the plant subsequently achieved sexual status in Britain (Simpson 1986) but the invasion remained restricted. Elton (1958) tentatively suggested some subtle nutritional deficiency as the cause, but there has been no research to explore this possibility. The fact that similar but less well-documented declines have been observed in independent introductions elsewhere in Europe as well as in the native range is all the more intriguing.

For the cane toad, another species for which several declines have been documented but no specific cause is strongly implicated, there has been some recovery of some crashed populations (W. Freeland, pers. comm. [2002]). It is possible that the crashes of this species are just a particularly dramatic example of the fact that many amphibian populations typically undergo drastic vicissitudes, often because of rainfall or lack thereof at just the right time. This is one reason for persistent controversy over whether there is really a worldwide decline in amphibians (cf. Pechmann and Wilbur 1994; Travis 1994).

For one of the seven regional collapses (the cane toad) and one species that has frequently crashed on islands (the giant African snail), a pathogen has been

suggested as causal, but in neither case is there strong evidence for this hypothesis, and for the toad no pathogen has been identified that might have caused the decline. Pathogens are often invoked, *faute de mieux*, for unexplained population declines of both native and introduced species (among the latter, the yellow-billed canary and Eurasian watermilfoil), but surely this should be an explanation of last resort, especially in the absence of an identified pathogen.

Of the seven invasions that collapsed over large regions, perhaps only for the least weasel on New Zealand, the yellow fever mosquito in Spain, the medfly in New South Wales, and the sea-rocket in California and Australia do explanations seem highly convincing based on all available evidence (competition with the stoat for the weasel, with the Asian tiger mosquito for the yellow fever mosquito, with the Queensland fruit fly for the medfly, and with *C. maritima* for the sea-rocket), and for the first two of these invasions there is no direct empirical, on-site demonstration that the claimed mechanism is operating. It is interesting that, for these four species, competition with a subsequently (or contemporaneously, in the case of the least weasel) introduced species is believed to have caused the crash. For two other species among more restricted invaders (the crested mynah and the budgerigar), competition with another invader has also been invoked as a cause of decline. As with most claims of interspecific competition, there is rarely direct evidence of a limiting resource and/or a mechanism, and some of these claims seem *ad hoc*. However, for the Mediterranean fruit fly in New South Wales, experimental research on a similar case in the Hawaiian islands (Keiser et al. 1974) greatly strengthens the hypothesis, just as experimental research on local declines of the yellow fever mosquito in the New World (e.g., Juliano 1998) bolsters the argument that competition has led to its disappearance from Spain. For a few other declines of introduced species, direct experiment or meticulous observation strongly implicates interspecific competition. For example, Luck et al. (1982) experimentally elucidated the replacement of the wasp *Aphytis lingnanensis* by *Aphytis melinus*; these were two of a series of three introductions of species of *Aphytis* for biological control of California red scale (*Aonidiella aurantii*) in which each species thrived, spread, but then contracted its range in the face of a subsequently introduced congener (Clausen 1978). By contrast, the wasp *Aphidius smithi*, released in North America to control the pea aphid

(*Acyrtosiphon pisum*), was largely replaced by the subsequently released *Acyrtosiphon ervi* (González and Gilstrap 1992). Although the timing and extent of the replacement strongly suggest that the later invader caused the decline of its predecessor, laboratory experiments have failed to explain the observation or establish a mechanism.

Often the more or less simultaneous decline of an earlier invader in the wake of a subsequent invasion leads to a reasonable conclusion that the latter has outcompeted the former, though direct evidence and even speculation about a mechanism are lacking. For instance, Allee et al. (1949) observed that, through medieval times, the Asian black rat (*Rattus rattus*) was the common house rat in Europe. The Norway rat (*Rattus norvegicus*), also from Asia, arrived in the 18th century and supplanted it as the common house rat. More recently, the black South American fire ant, *Solenopsis richteri*, which spread north from Mobile, Alabama, beginning in 1918, has been replaced by the red South American fire ant, *Solenopsis invicta*, everywhere within the range of the latter except in northern Mississippi (Tschinkel 1993), while hybrids between the two species are found in northern Mississippi and Alabama (Vandermeer 1986) and southern Tennessee (pers. observ.). The red fire ant almost certainly caused the retreat of the black fire ant, but the mechanism is unknown.

The crashes of reindeer populations on St. Matthew Island and probably St. Paul Island as well result from the confluence of typically drastic population fluctuations in this species, overuse of resources, and inability (because these were small islands) of populations to migrate so as to allow local vegetation recovery. Though a cold winter may have triggered the crash (as in mainland populations, e.g., Couturier et al. 1990), the collapse was inevitable because of the restricted area.

Other very restricted introduced populations, particularly on small islands (such as those of the Java sparrow and yellow-crowned canary on Mauritius, or the red-billed leiothrix on Kauai) but also at other sites (e.g., the grey mongoose in Italy) may be doomed to extinction, whereas the same species in a larger site would have persisted. This is even true if drastic population fluctuations do not typify a species. Such extinctions need not be an inevitable result of demographic stochasticity, which requires extremely small population sizes (Lande 1993), even smaller than those of the mongoose, sparrow, canary, and leiothrix.



Absence of metapopulation dynamics is an alternative possibility for collapse of invasions in small sites. It is possible that, in a larger area, a persistent metapopulation would have been established, so that local extinction would have been redressed by recolonization from nearby occupied sites. Although most clusters of populations termed 'metapopulations' have not been shown to act as metapopulations in this way (Harrison 1991; Harrison and Taylor 1997), at least a few (e.g., the pool frog, *Rana lessonae* [Sjögren Gulve 1994]) match this model. In such a species, an introduction that could not lead to a metapopulation simply because of inadequate area would be doomed, when it might have persisted indefinitely had a metapopulation been possible.

As for the practical significance of the fact that some well-established invasions collapse spontaneously, it is probably not huge. If this were a common phenomenon, it might be construed as an argument for a do-nothing management option. We do not claim that our survey is anywhere near exhaustive. For example, Pysek et al. (2002) refer to several introduced plants in the Czech Republic whose populations have waned greatly, though they provide no quantitative data to distinguish these from species that simply stopped spreading. However, though there are a few well-documented cases of decline, they are far fewer than examples of time lags before population explosions (cf. Kowarik 1995; Crooks and Soulé 1996, 1999). In those few instances in which independent populations of a species seem to collapse characteristically – such as *E. canadensis* and *A. fulica* – these histories argue for careful consideration of the do-nothing option. Aside from the expense invested in control measures, such measures might have non-target impacts that could be avoided. The introduction of *E. rosea* in a failed attempt to control *A. fulica* is doubly tragic; not only did it not work, but *Achatina* populations collapsed on their own whether or not the predator had been introduced.

It should be borne in mind, however, that, even in those few cases where there may be a reasonable expectation of decline in the absence of a specific management action, an introduced species can leave a trace long after it is gone. For example, an introduced species that reaches high densities, such as *E. canadensis* or *A. fulica*, and persists for a few decades could leave a permanent scar by causing extinction of a native species. Or an introduced plant may produce an allelopathic chemical that remains in the soil long after the plant has disappeared (see, e.g., Rice 1984; Grime 2001). The ecosystem impacts of the reindeer will

persist on St. Matthew Island even though they are now scarce, because the previously high populations overgrazed lichens, which are very slow-growing. It is also possible that a rapid crash of a formerly numerous invader could have an undesirable impact, especially if an introduced species has wholly or largely replaced a native species in interactions with other species. This was precisely the issue, for example, with the campaign to reduce populations of *Tamarix* spp. in the US southwest by biological control: the endangered southwest willow flycatcher (*Empidonax traillii extimus*) now nests in *Tamarix*, and there was concern that abrupt decline of the tree would be detrimental to the bird (Baskin 2002).

Prediction of the fate and impact of introduced species remains notoriously difficult, especially without detailed ecological knowledge of the invader and the recipient system. What appear at least superficially to be spontaneous population crashes are a minor phenomenon in invasion biology, but they do occur and demand both scientific attention and, in a few instances, consideration during the formulation of a management response.

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