

CHAPTER 13

Attributes of Invaders and the Invading Processes: Vertebrates

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13.1 INTRODUCTION

Population biologists have long wondered why some animals are extremely successful invaders (colonists), while close relatives are not. Are there special evolutionary attributes of species that tend to make some better than others at entering new communities and thriving in them? Are there any general rules that would permit an ecologist to predict which of an array of exotic species might be a potential invader (or perhaps more importantly, an economically damaging invader)? Or does the success of invaders normally depend on an interaction between attributes of a potential invader and features of the communities to be invaded? Or does chance normally dominate invasion processes? These questions are examined in this chapter from the viewpoint of vertebrates; it is based in part on earlier work on the attributes of animal invaders (Ehrlich, 1986).

13.2 WHAT IS AN INVADER?

I use the two terms 'invading species' and 'colonizing species' interchangeably for an organism that easily crosses barriers (with or without the help of *Homo sapiens*), rapidly establishes itself on the other side, and then expands its numbers and range relatively quickly in its new habitat. Most of the really successful animal invaders are ones that, for a variety of reasons, are able to cross major barriers because of their relationship with *Homo sapiens* (Elton, 1958). Thus the coyote has been able to expand its range because areas of human disturbance which are impassable barriers for wolves are relatively hospitable to *Canis latrans*. The principal exceptions to the need for a 'human connection' are creatures such as tardigrades that are passively wind dispersed and have become ubiquitous. No larger animals, however, approached ubiquity until humanity did.

13.3 PAIRED COMPARISONS

One approach to the problem of why some species are very successful invaders and others are not is to compare closely related species with very different records. The examples of successful versus unsuccessful sets of vertebrate species that I compared previously (Ehrlich, 1986) were: *Homo sapiens* vs other great apes; coyotes vs wolves; black and Norway rats vs other *Rattus*; house sparrow vs tree sparrow; blue-spotted grouper vs other groupers; and *Lutjanus kasimira* vs other snappers.

These cases clearly are dissimilar. At one extreme there are organisms such as the rats and coyotes that have invaded without any *deliberate* aid from humanity. In the middle are the sparrows, which were purposely introduced, but without systematic thought as to consequences (many avian species have been introduced around the world by colonists from Western nations who wanted familiar birds around them). At the other extreme are the reef fishes, which were transplanted by biologists with considerable knowledge of the organisms to be moved and the communities into which they were being introduced.

It seems obvious that the characteristics of successful invaders in these three groups might be very different. An additional category of invaders for which I did no paired comparisons are vertebrates introduced as biological control agents. It may, indeed, be stretching the definition of 'invader' to include them. After all, they are introduced specifically because it is believed, sometimes after very careful investigation, that an especially suitable environment—an empty niche—is awaiting. Ordinarily that most basic of resources, food, is present in superabundance.

Nonetheless, the fate of biocontrol agents can be instructive, and their introduction does not seem so different in principle from the introduction of, say, game birds or game fishes. For example, ferrets (*Mustela putorius furo*—a domestic version of the European polecat, *M. putorius*), stoats (*Mustela erminea*), and weasels (*Mustela nivalis*) were all introduced in large numbers into New Zealand in the second half of the last century. It was hoped that these energetic predators would end that island nation's plague of rabbits, but they did not (rabbits were eventually brought under control in the 1950s by spreading poisoned bait from airplanes and night-shooting). Interestingly, the mustelids were differentially successful; today stoats are common everywhere, ferrets are locally abundant, and weasels are generally rare (King, 1984).

Thus three organisms deliberately introduced into a land with few competitors and abundant prey had little influence on the size of the prey populations, and one of them was relatively unsuccessful. All three species are native and sympatric in Europe and the stoats and weasels have extremely broad distributions, suggesting that physical conditions in New Zealand are unlikely to be more favorable to stoats than to weasels. Instead, the differences seem to be due primarily to different diets (King, 1984). The stoat ordinarily feeds on small

rodents but does attack animals, such as hares, that are much larger than itself (Nowak and Paradiso, 1983). It dined in New Zealand on birds and to a lesser extent rabbits, possums, and rats. The large ferret (about eight times as heavy as the stoat) was originally bred, in part, to drive rabbits from their burrows. When rabbits were brought under control by other means, ferret populations declined.

The weasel is somewhat smaller than the stoat and has similar habits. The most likely explanation for the relative failure of the weasel is found in the abundance of prey of different sizes. In England its most common prey are voles (*Microtus*, *Arvicola*, *Clethrionomys*), which are much more abundant in woodlands than are their ecological equivalents, feral house mice, in New Zealand (King and Moors, 1979). Even though the three mustelid species were imported with the goal of controlling an abundant pest, their relative success seems to have largely been determined by their diets. These appear to be sufficiently different, however, so that all three species are able to coexist. These biocontrol introductions thus follow a pattern reminiscent of that seen in the lizard and bird faunas of the Caribbean and Hawaiian Islands respectively. There, closely related species with diets (as judged from body size or bill morphology) sufficiently different have coexisted, whereas the presence of close competitors has repeatedly led to extinctions (Roughgarden, 1986; Moulton and Pimm, 1986). Such patterns, of course, were first brought to our attention by Lack (1947).

13.4 ARE SOME SPECIES JUST NATURALLY GOOD COLONIZERS?

Evidence that intrinsic characteristics of vertebrate species can predispose them to be successful invaders comes from instances of some species *repeatedly* being successful invaders while close relatives *repeatedly* are less successful. For example, the house sparrow (*Passer domesticus*) occupied the entire United States in a little over 50 years after it was first successfully introduced. It had the help of additional releases by *Homo sapiens* and, possibly, an ability to disperse via railroad freight trains (Robbins, 1973). Other introductions have led to extensive ranges in South America, southern Africa, Australia, and New Zealand. The closely related tree sparrow (*Passer montanus*) has a range in Eurasia almost as large as that of the house sparrow. It was successfully introduced into North America at St Louis in 1870, but until the Second World War it was still largely confined to the St Louis area. Since then the tree sparrow has spread into central Illinois (Barlow, 1973), but it has not colonized with anything like the vigor of its close relative. Indeed, in some places it appears to have suffered some competitive displacement by *P. domesticus*. It is slightly smaller than the house sparrow, and in areas of eastern Asia where the house sparrow does not occur, *P. montanus* becomes a much closer commensal of humanity (Summers-Smith, 1973). The tree sparrow was introduced into Australia at about the same time as the house sparrow, but also has a much more restricted range there as well. It did not

successfully colonize New Zealand, a set of islands that in general have proven exceedingly vulnerable to occupation by exotics, but it has colonized some islands in the western Pacific, while failing to 'take' in Bermuda.

A similar case to that of the two sparrows is that of the rock dove or domestic pigeon (*Columba livia*) and its congener, the woodpigeon or ring dove (*Columba palumbus*). The former has spread from a presumed primitive distribution along the coasts of southern Europe, south Asia, and North Africa to occupy most of the northern hemisphere and substantial portions of the southern. The woodpigeon has a similar but larger original homeland, extending much further inland in Eurasia than did the rock dove. The woodpigeon reaches high densities feeding on crops, and is considered a pest; it thrives near human habitation. Yet it has hardly spread at all except by gradual extension of its original distribution. Two attempts to introduce the woodpigeon into North America, including one of 30 birds in New York, failed.

The extraordinarily successful invaders are the black or roof rat, *Rattus (Rattus) rattus*, and the Norway or brown rat, *R. (R.) norvegicus*. Both species are found throughout the world generally in association with human beings. The Polynesian rat, *R. (R.) exulans* is widely distributed in Southeast Asia, having spread through the islands of the Pacific by accompanying prehistoric human migrations (Wodzicki and Taylor, 1984). But more than 40 other species of the subgenus *Rattus*, a few of which are commensals with *Homo sapiens* in limited areas, have not become as widespread as even the Polynesian rat, let alone ubiquitous.

Gray and red wolves (*Canis lupus* and the closely related *C. rufus*) have undergone a dramatic decline in North America as a result of depredation by human beings (Nowak and Paradiso, 1983). With the exception of a gray wolf population in Minnesota and scattered reds in the coastal swamps of Louisiana and Texas, wolves are essentially gone from these coterminous United States. Their congener, the coyote (*Canis latrans*), with which they hybridize easily even though the species have had separate evolutionary histories since the late Pliocene, has proven to be a successful invader. The range of the coyote expanded dramatically while those of its relatives were shrinking.

As a final example, *Homo sapiens* has been the most successful invader of all, while its closest living relatives, *Pan troglodytes* and *Gorilla gorilla*, have been pushed almost to the brink of extinction.

13.5 CHARACTERISTICS OF GOOD INVADERS

What sort of biogeographic, ecological, genetic, and physiological attributes might one expect *a priori* to characterize successful and unsuccessful invaders? Table 13.1 (modified from Ehrlich, 1986) indicates some possible distinctions extracted from the ecological literature.

Most of these characteristics are elements of what can be summarized as 'broad

Table 13.1. Possible concomitants of invasion potential

Successful invaders	Unsuccessful invaders
Large native range	Small native range
Abundant in original range	Rare in original range
Vagile	Sedentary
Broad diet	Relatively restricted diet
Short generation times	Long generation times
Able to shift between <i>r</i> and <i>K</i> strategy (fishes)	Unable to shift
Much genetic variability	Little genetic variability
Gregarious	Solitary
Female able to colonize alone	Female unable to colonize alone
Larger than most relatives	Smaller than most relatives
Associated with <i>H. sapiens</i>	Not associated with <i>H. sapiens</i>
Able to function in a wide range of physical conditions	Only able to function in a narrow range of physical conditions

ecological amplitude.' Comparisons of closely related vertebrate species do not always support these *a priori* distinctions. At one extreme, there is no obvious reason why the tree sparrow does not colonize as easily as the house sparrow. I am tempted to speculate that *P. domesticus* simply outcompetes *P. montanus* in areas of human disturbance. Outside their native communities in Eurasia those may be the only areas invadable by either.

Almost as obscure is the reason for the relative lack of success of the Polynesian rat (known as the kiore in New Zealand) compared with black and Norway rates. The kiore has become a 'house rat' in Vietnam, Laos, Kampuchea, Malaya, Thailand, and Burma, and in most of these and the Philippines and Indonesia it is a serious pest of rice in the field and in storage. After it reached New Zealand, the kiore apparently played a role in the decimation of the flightless bird fauna there and is still a serious predator of birds' nests, native invertebrates, lizards, and so on. So on one hand the kiore seems to be quite a successful invader. On the other hand, with the arrival of black and Norway rats on New Zealand, the kiore declined, and it is now largely restricted to small, offshore islands. And the kiore has never spread northwestward through Eurasia or over the Australian continent, and has never, like *R. rattus* and *R. norvegicus*, invaded Africa or the western hemisphere. The kiore is smaller than the other two, but otherwise it seems to be their equal in invasion potential—and the house mouse is smaller still, and much more widely distributed. It is possible that poor competitive ability of the kiore (relative to the two ubiquitous rats) *on ships* has limited its distribution by denying it a means of dispersal.

The difference between invading coyotes and declining wolves is, in contrast, relatively clear. It seems to be a function of diet and social structure. Coyotes eat small game and carrion, wolves hunt large mammals cooperatively. Large areas

disturbed by humanity are barriers to wolves, especially since their social behavior makes them easy prey for hunters. Coyotes can cross the worst of these areas and thrive in many of them.

The reason that *H. sapiens* is the most successful colonizing primate is certainly its extreme employment of cultural evolution, which permitted the development of artifacts and survival techniques (clothes, shelters, tools, weapons) that allowed expansion into previously inaccessible habitats.

One characteristic of organisms that are good invaders is an ability to tolerate a wide range of physical conditions. Classic examples are the mosquito fish, a poeciliid (*Gambusia affinis*), which because of its use as a biological control agent now may be the most widely distributed species of freshwater fish, and the Mozambique tilapia, *Tilapia (Oreochromis) mossambicus*. *Gambusia* can survive in water as cold as 6° C and as hot as 35° C, extremely low oxygen concentrations, and salinities as high as twice that of seawater, given time to acclimate (Ahuja, 1964). *Tilapia* can tolerate 13–37° C and a wide range of oxygen saturations and salinities.

Both of these fishes also have reproductive strategies that appear to help make them successful colonizers (Bruton, 1986). *Tilapia mossambicus* is able to switch from a precocial to an altricial strategy when it finds itself in an unstable environment, relatively free of competitors, and to a more precocial strategy when competition is severe. *Gambusia affinis* is a live-bearer that produces a few well-guarded young and preys on the young of competitors. It seems possible, though, that physiological tolerances are more important, since other *Tilapia* are able to adjust their reproductive strategies and other *Gambusia* species share the live-bearing reproductive strategy of *G. affinis*. What we do not know is the degree to which the 'popularity' of *T. mossambicus* and *G. affinis* with introducers has affected their success relative to that of congeners.

Different innate responses to physical factors of the environment appear to explain the contrasting successes in North America of the European starling (*Sturnus vulgaris*) and the closely related Southeast Asian crested myna (*Acridotheres cristatellus*). While the former took the continent by storm, the latter, introduced into Vancouver in 1897, established itself but did not spread significantly. Studies in Vancouver, where the two species are sympatric, indicated that a lack of attentiveness to incubating eggs, and their resultant low temperature, led to low hatching rates. Furthermore, the mynas fed their young more low-protein vegetable food than did the starling, producing lower growth rates. In both cases the mynas retained habits appropriate to their tropical homelands, and relatively inappropriate to British Columbia (Johnson and Cowan, 1974). There must be other differences between these two species, however, since the myna has been a failure as a colonist virtually everywhere. For example, it took at least three attempts to establish it in the tropical Philippines where it has spread only in the vicinity of Manila (Long, 1981). It also has not managed to spread southward from Vancouver. Perhaps the myna simply is

unable to build a large enough population to provide sufficient dispersers; perhaps it can only persist in areas of high human disturbance.

Being native to a relatively stressful environment may well be one characteristic of a good invader. Many temperate zone or arid zone vertebrate species (or species whose natural ranges include such areas) successfully invade rather benign, moist, tropical habitats. For example, numerous naturalized members of Hawaii's tropical lowland bird fauna came from more rigorous climes. At least among birds there are very few examples of species indigenous to benign environments successfully invading stressful habitats (Long, 1981).

13.6 SIZE OF THE INTRODUCTION; FREQUENCY OF ATTEMPTS

Given intrinsic attributes that make an organism a potential invader, it would seem that the size of the introduction should be an important factor in the success of a given invasion. Larger invading groups should bring with them a larger ration of genetic variability, and should be less subject to stochastic extinction before there is a chance for the population to increase in size. What data there are on purposeful introductions, however, do not universally support this view. For instance, Himalayan tahr, the only vertebrate species to invade relatively undisturbed ecosystems in South Africa, did so by building a population based on a single pair. In that same nation the European starling population was based on an introduction of 18 individuals, and Indian mynas on perhaps 20–30. In contrast, an introduction of about 200 rooks (*Corvus frugilegus*) failed, even though there are few South African crows, and the Indian house crow has managed to establish itself in Durban on the basis of much smaller groups of invaders (Brooke *et al.*, 1986).

An analysis of avian introductions in Australia showed those of foreign birds to be statistically more likely to succeed if propagule number was large, while there was no significance of propagule size when Australia birds were translocated (Newsome and Noble, 1986). Overall one suspects that invasions will be more likely to succeed if the number of individuals introduced is large, everything else being equal. But it is a weak statistical association, and everything else never equal.

Everything else is never equal because random factors, environmental and demographic stochasticity but possibly also genetic stochasticity, must play a substantial role in the success of invasions. This is evident from repeated failures of 'good invaders' to become established. A pattern of frequent failure has been best documented for birds (Long, 1981); even European starlings and common mynas did not succeed in establishing themselves after each introduction. Eight pairs of house sparrows, one of the most successful colonizers, were released in New York in 1851, but failed to become established. Another 50 did not manage to establish a population when introduced in 1852. The first successful release was another 50 in 1853 (Long, 1981). The European starling did not become

established in two attempts in New York (1872, 1873), and 35 pairs or more released in a Portland, Oregon park around 1890 did not lead to colonization. Success came immediately, however, from the introduction in New York of two flocks of some 60 (1890) and 40 (1891) birds. On the other hand, attempts in 1875, 1889 and 1892 in Quebec all failed, even though the advancing front of starlings dispersing from the New York introductions swept through Quebec by 1920. There were several unsuccessful introductions of rooks into New Zealand before it finally 'took'. The ring-necked pheasant (*Phasianus colchicus*) is one of the most successful temperate-zone invaders, and yet its introductions have only succeeded about half the time (Long, 1981). Repeated early attempts to establish the species in the United States failed in areas where the birds are now plentiful.

Lack of repeated colonization attempts may be the principal reason that the woodpigeon has not spread as far as has the rock dove. Yet other birds, especially columbids such as the Senegal turtledove (*Streptopelia senegalensis*), spotted turtledove (*S. chinensis*), and the peaceful dove (*Geopelia striata*) seem to succeed whenever they are released. The frequency of failure for most species is probably considerably higher than indicated in the literature, however, since records of successes are much more likely to get into print than those of cases where establishment did not follow introduction.

13.7 INVASIBILITY

Some large regions may have communities that are generally less invisable by vertebrates than others. South Africa, for example, seems to be relatively resistance, Brooke *et al.* (1986) suggest that this is because the tip of Africa is a temperate extension of a large, tropical continent with an impressive suite of native predators and pathogens that evolved in the tropics and moved south. In contrast, New Zealand was 'easy'—with no native mammalian predators and very few predatory birds. European rabbits, a plague in New Zealand, have only been successful on offshore islands of South Africa. Rooks failed to invade South Africa, but succeeded in 'taking' in New Zealand and spreading slowly in spite of control measures there (Long, 1981). Mammals seem to have been less successful at invading Eurasia than other continents, possibly because it has a more diverse mammalian fauna than the New World (de Vos *et al.*, 1956).

Indeed, when the reasons for resistance of areas to invasion are discussed, competition is the one that seems most frequently mentioned. Support for this view is seen in the impressive *lack* of success that exotic birds have had in New Zealand forests not disturbed by humanity (Diamond and Veitch, 1981; Clout and Gaze, 1984)). On the islands of New Zealand's Hauraki Gulf, which are virtually devoid of mammalian predators and have no introduced browsing mammals, six exotic passerines (five from Europe and one recently self-introduced *Zosterops* from Australia) are essentially absent from climax native

forest (Diamond and Veitch, 1981). On one offshore island, Cuvier, there were once cats, wild goats, and domestic stock, and four European bird species and the *Zosterops* were breeding in the forest. In 1959 the cats and goats were removed, and the stock were fenced. In 5 years a dense forest understory had regenerated; the four European exotics had disappeared, and the population of *Zosterops* had declined precipitously. Diamond and Veitch conclude that exotics are excluded from intact climax forest bird communities, and can only invade browsed forests where the native avian community has been decimated and the forest structure has been altered.

Native passerines in Hawaii are almost entirely confined to fragments of relatively undisturbed habitat, mostly above 900 m (Berger, 1981; Scott *et al.*, 1986). A large number of introduced bird species appear to be competing to some degree in the disturbed lowlands, and may be approaching a dynamic immigration—extinction equilibrium (Moulton and Pimm, 1983). The chances of two invading species both persisting is, as discussed earlier, in part an inverse function of their similarity in body size or bill morphology, which are considered an indirect measure of competition. Whether undisturbed Hawaiian bird communities, like those of New Zealand, were originally invasion resistant has not been determined, but seems a reasonable surmise since there are residual lowland forests dominated by native birds.

Thirty-three species of mammals have been successfully introduced into New Zealand, which had no endemic mammals except bats. None of these exotics is confined to areas of severe human disturbance, and several are abundant in native forests (Gibb and Flux, 1973). In contrast, New Guinea has a rich native mammalian fauna—some 200 species—and few successful invaders (Diamond and Case, 1986). Even the black rat is largely restricted to settlements, and the Norway rat is scarce, in striking contrast to the New Zealand situation.

Similarly, the two reptile species that have been successfully introduced to Australia are largely commensal with *Homo sapiens*. Both are geckos (*Hemidactylus frenatus* and *Leptodactylus lugubris*) that live mostly on insects attracted to house lights (Myers, 1986). The only successful amphibian species, is *Bufo marinus*. This organism is an extremely successful invader in many areas, and is not restricted to areas of human disturbance. Its ultimate distribution is expected to be determined by climatic barriers (Floyd and Easteal, 1986).

Detailed work by Jonathan Roughgarden and his colleagues (e.g. Roughgarden, 1986) has shown that the success of *Anolis* lizards invading Caribbean islands is largely a function of the anole community already established. Invasion of islands already containing an anole species of the same size is difficult or impossible, even though the lizard fauna of those islands is depauperate—being depauperate is not in itself enough to make a fauna invulnerable.

The degree to which intact freshwater fish communities are invulnerable is unclear (e.g. Moyle, 1985). There seems, however, little doubt that human-altered systems are more likely to support invaders than undisturbed lakes, rivers, and streams.

13.8 WHAT CONTROLS THE SUCCESS OF INVASIONS?

So far I have focused primarily on broad patterns, but how is the fate of any given introduction determined? It is evident that the success of any given introduction depends on an interaction between the characteristics of the invading species, the communities already established in the recipient area, and that area's physical environment. But, unfortunately, neither invaders nor environments are static. Consider some of the variables on the invader side of a vertebrate introduction:

1. Number of individuals.
2. Sex ratio.
3. Physiological status—are individuals mature, pregnant, at an appropriate state of the breeding cycle, healthy, acclimated, etc.
4. Genetic composition—including ecotype of origin and amount of genetic variability present.
5. Behavioral status—experience of individual(s), social relationships within group.

On the physical/biological environment side of the equation the variables include:

1. Season.
2. Weather.
3. Size and structure of populations of resource organisms.
4. Size and structure of populations of competitors.
5. Size and structure of populations of predators.
6. Size and structure of populations of parasites and pathogens.

Many of these factors are discussed by Bump (1963) in connection with the introduction of grouse into North America. Twelve attempts to establish capercaillie (*Tetrao urogallus*) and 10 to establish black grouse (*Tetrao tetrix*) all failed. The failures occurred even though climatic conditions were very similar in donor and recipient areas, all of the 40 genera of plants known to supply them with buds, leaves, seeds, and berries as food in Europe were present in the recipient area, and the numbers released in most cases should (by standards of successful introductions) have been adequate.

Grouse tend to show cycles of abundance, and Bump attempted to determine if either the state of the cycle of the introduced birds or of native potential competitors could explain the failures. There were, however, no obvious patterns. For example, in the 10 cases of failed capercaillie introductions for which state of cycle of the invaders could be estimated, in two the capercaillie were from populations close to their peak, two on the upswing, and six at the bottom. Seven of the black grouse introductions were made from populations probably near peak abundance, and one on the upswing. The ruffed grouse (*Bonasa umbellus*) is a close North American relative of the two European species. The ruffed grouse

were near the peak of their cycle for 8/12 of the capercaillie and 6/10 of the black grouse liberations.

What, then, could be responsible for the failures? It seems unlikely that these species have their mating behavior in some way deleteriously modified by the process of capture, transport, and release (most were wild-trapped). Capercaillie were successfully reintroduced into Scotland, where they had been exterminated, using 49 individuals wild-trapped in Sweden. Poor condition of individuals after transport could very well be a factor in the lack of success in North America, but the data are inadequate to evaluate this. Bump's basic conclusion is that success in introductions only occurs when all or nearly all the crucial factors are 'in productive conjunction.' This could be modified into an 'invasion law of the minimum'—the success of an introduction is likely to depend on whatever factor (or interaction of factors) is in the least auspicious state at the place and time of the attempt. It is tempting to speculate that grouse are very vulnerable to predators, especially if they are not in prime condition. Ruffed grouse are subject to the depredations of hunters and predators such as foxes, lynxes, feral dogs and cats, goshawks, and great-horned owls and a variety of nest robbers. In the scramble to become established and familiar with new territory, many or most of the introduced birds may become victims. Unfortunately comparisons of predator populations in the North American and Scottish release sites are not available.

There is also a general pattern of lower invasibility in the Tetraoninae (grouse) compared to members of other subfamilies of the Phasianidae, Phasianinae (pheasants and partridges), Odontophorinae (quail), and Numidinae (guinea-fowl) Long, 1981). The chukar (*Alectoris chukar*; Phasianinae), for example, has been introduced with great success to many arid, mountainous parts of western North America. So in this case, as in so many others, there would appear to be subtle interactions between the properties of the invaders and the state of the ecosystem invaded. These interactions may make the probability of a grouse introduction succeeding in broadly 'suitable' habitat always smaller than the probability of success of a ring-necked pheasant (or house sparrow or Norway rat) introduction.

13.9 CONCLUSIONS

Ecologists can make some powerful and wide-ranging predictions about invasions. For instance, vertebrates will generally be more successful invaders than herbivorous insects, since the latter tend to be monophagous or oligophagous and can only colonize places in which suitable plants are already established. Ecologists (on the basis of observed patterns of success and knowledge of their biology) can predict that most organisms will not be successful invaders, and that among those that are invasive, most colonization 'attempts' will fail (due primarily to environmental and demographic stochasticity). Indeed, most of the *a priori* assumptions that I listed, representing an approximation of a

consensus of trained ecologists, seem to be valid in many cases. And the rule that human disturbance will almost always pave the way for vertebrate invasion seems quite robust.

On the other hand, ecologists cannot accurately predict the results of a single invasion or introduction event. Even the arrival of a flock of starlings or house sparrows, or a pregnant Norway rat, in an apparently hospitable area and at a favorable time, is no guarantee of successful establishment.

The inability to make the latter kinds of prediction should not be considered a failure of ecology as a science—it does not necessarily represent a lack of adequate theory or a failure of the discipline (Ehrlich, 1986). Physicists, after all, cannot predict which of two identical radioactive nuclei will decay first or which of a series of nearly identical missiles launched from the same silo will come closest to the target. Moreover the task of ecologists in making predictions about potential invaders and invasions is much more complex. They are attempting to predict the fate of diverse, often little-known organisms launched in varying numbers at diverse, complex, usually barely-studied environments.

In spite of this, ecologists can say a great deal about both the probability of invasion success of different organisms in different environments (and the possible consequences of that success)—even if they can not yet generate probability distributions such as those associated with nuclear decay. Clearly we should strive to develop better predictive tools, including mathematical models for the behavior of invaders in some groups (and most successful models will almost certainly be group-specific). But, considering the enormous complexity of the problem, what can already be predicted is far from trivial.

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