

SEE ALSO THE FOLLOWING ARTICLES

Ballast / Canals / Eutrophication, Aquatic / Great Lakes: Invasions / Invertebrates, Marine / Mediterranean Sea: Invasions / Seas and Oceans

FURTHER READING

- Kasymov, A. G. 1987. *Biota of the Caspian Sea*. Baku: ELM. [In Russian.]
- Mordukhai-Boltovskoi, F.D. 1969. *Guide to fauna in the Black and Azov seas*. Kiev: Naukova Dumka. Ed. Vodyanitsky V. [In Russian.]
- Shiganova, T.A., H.J.D. Dumont, A. Mikaelyan, D.M. Glazov, Y.V. Bulgakova, E.I. Musaeva, P.Y. Sorokin, L.A. Pautova, Z.A. Mirzoyan, and E.I. Studenikina. 2004. Interaction between the invading ctenophores *Mnemiopsis leidyi* (A. Agassiz) and *Beroe ovata* Mayer 1912, and their influence on the pelagic ecosystem of the northeastern Black Sea (33–70). In H. Dumont, T. Shiganova, and U. Niermann, eds. *The Ctenophore Mnemiopsis leidyi in the Black, Caspian and Mediterranean Seas and Other Aquatic Invasions*. NATO ASI Series, 2. Environment. Kluwer.
- Shiganova, T., and H. Dumont. 2010. Non-native species in the inland southern seas of Eurasia. Berlin: Springer.
- Zaitzev, Y.P., and B.G. Alexandrov. 1998. *Biological Diversity*. Ukraine N.Y., U.N. Publ. 7.

PREDATORS

MICK N. CLOUT

University of Auckland

JAMES C. RUSSELL

University of California, Berkeley

Predators are animals that kill other animals for food. Examples of invasive introduced predators extend across the animal kingdom and include many species of insects, spiders, mollusks, fish, amphibians, reptiles, birds, and mammals. Predatory species have been deliberately introduced outside their natural range for a variety of reasons. These include companion animals (e.g., dogs, cats); species introduced as fur bearers, for sport or for aquaculture (e.g., mink, foxes, salmonid fish); those introduced for biological control purposes (e.g., predatory insects, cane toads, mustelids); and many that were simply introduced as novelties or for “faunal enrichment” (e.g., ornamental fish, frogs, birds). Many invasive predators, especially arthropods and rodents, but also snakes and marine mollusks, have also been introduced accidentally with cargoes or by “hitchhiking” in or on vessels.

IMPACTS

The impacts of invasive predators on native species and natural ecosystem processes are arguably more severe than those of other types of introduced species. This is because,

by definition, a predator kills its prey. Predation therefore has a more severe and direct effect than does a herbivore eating part of a plant, or any species (plant or animal) competing with others for resources. An analysis of the IUCN database of known extinctions of species over the past 500 years reveals that most have occurred on islands and that terrestrial vertebrates have disproportionately gone extinct, compared with plants. This analysis also reveals that predation (by itself or in combination with other factors) has been a cause of extinction for approximately 80 percent of all terrestrial vertebrates. Predation by humans has, of course, been a cause of such extinctions in several cases.

The mechanisms by which predation occurs can vary greatly between predators. Some “super-predators,” such as large carnivores, are at the top of the food chain. These predators usually eat entire organisms at any life stage (e.g., young through adult). Other “mesopredators,” such as small omnivores, may rest lower down on a food chain, above their prey but below other higher-order predators. These predators may prey upon only specific life stages of their prey, such as vulnerable young. These relationships between predators and prey in an ecosystem can be represented by simple food web diagrams (Fig. 1). Predators

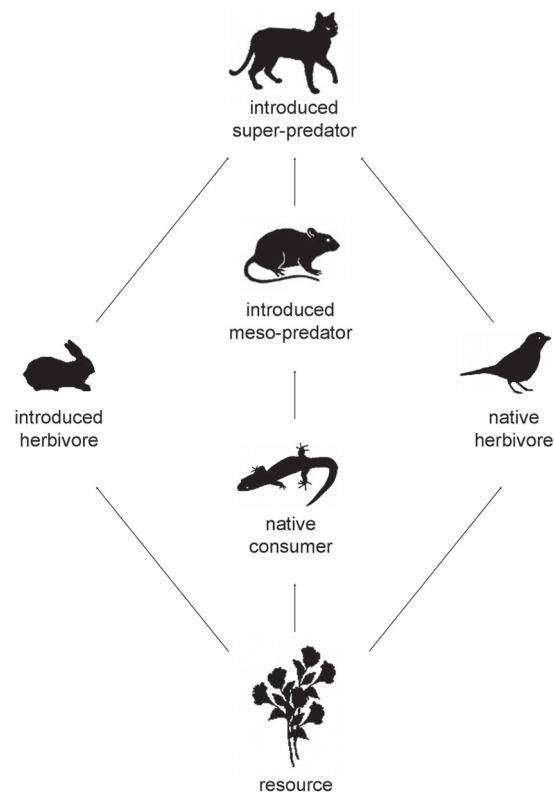


FIGURE 1 Simple food web with two introduced predators. Arrows represent the flow of energy.

can also switch between different prey, based upon seasonal availability or relative abundance of prey species. Because of these intricacies of predation, an individual-level impact (e.g., a predator eating a prey) may not lead to a population-level impact (e.g., a species being affected by predation). The overall population-level effect of predation will depend not just on prey survival rates but also on their relative birth rates (i.e., their ability to replenish their population size).

CASE STUDIES

Dogs (*Canis domesticus*) were among the first predators to be introduced by people. For example, dingoes were introduced to Australia at least 3,500 years ago and contributed to the extinction of several endemic Australian mammals. These included the thylacine, an endemic predatory marsupial that apparently suffered from competition from dingoes. This makes the point that introduced predators can adversely affect other predator species in addition to their prey. Another domestic predator that has been widely introduced by people is the cat (*Felis catus*). The impact of feral cats has been devastating in many ecosystems to which they have been introduced, especially on oceanic islands where many species have not evolved defenses to the tactics of predatory mammals, such as hunting nocturnally and by scent.

The introduction of predators to control pest species has a recent record of many successes (especially with arthropod introductions), when proper risk analysis precedes the introduction. Unfortunately, the history of biological control is also littered with some very bad mistakes. One of the most notoriously disastrous attempts at biological control was the introduction of predatory snails and a predatory flatworm to several tropical islands beginning in the 1950s to control the African giant snail (*Achatina fulica*), itself an introduction. Control of the target species remained elusive, but the introduced predatory snails caused the extinction of several species of endemic snails on Tahiti, Hawai'i, and other islands. Another biological control disaster was the attempt to control introduced rabbits (*Oryctolagus cuniculus*) in New Zealand in the 1880s by releasing predatory mustelids. Control of rabbits was not achieved, but the mustelids (especially stoats, *Mustela erminea*) preyed extensively on native wildlife and contributed to the extinction or decline of several endemic bird species. Similarly disastrous effects have resulted from the introduction of another mustelid, the small Indian mongoose (*Herpestes javanicus*), to various tropical islands as a potential biological control agent



FIGURE 2 Black rats (*Rattus rattus*) are among the most widespread invasive rodent species and have damaged native biodiversity on many islands around the world. (Photograph courtesy of James Russell.)

for rats in sugarcane fields. Control of rats was generally not achieved, but losses of native wildlife often occurred due to mongoose predation.

Introduced rodents (including *Rattus* species and house mice) are now present on every continent except Antarctica and in over 80 percent of the world's archipelagoes (Fig. 2). Invasive rodents have been implicated in over 50 percent of vertebrate extinctions on islands. Extinctions of vulnerable species typically occur rapidly after the arrival of predatory rodents and can have flow-on effects to the entire ecosystem. For example, the extinction of seabirds on islands alters the flow of resources from the marine to the terrestrial systems, an important source of nutrients for plants and insects. Even after introduced rodents have been removed, it may be a very long time, if ever, before ecosystem processes can be restored to their status prior to invasion.

Several species of predatory social invertebrates (ants and wasps) have invaded many parts of the world through accidental introduction and have had severe impacts on native species and ecosystem processes. Notorious examples include red imported fire ants (*Solenopsis invicta*), yellow crazy ants (*Anoplolepis gracilipes*), and the common wasp (*Vespula vulgaris*). Each of these species is omnivorous (scavenging, and then harvesting sugary excretions), but also predatory.

Red imported fire ants are generalist predators that have now been accidentally introduced to many parts of the world and prey on a wide range of invertebrates and some vertebrates, including reptiles and nesting birds. They are capable of transforming the structure and composition of entire communities. Yellow crazy ants are similarly invasive, generalist predators that form supercolonies, recruit rapidly to food resources, and aggressively disrupt invertebrate communities. A specific example of their impacts is on Christmas Island, in the Indian Ocean,

where they formed associations with honeydew-secreting Hemiptera, increased rapidly in abundance, and killed vast numbers of native land crabs (*Gecarcoidea natalis*) that are key herbivores in the local rainforest ecosystem.

In the honeydew beech (*Nothofagus*) forests of New Zealand, invasive common wasps reach very high densities in summer and fall, fueled by abundant honeydew excreted by native scale insects. These wasps deplete the honeydew and compete with native wildlife for this resource. They also prey on a range of native invertebrates, including spiders, moths, and stick insects. Probable elimination of some species of spiders from honeydew beech forests by these invasive wasps has been demonstrated. Those species of native moths with a caterpillar stage that coincides with the peak wasp season are also eliminated from wasp-invaded forests.

One of the best-documented recent invasions by an accidentally introduced vertebrate predator is that of the brown treesnake (*Boiga irregularis*) on the island of Guam. This species arrived in Guam shortly after World War II, probably in the undercarriage of military aircraft. Over the next 40 years, 17 of 18 native bird species on Guam were severely affected by snake predation. Twelve of these bird species became extinct as breeding residents and others suffered declines of more than 90 percent. The snake is also a major predator on young of the endangered Marianas flying fox (*Pteropus mariannus*). Overall, it has transformed the natural ecosystems of Guam. By the time it became clear that the brown treesnake was responsible for these extinctions and declines, it was too late to react. In addition to its effects on biodiversity, the brown treesnake also has many nonbiological impacts, such as regularly causing power outages through short-circuiting electricity transformers and crawling into the bedrooms of young children, where its nonpoisonous bite can still be damaging.

Invasive predators also have severe impacts in marine and freshwater ecosystems. For example, the introduction of Nile perch (*Lates niloticus*) to Lake Victoria in Africa has apparently caused the extinction of hundreds of species of endemic haplochromine cichlid fish and has transformed the lake ecosystem and its environs. Nile perch are now used extensively by local people as a food resource, and preservation of these large oily fish is commonly done by smoking. This has raised the local demand for firewood and has led to increased levels of deforestation around the lake. However, the availability of an abundant food source has also led to increased economic demand for Nile Perch, both from within Africa and overseas.

INDIRECT EFFECTS

Introduced predators can also have complex indirect effects on ecosystems by changing how other species interact with one another. For example, by driving a prey species to extinction, an invasive predator may also affect other species that depend on this prey. The presence of other introduced species can also create complex interactions. For example, one invasive predator may prey on another, or an invasive predator may depend on an invasive herbivore as its main prey.

Because invasive predators often prey on other introduced species, their introduction to (or removal from) ecosystems where such interactions occur can have unexpected consequences. On sub-Antarctic Macquarie Island, the introduction of European rabbits in 1879 was followed shortly afterward by extinction of the endemic parakeet (*Cyanoramphus novaezelandiae erythrotis*). It is now thought that the introduction of rabbits supported a substantial increase in the numbers of previously introduced feral cats, which then drove the vulnerable parakeet to extinction. In the 1970s the control of rabbits, in order to protect the island's native vegetation, was achieved through the release of a *Myxoma* virus. This led to a diet switch by the cats to seabirds. Control and then eradication of cats from Macquarie Island was therefore undertaken. Rabbits have once again increased in numbers, although it is unclear whether this release is attributable to the removal of cats or a decrease in efficiency of viral control. Vegetation cover on Macquarie has also changed with rabbit density, although this effect has been confounded by climate warming over the past 50 years.

On Little Barrier Island (New Zealand), feral cats were impacting adult survival of threatened Cook's petrels (*Pterodroma cookii*). However, the nesting success of Cook's petrels paradoxically decreased after the eradication of feral cats. The probable explanation is that the impact of invasive Pacific rats (*Rattus exulans*), which are nest predators, increased after cat eradication, owing to a "mesopredator release" effect. When the rats were also eradicated from Little Barrier Island, the nesting success of Cook's petrels improved dramatically, in the absence of any invasive predators. Such examples highlight the importance of understanding the interactions between predators and their prey when planning for action against invasive species for conservation purposes.

Invasive predators can sometimes have ecological effects that extend beyond those on their prey: their influence can potentially extend to the very foundation of food webs, through "trophic cascades." Well-documented examples of this effect come from the Aleutian Islands,

where introduced Arctic foxes (*Alopex lagopus*) and brown rats (*Rattus norvegicus*) prey on seabirds and greatly reduce their abundance. On islands invaded by foxes, the loss of seabirds disrupted their transport of marine nutrients to the land. This had flow-on effects to soil fertility and ultimately resulted in radical changes to the vegetation, changing grassland to communities dominated by shrubs and forbs. On islands invaded by rats, the loss of seabirds caused an increase in intertidal invertebrates which seabirds preyed upon, and a decrease in algal cover that the invertebrates fed upon.

Predators can also cause shifts in the biology of their prey. When predators selectively target only some individuals in a population, traits in the prey population can evolve over time. Introductions of the predatory ground-dwelling curly-tailed lizard (*Leiocephalus carinatus*) on Caribbean islands caused brown anoles (*Anolis sagrei*) to increase the height at which they perched in trees. Introduced salmonids in Sierra Nevada alpine lakes preferentially target large *Daphnia*, causing subsequent generations to be selected for smaller body size. Such ongoing selection processes at the population level will ultimately change the evolutionary pathway of the prey populations.

The dynamics of predator–prey populations are commonly studied using predator–prey (also known as Lotka–Volterra) population models. These mathematical models couple the population size, birth rates, and death rates of predators to their prey. The simplest models relate only one predator and prey to each another (Fig. 3), but many more complex models can be examined, incorporating such factors as the carrying capacity of each population

in the environment, the presence of alternative predators or prey, or the effect of seasons or human harvesting on populations. Such models allow the prediction of long-term outcomes for populations, such as population size fluctuations, coexistence of the predator and prey, or extinction of the prey species.

CONTROL/ERADICATION

Because invasive predators can have such severe effects, their control or eradication usually benefits native species and ecosystems, provided it does not result in unanticipated indirect effects. On geographically isolated areas, such as on islands or within fenced sanctuaries, it is possible to eradicate predatory invasive vertebrates, provided that the removal rate is faster than the population growth rate. However, in most situations, eradication is impossible, and control is the only option. Well-established invasive predators occupying large areas of habitat on continents, large landmasses, or large water bodies usually present insurmountable eradication challenges and the eradication of invertebrates is generally more difficult than vertebrates. For these reasons, prevention is always better than cure. It is generally far more cost effective to prevent biological invasions, or (failing that) to detect and eradicate newly established populations, than to manage the consequences of widespread, well-established invasive predators. Reinvasion following eradication is also possible, whether intentional or accidental. It is therefore important to have measures in place to detect invasive predators in the early stages of invasion, allowing for eradication before their severe effects on other species become irreversible.

SUMMARY

Predators are a natural part of all environments, and their presence is vital for maintaining a balance in nature, although population sizes of predators and prey will always fluctuate over time. Introduced predators, however, can drastically change ecosystems, as shown by examples here from different ecosystems across the world. Deliberate introductions of invasive predators for biological control purposes, or for other reasons, therefore need to be subject to rigorous controls. Accidental introductions, especially of invertebrates and commensal rodents, will continue, and no area can ever be considered completely safe from them. We are only now beginning to understand fully the consequences of predator introductions, as mathematical models and field studies suggest that the introduction of invasive predators can have long-term effects on ecosystems that they invade.

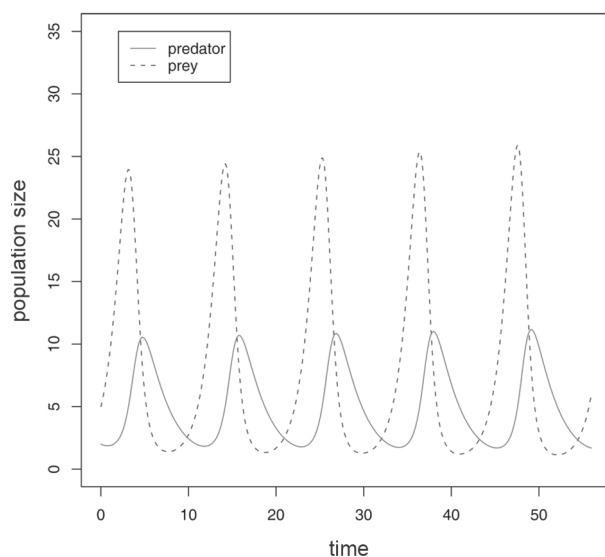


FIGURE 3 Standard predator–prey model with cyclic population dynamics.

SEE ALSO THE FOLLOWING ARTICLES

Biological Control, of Animals / Brown Treesnake / Carnivores / Eradication / Fishes / Rats / Small Indian Mongoose / Wasps

FURTHER READING

- Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: Impact, control and control impact. *Biological Reviews* 78(3): 347–383.
- Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307(5717): 1959–1961.
- Goldschmidt, T., F. Witte, and J. Wanink. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in sublittoral areas of Lake Victoria. *Conservation Biology* 7(3): 686–700.
- Wiles, G. J., J. Bart, R. E. Beck, and C. F. Aguon. 2003. Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. *Conservation Biology* 17(5): 1350–1360.

PRIORITIZATION

SEE RISK ASSESSMENT AND PRIORITIZATION

PROPAGULE PRESSURE

RICHARD P. DUNCAN

Lincoln University

Propagule pressure is a measure of the number of individuals of a species arriving in a region to which they are not native. It has been identified as a key factor determining whether species introduced to a new region are likely to establish wild populations; put simply, the more individuals that arrive, the greater the chances of successful establishment. It is also a key factor in determining the pattern and rate of subsequent spread of species throughout a newly invaded region.

MEASURING PROPAGULE PRESSURE

Propagule pressure (also termed introduction effort) is a term describing the number or rate at which propagules enter a region. For species with good records of their introduction and release, it is often possible to distinguish two components of propagule pressure: the number of individuals included in any one release event, and the number or rate of discrete release events. Birds that were introduced to New Zealand in the nineteenth century under the auspices of the acclimatization societies, for example, arrived in shipments for subsequent release into the wild. The greater the number of shipments (discrete release

events) or the greater number of individuals included in each shipment, the greater the propagule pressure.

In many situations, it is difficult to determine the number of individual propagules of a species that arrive in a region, and hence to measure propagule pressure directly. This is especially true for accidental introductions, which typically go unrecorded. It is also true for plants introduced initially into cultivation, where propagule pressure is often a function of the amount of seed escaping into the wild, which is determined by the number of individuals planted and the rate of seed production and dispersal, all of which can be difficult to quantify. As a consequence, studies often use surrogates for propagule pressure—some measure known or considered to be highly correlated with it. Boats, for example, are the primary vector by which invasive zebra mussels are transported between lakes in North America, and estimates of boat traffic between invaded and noninvaded lakes thus provides a useful surrogate for propagule pressure.

THEORETICAL UNDERPINNINGS

There is a strong theoretical justification for the link between propagule pressure and the probability that a species will establish a population in the wild. The link stems from the theory and observation that large populations are less likely to go extinct than small populations for several reasons. First, large founding populations are less likely to decline to extinction than are small populations, due to stochastic fluctuations owing to demographic or environmental stochasticity, or to natural catastrophes. Second, large populations are less prone to negative effects, such as inbreeding or difficulty in finding mates, which can occur at low population densities (Allee effects). Third, greater propagule pressure associated with a greater number of release events may improve establishment by increasing the chance that at least one release population encounters favorable conditions for population growth.

The combined effect of these factors can be summarized as a curve relating the probability of establishment to the number of propagules arriving, termed the establishment curve (or dose–response curve). The theoretical shape of this curve is determined by the relative role that various processes play in affecting establishment, but Leung et al. (2004, *Ecology* 85: 1651–1660) have derived a simple yet general form for the relationship. If we define a population as establishing at a location to which it is released if at least one propagule from the release event establishes, then the probability of establishment