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## Introductions of wildlife as a cause of species extinctions

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Introduced animals, particularly mammals, continue to extinguish indigenous species in many parts of the world. This effect is greatest on oceanic islands but continental biotas are also affected. Case histories are used to illustrate difficulties of separating alien animal effects from other extinction agents, and of predicting outcomes. Further research is needed on synergistic and flow-on effects that may follow establishment of a new alien species. Combatting the introduction problem is seen as primarily one of attitude rather than of scientific understanding. It is recommended that in each country: risk analyses are made to identify problem species likely to be introduced; preventive measures are maintained against invasions by these aliens; contingency plans are established for rapid responses to invasions; intensively managed refuge areas are created to protect vulnerable indigenous species from alien species already present; further research is coupled with these actions; information on the introduction problem is disseminated more widely within countries; and international sharing of information on preventive and control measures is promoted more vigorously.

*Key words: alien mammals, synergistic effects, run-on effects, species declines, endangered species*

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Species extinction is one of many effects that result from introduced mammals and birds. The effect is greatest on islands but some continental extinctions are also attributable to introductions. A few alien species readily adapt to new countries: house sparrows *Passer domesticus*, starlings *Sturnus vulgaris*, cats *Felis catus*, and commensal rodents for example. Such successful animals often replace indigenous species to make formerly distinctive biotas more alike.

Extinction of a species is the end-point of a population decline; most often declines of several subpopulations that originally constituted the species. In early stages it is often not possible to distinguish an ongoing decline from fluctuations in population numbers that affect all species.

Extinctions caused by alien species pose difficult questions. How can we untangle effects of an alien from other causes of extinction? How can we predict effects of an alien on resident species? What options are there for pre-

venting or reducing species declines caused by alien species?

I will illustrate these difficulties with examples taken mostly from islands, concentrating on alien mammals, and searching for any principles that may help to reduce the problem. The global extent of the problem and the rate at which it continues have been discussed elsewhere (e.g. Holdgate 1967, Long 1981, Lever 1985, Atkinson 1989).

### Separating effects of introduced species from other agents of extinction

Four agents of extinction are commonly recognised: habitat destruction and fragmentation, hunting-related overkill, introduced species, and indirect flow-on effects such as chains of extinction (Diamond 1989). Introduced species do not act independently of other

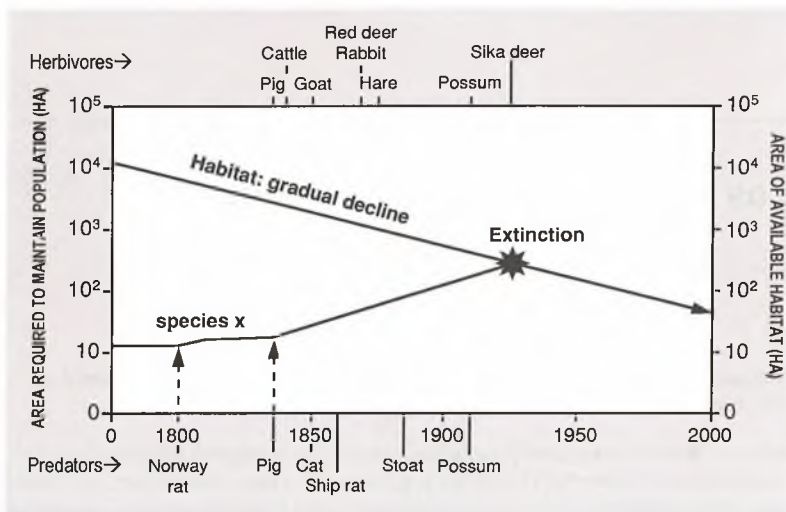


Figure 1. A conceptual model of interaction between habitat loss and introduced herbivores and predators in New Zealand. Predation by Norway rats and food competition by pigs both increase the land area required by species 'x' for it to remain viable. By 1925 the remaining suitable habitat has declined to an area less than that required by species 'x' and it becomes extinct.

agents; their interaction with habitat loss is particularly important (Fig. 1).

It is not acceptable to carry out controlled experiments with threatened species, manipulating first one and then another agent. We must either learn from our mistakes while attempting to halt a species decline, a 'research by management' approach, or we must learn from case histories analysed retrospectively (e.g. Atkinson 1977, 1985, Taylor 1979).

### Identifying all effects of an introduced species

Known effects are predation, browsing/grazing (and burrowing), hybridization with or reproductive disruption of resident species, food or nest-site competition, disease transmission, indirect flow-on effects, or a combination of these processes. As shown below, all possible effects must be considered when assessing risks posed by an introduction which means that we must understand the biology of the alien species.

#### Pacific rats *Rattus exulans*

Pacific rats reached New Zealand with the first human immigrants. European naturalists last century considered it a 'harmless vegetarian', a belief still held by some. Both circumstantial and direct evidence of predation by Pacific rats on invertebrates and vertebrates now shows that they have probably been responsible for many local and total extinctions of larger species of flightless beetles and weevils, giant wingless grasshoppers (wetias), land snails, frogs, lizards, and tuatara, small seabirds and landbirds

(Atkinson & Moller 1990, Towns & Daugherty 1994). Similar effects of this species resulting in extinctions are identified elsewhere in the Pacific by Olson & James (1982) and Steadman (1989).

### Separating effects during intensive studies and species recovery programmes

#### Lord Howe woodhen *Tricholimnas sylvestris*

The Lord Howe woodhen is one of the few endangered species whose decline has been thoroughly investigated. Intensive field work eliminated potential decline factors one by one until it became clear that pigs *Sus scrofa* were likely to be the crucial factor by eating adult birds and destroying nests and eggs (Miller & Mullette 1985). The hypothesis was tested by destroying

the pigs and beginning a programme of captive breeding with three pairs of woodhens taken from the remnant population on Mt Gower in 1980. The first birds were released into the wild in 1981. By 1987 the woodhen population had increased from the 6 - 10 breeding pairs recorded between 1969 and 1980, to 50-60 breeding pairs between 1987 and 1993 (Caughley 1994). Caughley remarked: "The steps followed for the woodhen - diagnose the agent of decline, neutralize the agent of decline, re-establish the species of concern - may serve for almost any other troubled species." Unfortunately, diagnosing all agents of decline is sometimes more difficult.

#### Kakapo *Strigops habroptilis*

New Zealand's nocturnal flightless parrot, the kakapo, is the only lekking parrot known (Merton et al. 1984) and is listed among the world's 20 most threatened bird species. Originally distributed throughout the country, its range has shrunk dramatically since human arrival largely as a consequence of predation and competition from introduced mammals. In 1895-1907, a pioneer attempt to use islands in Fiordland as safe refuges for the species failed when stoats *Mustela erminea* swam the water gaps separating these islands from the mainland (Hill & Hill 1987).

The kakapo is now extinct on the mainland but was rediscovered in 1977 on Stewart Island (where stoats are absent) and the first female kakapo was found since the beginning of the century. Cats were preying on the birds so every kakapo that could be found was transferred to three smaller offshore islands. Currently, 50 birds are

known: 19 females and 31 males. Pacific rats are present on two of these islands and because the rats sometimes eat eggs and nestlings, and may compete with kakapo for high-quality food such as fruit, there are plans to eradicate them.

The kakapo has small clutches and breeds at intervals of two to five years, apparently in response to environmental cues that are not yet clearly identified. Since 1981 they have laid at least 46 eggs, although many were infertile and only 20 hatched. Of these, six have fledged but without intervention only two would have survived. The problems of infertility and chick survival have to be overcome. Video scanners are being used to obtain vital information on matings, and sound deterrents are being trialled to prevent rats from reaching nests. Although many of the factors that have led to kakapo decline are diagnosed, our understanding of this amazing parrot is as yet insufficient to allow us to reverse its decline.

### **Predicting effects of an introduced species**

In spite of many symposia devoted to this question, it is still extremely difficult to predict the effects of a new introduction (*cf.* Lodge 1993, Atkinson & Cameron 1993).

Direct effects of some introduced mammals are, however, already well known. On islands, nine species of mammal: humans, goats *Capra hircus*, rabbits *Oryctolagus cuniculus*, pigs, cats, mongooses *Herpestes auro-punctatus*, ship rats *Rattus rattus*, Norway rats *R. norvegicus* and Pacific rats, are the most widespread causes of extinctions (Atkinson 1989). Their impact (excepting that of humans) is much less predictable on continents. However, if no previous extinctions have been associated with an alien, as with the brown tree snake (below), effects are seldom predicted.

### **Extinctions resulting from direct effects of a single introduced species**

The brown tree snake *Boiga irregularis* reached the island of Guam most probably during the 1940s. Savidge's (1987) study correlated its range expansion with range contraction of the forest avifauna at the time. She examined pesticides, competition with introduced species, habitat loss, disease (Savidge et al. 1992), and predation by dogs, cats, rats, and monitors (Varanidae), as well as the snake. She concluded that, between 1963 and 1986, predation of eggs, nestlings and adults by the snake resulted in declines or extinctions of 10 of the 11 species of native forest bird previously present. On Guam, the snake has few competitors and no significant predators and, by using small native reptiles as alternative prey, can maintain high rates of predation on the birds.

### **Extinctions resulting from interactions between several introduced species**

#### **Cats and rabbits on Macquarie Island**

Interactions between two or three introduced species can eliminate an indigenous species as shown by loss of the Macquarie Island parakeet *Cyanoramphus novaehollandiae erythrotis* (Taylor 1979). Parakeets of the genus *Cyanoramphus* are commonly hole-nesters in trees although on tree-less Macquarie Island, the formerly abundant endemic parakeet nested under tussock grasses. In spite of nesting and feeding on the ground, they coexisted with cats and dogs for over 60 years and were still numerous in 1880. This result might not have been predicted from either the habits of parakeets or those of cats. The weka *Gallirallus australis*, a large rail endemic to the New Zealand mainland, was introduced to Macquarie Island in 1872 and again in 1879. Like the cats, it remained scarce until at least 1880. Rabbits were introduced in 1879 and spread rapidly. Cats and wekas both increased soon afterwards and were numerous on the island by 1891. The parakeet became extinct in the same decade: 1881-90. Taylor (1979) points out that before the introduction of rabbits, and wekas, the number of cats would have been limited by scarcity of winter food; comparatively few seabirds remain during winter. Rabbits provided an abundant year-round food supply enabling cats to increase and prey on the parakeets throughout the year. It is possible that weka predation on parakeets also increased. This illustrates a synergistic effect of two (or three) introduced species. It also shows how availability of a new and alternative prey for the cats (and wekas) at a critical time of the year increased predator pressure on a particular prey (Davis 1957), in this case one that was vulnerable.

### **Extinctions resulting from flow-on effects of introduced species**

Even when an introduced species does not directly eliminate a species, its feeding or other activity may result in flow-on effects that result in extinctions.

#### **Australian brushtail possums *Trichosurus vulpecula* in New Zealand**

Effects of possums, introduced to New Zealand last century, are widespread with the major impact being on lowland forests. Foliage, flowers, fruit, fungi, ferns, bark and seedlings are eaten selectively, with respect to species, in all layers of the forest. Some populations of palatable species are destroyed while others remain little damaged. The forest canopy opens and less palatable species become dominant. As strong climbers, possums move freely through the forest giving them opportunities to eat eggs, or kill nestlings and adult birds that they may en-

counter. Many invertebrates are also eaten. Not all this behaviour is opportunistic; large moths are actively hunted and probably large landsnails as well (G. Elliott, pers. comm.). Possums den in thick foliage or holes, both in large trees and on the ground thus making competition for nesting and roosting sites another effect that could contribute to a species' decline.

Although no extinctions have yet been attributed to possums they have brought about marked declines of some species. The five extant species of endemic leafy mistletoes (Loranthaceae) are semi-parasitic shrubs that are severely browsed by possums in many parts of the country, sometimes resulting in their local disappearance (Ogle & Wilson 1985). However, these declines are unlikely to result solely from the direct effect of possums. Pollination of *Peraxilla*-mistletoes is greatly increased by native nectar-feeding birds, particularly bellbirds *Anthornis melanura* and tui *Prothemadera novaeseelandiae*, which open the flowers when seeking nectar (Ladley & Kelly 1995). These birds are themselves likely to be adversely affected by two flow-on effects of possums. They are partly dependent on nectar-producing flowers (additional to those of the mistletoes) as well as on fruit; both items are preferred foods of possums. Second, where possums are at high densities, the reproductive success of these birds is likely to be reduced by possums through nest disturbance and predation (Fig. 2).

Unlike the mistletoe example, most flow-on effects are only surmised. As many direct effects of possums on plants and animals are now identified, it is inconceivable that these are not producing indirect effects. Food competition with animals is inevitable, particularly birds and invertebrates in the nectarivore, frugivore and foliovore guilds. Most extant New Zealand forest birds rely on invertebrates for significant parts of their diet (Atkinson & Millener 1991) so that reduced invertebrates are likely to affect these birds as well. We are dealing with a network of flow-on effects in which few pathways are identified and none, so far as native species are concerned, are quantified.

### Rabbits in arid Australia

The rabbits in arid Australia are an excellent example of the interactions between introduced species as well as possible flow-on effects on a continent. Morton (1990) identified 11 extinctions and 20 major declines among the 72 species of mammal known to have been present in inland arid Australia. Affected mammals are mainly medium-sized and herbivorous or om-

nivorous (Burbidge & McKenzie 1989). Morton demonstrated that, even in pre-European times, life for such mammals was marginal in what is an exceptionally infertile environment where productive areas are patchy in space and time. To explain the declines he examined the possible role of droughts, climatic change, introduced predators, mice, stock, disease, pastoralism, rabbits and altered patterns of fire. He concluded that the primary cause of the extinctions was habitat modification brought about by "cattle, horses, sheep, goats and, especially, rabbits". Other factors he considered to be secondary. Morton suggested that stock were held on country long after the vegetation could support them and, together with enormous populations of rabbits, depleted the patchy sources of nutritious growth that formerly supported the native mammals. Morton acknowledged a flow-on effect of high rabbit numbers in generating "unusually high densities of predators" but believed that the impact of predators had been over-emphasised. This conclusion must be questioned as all three of the larger introduced predators of native mammals in arid Australia, the dingo *Canis familiaris*, fox *Vulpes vulpes* and cat, are known to respond numerically to high rabbit numbers. Corbett (1995) has concluded that up to 10 species of medium-sized native mammals of this zone have been eliminated by the dingo since 1930.

### Preventing introductions of species likely to cause extinctions

There are often both economic and conservation reasons for preventing an animal from establishing in a new country. When new introductions are proposed, the burden of proof that no harmful effects will result should always be

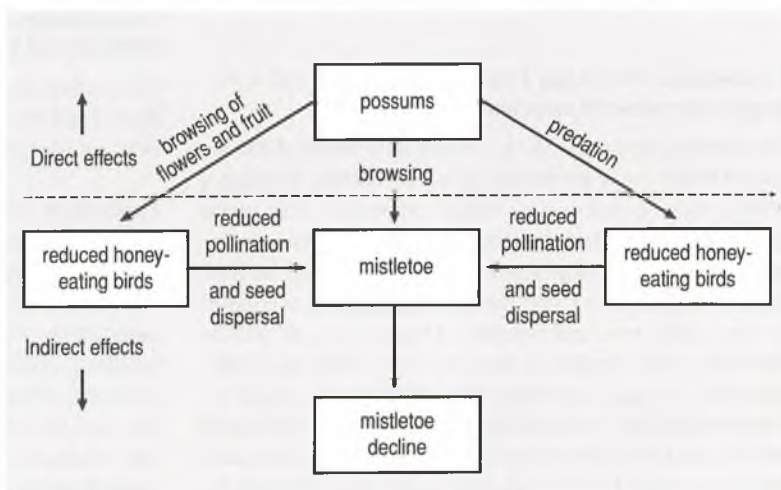


Figure 2. Direct and indirect (flow-on) effects of Australian possums on *Peraxilla*-mistletoes in New Zealand.

with those most likely to benefit from the introduction (Ruesink et al. 1995). Strict quarantine controls must remain as national priorities, but national boundaries are not recognised by animals. Once a species reaches a continent, unless it is detected and eradicated quickly, its further spread is likely to be governed by ecological factors alone. On islands, quarantine measures by governments, public education, and specific preventative action by interest groups, can all reduce risk of invasion by alien vertebrates.

Commensal rodents are among the more difficult animals to exclude from islands. Preventive measures include rodent proofing of all boxes and crates taken to an island, close inspection of cargoes, permanent poison-bait stations maintained within 200 metres of any landing point, and rodent destruction kits with contingency plans for dealing with rodent escapes from shipwrecks, moored vessels, or landed cargo (Moors et al. 1992). The weakest link in executing such precautions on a government-controlled island is maintaining these measures at times when experienced staff are replaced by new staff. With privately owned islands, effective precautions are dependent on the understanding and goodwill of the owner. For example, Frégate Island (210 ha) was one of four rat-free islands in the central Seychelles group. It supports the last natural population of the Seychelles magpie robin *Copsychus sechellarum* as well as populations of Seychelles fody *Foudia sechellarum*, Wright's skink *Mabuya wrightii*, Bronze gecko *Ailuroonyx sechellensis*, a giant tenebrionid beetle and a large scorpion. These threatened endemics of the Seychelles may all be vulnerable to rats. In 1995, Norway rats reached the island with stores brought by boat for a small tourist facility. Since then building materials have been barged to the island for an expanded tourist lodge. Rats are now spreading across the island and requests to the owner and to conservation organisations for adequate money to eradicate them have so far been unsuccessful (D.V. Merton, pers. comm., April 1996).

## Reducing negative effects of introduced species

### Islands as refuges for threatened species

Islands have become refuges for threatened species throughout the world because they often remain free of particular alien animals. In New Zealand, many bird, reptile and invertebrate species have survived only on offshore islands >1 km from the mainland (e.g. Towns & Ballantine 1993). This refuge principle has been exploited by translocating many species threatened on the mainland to islands and eradications of alien mammals (Veitch

1994) have greatly increased the number of islands available as refuges. Elsewhere in the world, notable eradication successes include the eradication of rabbits from Phillip Island of the Norfolk Island group and from Round Island, Mauritius.

### Mainland habitat refuges

Some methods of protecting threatened species by localised control of alien predators or herbivores on the New Zealand mainland, with or without fencing, may be relevant to continents. The longest running case is that of the northern royal albatross *Diomedea epomophora sanfordi* colony at Taiaroa Head, Otago Peninsula in the South Island (Robertson in press). Albatrosses first attempted to nest there between 1890 and 1920 but these and subsequent attempts failed until protective measures began in 1936; a fence was built to exclude humans and their dogs although controlled public viewing through an observatory has been allowed since 1972. Cliffs and beaches at each end of the fence render it ineffective in excluding the alien predators most dangerous to albatrosses, i.e. stoats, ferrets *Mustela furo* and cats. Therefore, these predators have been controlled by year-round trapping maintained for over 40 years and the colony now numbers 27 breeding pairs.

A second example concerns yellowheads *Mohoua ochrocephala*, a threatened species of hole-nesting birds living in forests of southern beech *Nothofagus* spp. in Fiordland, which are vulnerable to stoats. Beech trees seed heavily at intervals of 3-5 years, mice *Mus musculus* increase and then stoat numbers erupt with increased predation on yellowheads. O'Donnell et al. (1996) have shown that intensive trapping of stoats at these times can increase breeding success of yellowheads even though stoats infiltrate from the surrounding untrapped area.

A third example centres on predator control in a 1,400-ha forest at Mapara, central North Island, which is managed to safeguard a declining population of the endangered kokako *Callaeas cinerea* (Callaeidae). The forest was fenced to exclude stock from the surrounding farmland (Saunders 1990) and possums and rats controlled by trapping, hunting with dogs, and poisoning, continued each year since 1989. More recently, time-lapse video-monitoring (Innes et al. 1994) has identified ship rats and possums as the most important predators of kokako. Through all these measures the decline in numbers of adult kokako has been reversed; in the 1994/95 breeding season 18 pairs of kokako attempted to breed (previously never more than 10 pairs) and 55 chicks were fledged (P. Thomson, pers. comm.). Both here and in the previous example it may prove unnecessary to control predators each year.

These successes, particularly the effectiveness of aeri-

al and ground-based poisoning of possums and rats at Māpara (Innes et al. 1995), have stimulated rethinking of what might be possible in mainland areas with sustained concentrated management. It has led to the realisation that habitat refuges, if selected carefully, have potential for protecting threatened species and for restoring some indigenous communities to a functioning state more like that of earlier times. A proposal is now being tested to surround a 252-ha forest catchment near Wellington with a new design of fence that would exclude all mammalian predators and herbivores. This would create a refuge for vulnerable species that disappeared from the mainland many years ago (Lynch 1995).

## Discussion and recommendations

In his penetrating review of conservation biology, Caughley (1994) distinguishes 'small-population' and 'declining-population' paradigms. While acknowledging the contribution made by 'declining-population' studies in saving endangered species, Caughley points out that this approach lacks a unifying theory. This is fair criticism. Improvement in our theoretical understanding of extinction mechanisms is needed both for recovery and advocacy programmes. Interactions between introduced animals and habitat loss (see Fig. 1) may be a useful starting point for developing a more comprehensive theory. But central to the introduction problem is preventing alien species from entering new countries. This is more a question of changing people's attitudes than one of scientific understanding.

Because economic benefits have often followed intentional introductions of species to new lands, negative effects on indigenous species are frequently discounted unless of economic or health significance. Allied to this is widespread ignorance of the full consequences of invasive species, ignorance that could be partly dispelled with more effective communication of research results.

For these reasons, all countries should take active measures that will reduce the frequency of introductions, mitigate the effects of aliens already established, and promote interchange of research results. Seven such measures are recommended:

- 1) Analyse invasion risks to identify (i) problem species likely to be introduced and (ii) high-risk areas with vulnerable indigenous species (e.g. islands).
- 2) Develop measures to prevent invasions by problem alien species (see earlier discussion).
- 3) Develop contingency plans for rapid responses to invasions and emergency protection of vulnerable species or high-risk areas.
- 4) Disseminate information about the introduction problem to a wide range of people, especially children, and officials from government and local authorities who are responsible for preventing undesirable introductions. Time-lapse video films should be regarded as an essential tool for identifying predators and demonstrating their effects.
- 5) Where problem alien species are already established, select and intensively manage refuge areas, using high-technology fencing where necessary, to protect populations of vulnerable species.
- 6) Promote further research into both single-factor relationships between alien and indigenous species, and the synergistic and flow-on effects of particular alien species. This will underpin the risk analysis of 1) and the advocacy of 4) above.
- 7) Promote further international sharing of information on preventive measures and control techniques suitable for various introduced species.

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