Biological Invasions: a Global Perspective
Edited by J. A. Drake *et al.*

CHAPTER 21

Ecological Effects of Controlling Invasive Terrestrial Vertebrates

MICHAEL B. USHER

21.1 INTRODUCTION

21.1.1 The perception of the problem

In concluding the British meeting of the SCOPE programme, Holdgate (1986) posed three questions, one of which was 'what management strategies are appropriate to control invading species?' In reply, he said of Great Britain 'very little consideration is given to management questions'. In reviewing the worldwide literature on introduced vertebrates, it is apparent that there is a wealth of data documenting introduced and invasive species, far fewer data recording accurately the habitats that are invaded, very few data on the subject of controlling the introduced species, and extreme scarcity of data on the effects of control on the biota of the invaded environment. Both Brown (this volume) and Ehrlich (1986, this volume) have documented invasive vertebrate species, and hence this paper will concentrate on their management.

Although there are relatively few published data on management, conservationists, in particular, are aware of the potential effects of invasive species and of the formidable management problems that they can pose. An example of this concern is Henderson Island, an uninhabited island of about 4000 ha in the Crown Colony of the Pitcairn Islands (South Pacific; 24° 22′ S, 128° 18′ E). Four of the 17 species of birds breeding on the island are endemic (Bourne and David, 1983, 1985, 1986), as are 10 of the 63 species of ferns and flowering plants. In April and May 1983 many conservation organizations lobbied the British Government to prevent the development of an airstrip and private recreational facilities on the island. The case was made on the grounds of the effects of invasive species (especially black or brown rats) coming with human visitors and of the management impracticability of zoning the island into separate developed and conserved sections. Eventually, Her Majesty's Government's reply (*House of Lords Hansard*, 15 December 1983, col. 385) rejected the development proposals 'on administrative and environmental grounds'.

Another example of the perception of the problem of controlling invasive mammals is the management policy of Barrow Island (Western Australia) during the development, since 1966, of a commercial oil field (Butler, 1987). This island has a varied community of native marsupial mammals (Butler, 1970), and stringent, almost draconian, powers are available to the oil industry's management to conserve the flora and fauna and prevent the colonization of the island by non-native species.

Both the Henderson Island and Barrow Island examples show that the perception is that it is extremely difficult, or impossible, to control invasive vertebrates before they have damaged, often irreparably, the native biota of islands. Perception can, however, be dangerous; the recent discussions of *Rattus* species have indicated that colonization by *R. exulans* (Polynesian rat) may not necessarily lead to the loss of endemic island species (*R. exulans* exists on Henderson Island, for example), but that colonization by either *R. rattus* (black rat) or *R. norvegicus* (brown rat) is more likely to lead to species losses (Atkinson, 1985). However, Diamond (1985) considered that it is not inevitable that these *Rattus* species would arrive on all rat-free islands. Despite these comments, case studies from around the world, and especially from oceanic islands, have shown that native populations can be greatly reduced or exterminated by invasive mammals, but equally Holdgate's (1986) remarks indicate that control measures have often not been either attempted or completely documented. The aims of this chapter are to investigate how frequently control measures have been attempted and to ask how frequently control might be successful.

21.1.2 The scope of this paper

The word 'control' is not necessarily used in the sense of 'eradication'; once an invasive species is established, eradication may well be impossible. Control will, however, refer to the management of that species so that its effect on other biota, or on the environment, are acceptable. Such a definition begs one question; to whom are the effects 'acceptable'? Acceptability has to be defined in relation to the aims of managing the piece of land that carries the invasive population. The situation is analogous to pest management; the manager has to decide how much inconvenience is acceptable, and once that has been decided a management strategy can be devised. Hence, in the remainder of this paper, control will relate to the management of the population of the introduced species, not necessarily to its eradication.

Management can have three different kinds of effects. First, there are the effects on the alien species itself. There are very few studies that relate to this effect, especially for vertebrates, but they are reviewed in Section 21.2. Second, there are the effects on the other biota in the community that has been invaded. The majority of studies address these effects, and these are reviewed in Section 21.3. Third, there are the effects on the abiotic environment. There are very few data that could be used to investigate these effects. Indeed Verkaik (1987) specifically stated that the muskrat control programme in the Netherlands had failed to gather reliable data on the effects of control on the 'burrow-digging time'. In Australia, Backhouse (1987) indicated that invasion of nature reserves by plant and animal pests led to 'habitat degradation'. However, due to the lack of precise data, this third set of effects will not be addressed further.

After reviewing the effects of management on both the invader and the invaded, the final Sections, 21.4 and 21.5, aim to make some prognoses and draw some conclusions. The reasons for wishing to control invasive species are frequently related to conservation activities, and hence the prognoses will be based not only on the review material in Sections 21.2 and 21.3, but also on the data compiled by the Working Group studying Invasions into Nature Reserves (see Macdonald *et al.*, this volume, and Usher (1988)).

21.1.3 The frequency of control measures

If the terrestrial vertebrates are divided into three groups—mammals, birds, herpetofauna—one finds some interesting differences in the approaches of land managers to the control of invasive species. All three groups feature prominently in lists of introduced species, e.g. in Moulton and Pimm's (1986) study of introduced species in Hawaii, they recorded that 22 out of 53 passerine bird species introductions on individual islands persisted, as did 68 out of 74 mammal species introductions and 48 out of 53 reptile species introductions. Mooney *et al.* (1986) recorded 17, nine and five species of invading mammals, birds and herpetofauna respectively in California. In southern Africa, the situation is similar, with species of these three terrestrial vertebrate groups being introduced (Brown, 1985; Griffin and Panagis, 1985; Brooke *et al.*, 1986). However, although all three groups have been introduced, the approach to control differs.

There seems to be almost no control of invasive amphibians and reptiles, although control measures may need to be adopted in the future for some species. *Bufo marinus* (giant toad) was introduced into Queensland from South America in 1935 to control coleopteran pests of sugar cane, but it is now posing a threat to native fauna. Floyd and Easteal (1986) considered two strategies for its control; first, a campaign to prevent its further spread by prohibiting transportation of produce and agricultural machinery from toad-inhabited to toad-free areas, and, second, by reducing the population density in toad-inhabited areas. The former is still being discussed, and methods for the latter have not yet been investigated in Australia.

There are rather more data for the control of birds, some of which can be considerable pests, e.g. the control of *Quelea quelea* (red-billed quelea), a native but invasive pest of grain crops in Africa (Ward, 1979). In some instances an active form of control is not wanted since birds provide a recreational activity for a portion of the population. This is the case, in Sweden, of *Branta c. canadensis* (Canada goose) which provides sport for the wildfowlers (Fabricius, 1983). Casual control of birds is more frequent. In Australia, for example, farmers in particular have shot many of the 27 species that have become established (Newsome and Noble, 1986). Active control operations of introduced bird species are rare; Brooke *et al.* (1986) recorded the unsuccessful attempt to eradicate *Corvus splendens* (Indian house crow) from Zanzibar, whilst Falla *et al.* (1966) reported the deliberate extirpation of *Pycnonotus cafer* (red-vented bulbul) from New Zealand. In the Hawaiian Islands, Berger (1981) recorded the attempted extermination of *Urocissa erythrohyncha* (red-billed blue magpie); S. L. Pimm (personal communication) is reasonably certain that the campaign was successful as there are no recent sightings of the species. Several single individuals of *Sturnus vulgaris* (starling) have been seen in the Hawaiian Islands, and all have been shot (S. L. Pimm, personal communication) so that the species has never become established. Despite these examples, the usual attitude towards invasive birds tends to be *laissez-faire*, and can be summed up by quoting a discussion of *Passer domesticus* (house sparrow) in Africa (Brown, 1985): 'It would be almost impossible to eliminate this species from SWA/Namibia, as recolonization from adjacent areas would probably take place as quickly as areas could be cleared. No control of this species has been attempted, and none is recommended.'

There are many more examples of the control of invasive mammals. Considerable experience has been gained in New Zealand on their control (Lockley, 1970; King, 1984) and the most successful campaigns have been on islands where the aim was total eradication. Although New Zealand scientists may have pioneered invasive mammal control methods (see, for example, the review by Wodzicki and Wright (1984)), examples of such control can be found from all continents except Antarctica, which has yet to be invaded successfully by species such as *Rattus norvegicus* (brown rat) or *Mus musculus* (house mouse). A number of these species has, however, become established on subantarctic islands, and on these control methods appear to have been reasonably successful. An example is the control of *Felis catus* (feral cat) on Marion Island by the feline panleucopaenia disease (Aarde and Skinner, 1981; Aarde, 1984; Howell, 1984; Rensburg, 1985a).

Although there are now a considerable number of examples of the control of invasive mammals, there are few examples of the control of invasive birds, reptiles or amphibians. The remainder of this paper will, therefore, concentrate on the control of mammals.

21.2 THE INVASIVE SPECIES

In general, management tends to concentrate on the ecosystem or on the rare and endangered species which it is hoped to help, and only to think of the invasive species as something to eliminate. One could view this as the 'only good rat is a dead rat' mentality. However, before analysing the effects of control on species and ecosystems, it is as well to ask what effects the control measures will have on the invasive species itself. A perception of the possible effects may be important in determining on appropriate management strategy. In this section two possible effects will be considered—ecological and genetical—though the concept of the two often overlap.

21.2.1 How is the invasive species' ecology affected by control?

Although this question has not been studied in detail, it is apparent that control measures can result in the realization of a larger than normal reproductive capacity. *Myocastor coypus* (coypu) populations in England have a large proportion of young animals, which Gosling *et al.* (1981) attributed to the intensive and prolonged trapping. Verkaik (1987) found that *Ondatra zibethicus* (muskrat) in the Netherlands had a relatively large reproductive capacity, had a large proportion of the females reproducing, and had a high juvenile survival rate. She also attributed these findings to the control campaign. The data for both the coypu and muskrat indicate that, at the relatively low densities maintained by management, the populations are not being regulated by density dependent effects which are likely to operate in higher density, natural populations.

Another interesting effect could be thought of as a very short-term co-evolutionary process. Gerell (1985) recorded the behaviour of *Mustela vison* (mink) and the breeding success of *Somateria mollissima* (common eider) on islands in southern Sweden. Invasive mink caused widespread destruction of colonies of breeding birds, which were subsequently only able to nest successfully on the outer, mink-free islands (R. Gerell, personal communication). Later, the birds have started to nest again on islands occupied by a stationary population of mink, and it thus appears that co-existence of the birds and mink is possible. R. Gerell (personal communication) considers that an ecological effect of controlling mink would be a delay in the adaptation of the sea birds to the new predator.

Although there are relatively few data, control of an invasive mammal may mean that, although many adults are removed, the remaining individuals realize a large reproductive rate and have a greater juvenile survival rate. As demonstrated for the mink in Scandinavia (R. Gerell, personal communication), this large reproductive rate means that the effects of a campaign to control an invasive mammal can be of short duration. Resurgence of *Oryctolagus cuniculus* (rabbit) after myxomatosis, or of coypu after a succession of cold winters, indicates that the ecological effects of control on the invasive species itself need further study. In the terms of the models discussed by Williamson (this volume), what is the effect of control on the life history and demography, represented either r or by R_O, of the population?

21.2.2 Are there genetical effects?

Control changes the environment of thę invasive species such that the great majority of the population is at risk and only a few individuals survive. If these few individuals are a truly random sample of the whole population, there may be no genetical influence of the control other than a possible loss of genetic variability. If, on the other hand, the few individuals surviving have special characteristics that increased their probability of survival, then one has a selective pressure and the possibility of genetic change conferring increased resistance in the invasive species.

An example of such adaptive change is the control of *Rattus norvegicus* (brown rat) by the anticoagulant poison warfarin. The use of warfarin began in 1950, and the first case of resistance was reported in Scotland in 1958. By 1972, there were three well-established resistant populations in Great Britain (Berry, 1977). Resistance is determined by a single dominant gene, and homozygous animals with this gene require about 20 times more vitamin K, which is an essential part of the blood-clotting mechanism, than ordinary rats. Berry (1977) discussed the engima of why, in the resistance area, the incidence of resistant rats stabilized at about 50% of the population, and he argued that this was a trade-off between the benefits of resistance and the disadvantage of large vitamin K requirements. Genetical aspects of warfarin resistance are discussed by Bishop *et al.* (1977) who showed that the heterozygote for the resistant allele, Rw_2, may be at a selective disadvantage in the absence of warfarin.

Another example of genetic change of an invasive species relates to the control of *Oryctolagus cuniculus* (rabbit) by the myxomatosis virus. When this virus was first spread in Britain in 1953, rabbit mortality was about 99%; the survivors had contracted the disease but recovered (Fenner, 1983). After six ensuing epidemics, mortality rates dropeed to about 40%. At first sight this may appear as a genetic change in susceptibility in the rabbit population, but such a change is confounded by decreasing viral virulence (Berry, 1977) and by a behavioural change in the rabbits (L. M. Cook, personal communication). In Britain, unlike Australia (Ross and Tittensor, 1986), myxomatosis is transmitted by *Spilopsyllus cuniculi* (rabbit flea) in burrows, but as the myxomatosis epidemics occurred rabbits tended to den less frequently in burrows and more frequently in open habitats where there was less contact with fleas. There is, however, still controversy (discussion of Ross and Tittensor, 1986) as to whether the behavioural change affected the rate of myxomatosis transmission.

These two examples, of control by chemical and disease agents, indicate that there may be genetical consequences which will, in time, make control successively more difficult. Although the whole subject of resistance to poisons and diseases is well documented in the literature on the control of invertebrate pests and microbes, it is less well known for invasive vertebrates. However, scenarios can be envisaged for selection pressures resulting from many forms of control. Consider, for example, a population of trap-happy and trap-shy animals. If all of the former are trapped and killed, the proportion of trap-shy animals in the population would increase with the subsequent difficulty in controlling that population (assuming, of course, that such a behavioural trait can be inherited).

The variety of genetical consequences of control is largely unknown. However, these consequences, or the possibility of them, should be borne in mind when considering a control programme.

21.3 THE INVADED COMMUNITY

The effects of control can be thought of as being either species-oriented or community-orientated. These two approaches will be considered in detail in the following two sub-sections. However, these are not the only effects which might be observed. With a pool of introduced species present, is the control of one of them likely to alter the ability of others to invade the environment? This question will be addressed in the third sub-section below. Finally, the unwanted side-effects of control will be reviewed.

The aim of this section is to select examples of each of the topics, and not to gain a complete coverage of all of the control methods available. A recent report (Daly and Goriup, 1986) documented the methods of *Capra hircus* (feral goat) control on small islands, drawing examples from around the world, assessing the effectiveness of control and indicating some of the economic aspects of eradication/control campaigns. A series of similar reports for other feral mammals would be an extremely useful addition to the literature.

21.3.1 Does control affect rare and endangered species?

This question can be assessed in two parts: the control of herbivores and the control of predators. The former seldom kill the plants that they graze, but subject the plants to stunted growth and long periods when reproduction may be impossible. The latter kill their prey and hence are able to reduce the prey population to very low levels.

There are a number of examples of successful herbivore control. On Raoul Island (New Zealand), after the dense *Capra hircus* (goat) population was shot and poisoned in 1982/3, Parkes (1984) recorded that most of the palatable native species were then able to regenerate. Within 2 years rare and endangered plants such as *Hebe breviracemosa, Homalanthus polyandrus* and *Boehmeria australis* var. *dealbata* were increasing in abundance, though others such as *Pisonia umbellifera, Pittosporum crassifolium* and *Asplenium shuttleworthianum* have remained rare. On Round Island (Mauritius) the palm *Latania loddigesii* was once dominant but is now rare. North and Bullock (1986) stated that all existing individuals were about 150 years old, being those that become established before burrowing and grazing mammals were introduced. Recent elimination of the goat and reduction in the rabbit population by shooting in 1976 have allowed *L. loddigesii* to regenerate. North and Bullock (1986) concluded that the reduction in herbivore pressure had allowed both palm regeneration and the ground vegetation to recover, but that some species—for example *Hyophorbe lageni-*

caulis (bottle palm) and *Dictyosperma album* (hurricane palm)—are now very rare and require artificial propagation and re-introduction. The authors advocated the continued reduction, or preferably the eradication, of the rabbit population. Further examples of the effects following reduction of herbivore pressure are given by Brockie *et al.* (1988).

It is not always possible to predict which of the rare and endangered species will increase their population sizes when herbivore pressure is released, and which will continue either to decline or to remain at very low densities. The solution to this problem is probably that of understanding the minimum viable population size. For many invasive mammals (e.g. the Scottish muskrats described in Section 21.3.4) a founder population can be extremely small. However, for many non-invasive species small populations appear to have lost the ability to increase in size. This would seem to be the case for *H. lagenicaulis* and *D. album* on Round Island, together with *Fernelia buxifolia*, thought to be extinct but subsequently re-discovered on the island. Although North and Bullock (1986) recommended a programme of nursery rearing and re-stocking, using Round Island stock, there seems to be no knowledge of whether sufficient genetic variability remains for re-stocked individuals to grow into viable populations. An example of the extreme loss of genetical variation is of *Trochetiopsis melanoxylon* (St Helena ebony), a small tree or shrub once common on St Helena; mature trees were felled particularly for the local tan bark industry, and seedlings and saplings were grazed and browsed by goats. The species was thought to have become extinct by the mid-19th century (Cronk, 1986a), but two individuals were recently re-discovered growing on a steep cliff-face. These two individuals would appear to be of a cliff genotype that develops only into a small prostrate bush (*ca* 1 m diameter) rather than into a small tree to 4 m high.

There seem to be less undesirable genetical effects following the control of predators. Shepherd (1981) suggested that *Canis familiaris dingo* (dingo) selected juvenile kangaroos, thereby limiting the rate of increase of their populations. Comparisons across the New South Wales/Queensland border fence indicated that *Macropus rufus* (red kangaroo) populations increased when dingos were controlled. An excellently planned experiment in Western Australia (see Kinnear *et al.*, 1984, for background information) is indicating that control of *Vulpes vulpes* (fox) and *Felis catus* (feral cat) allows small, isolated populations of *Petrogale lateralis* (rock wallaby) to increase three- or four-fold over a period of only 4 years (see Figure 21.1). This experiment, with replication of controlled and uncontrolled alien predator populations on five rocky hill outcrops, should provide valuable information when all of the monitoring data are analysed.

The control of invasive mammals can also have some striking effects on bird populations, as shown in many of the studies in New Zealand (King, 1984). One example is Veitch's (1983) work on Little Barrier Island where *Natiomystis cincta* (stitchbird), which had once been common throughout the North Island of New Zealand, had its last remaining population of about 500 birds threatened by feral

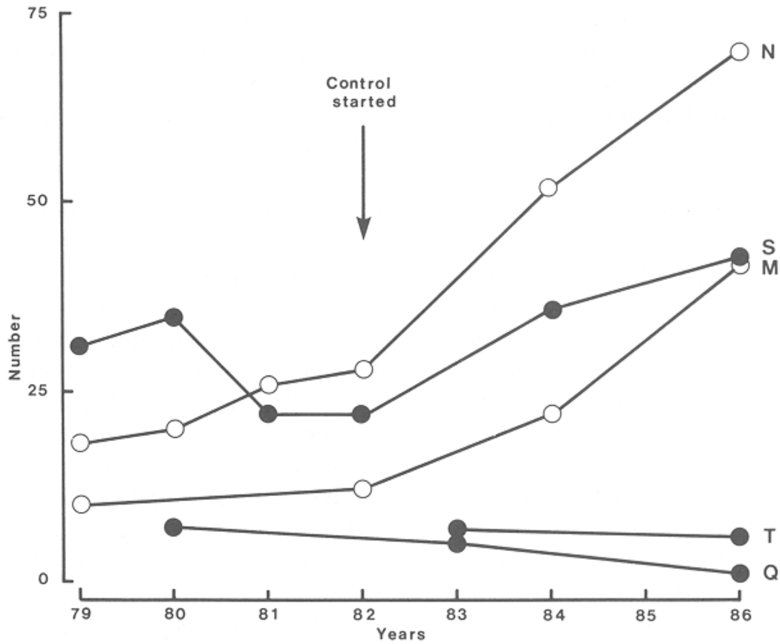

Figure 21.1. Population estimates of *Petrogale lateralis* (rock wallaby) on five rocky hills in the wheatbelt of Western Australia. The fox and feral cat populations were controlled on two of the hills (M and N) between 1982 and 1986, whereas the populations were uncontrolled on hills Q, S, and T. Between 1982 and 1986, rock wallaby populations increased by an average of 10% on hills where predators were controlled and by an average of 43% on hills without control (unpublished data provided by J. E. Kinnear)

cats. Extermination of the cats resulted in a rapid six-fold increase in the stitchbird population, which was then used to re-introduce the species to islands where it had previously occurred. There appears to be no suggestion that genetical variation in the stitchbird population had been lost.

On subantarctic Marion Island the feral cat population has been reduced by the spread of a feline parvovirus. Between 1974 and 1976, when cats were abundant, van Aarde (1980) estimated that a single cat would kill an average of 213 petrels (*Halobaena, Pachyptila, Procellaria* and *Pterodroma* species) per year. However, after control of the cats, field data collected between 1981 and 1983 (van Rensburg, 1958b) indicated that the residual cats were replacing petrels in their diet with *Mus musculus* (house mouse) and that there was now no evidence of predation on *Pterodroma brevirostris* (Kerguelen petrel). The interesting feature is that the introduced cat, at low population density, was feeding mainly on the introduced mouse, and was having a smaller effect on the native nesting bird species. The total consumption of mice was similar in high and low density cat populations, and hence it appears to be the preferred prey species.

Control of invasive predators appears to be successful in allowing native prey species to increase their population sizes. However, minimum viable population sizes for field populations have yet to be determined experimentally. Most suggestions are in the range 50–500 (reviewed by Usher, 1987b) and hence the example of the stitchbird in New Zealand would hardly be at the minimum viable size. However, the small, isolated rock wallaby populations in Western Australia were all below the suggested minimum of 50 when alien predator control started. Practical experience of minimum viable population sizes may be useful in assessing the theoretical considerations that form the foundation of these ecological and genetical hypotheses. The rock wallaby example (Figure 21.1) shows that the three populations with 10 or more animals (two with predator control, one without) increased in size between 1982 and 1986, whereas the two populations with less than 10 animals (neither with predator control) both decreased. Do these data suggest that the minimum viable population size is about 10, approximately the number of muskrats that initiated the Scottish population? Such a comparison may, however, be misleading since, on the one hand, there is a small sample from a large population that establishes and increases rapidly whilst, on the other hand, there is a species that might have maintained a small population for a number of generations. The length of time that a population has remained at small size may be an important factor.

21.3.2 Does the community recover?

Amongst the earliest experiments investigating the effect of herbivore control on vegetation were the rabbit-proof exclosures on the Breckland grasslands (Watt, 1957). The data, collected over a 21-year period beginning in 1936, are amongst the most detailed, long-term data available for ecological analysis and for modelling (Usher, 1987a). Although these data related to small exclosures, more recent data on rabbits have investigated their effect on larger areas. North and Bullock (1986) indicated that a reduction of rabbit numbers on Round Island (Mauritius) had allowed the ground vegetation to recover and some palms to regenerate (discussed in Section 21.3.1). However, the new community, although visually similar to the pre-rabbit community, was less diverse since some of the rarest native species failed to regenerate. Myers (1986) adapted a 'picture model' of the vegetation/rabbit/predator system in Australia indicating that an invasive predator, controlling the invasive herbivore, is likely to result in an improved vegetation cover (though Myers avoided a discussion of whether it would be native or introduced plants that benefit).

A number of studies in New Zealand, and oceanic islands administered by New Zealand, show the effects of controlling large herbivorous mammals (Wodzicki and Wright, 1984). The eradication of *Ovis aries* (feral sheep) on the northern half of the subantarctic Campbell Island (separated from the uncontrolled southern half by a trans-island fence) led to a spectacular regeneration of the native endemic flora, especially the herbfield, turf meadow and upper alpine tall rush associations (Meurk, 1982). On two of the smaller Chatham Islands, eradication of sheep in the 1960s led to a change in the vegetation back to native forest (Ritchie, 1970) so successfully that these islands are now essential for the conservation of two endangered species, *Cyanoramphus auriceps forbesi* (Forbes parakeet) and *Petroica traversi* (Chatham Island robin). An 80–90% reduction of *Cervus elaphus* (red deer) in the Fiordland National Park resulted in the alpine and subalpine vegetation recovering spectacularly (Evans *et al.*, 1976), and control of both red deer and goats in the forests of the Ruahine Range (Cunningham, 1979) changed the forest, which had been modified 'to the point of collapse', to a forest that showed signs of recovery. The examples from New Zealand could be extended, but they demonstrate two important points. First, control of invasive herbivores leads to the recovery of the plant community, at least structurally. The speed of recovery is obviously dependent on the composition of the community, being fastest for grasslands and herbfields and slowest for forests. Second, complete studies of recovering ecosystems are very rare, so it is generally not possible to assess whether recovery results either in a less diverse community (e.g. the Round Island study) or in a community as diverse as that which existed pre-colonization by invasive herbivores.

The same general remarks can be applied to the control or eradication of predators. In southern Africa, Cooper *et al.* (1985) reviewed the effects of introduced mammals on island biota. At Marcus Island (South Africa), serious damage to breeding birds followed constructions of a causeway linking the island to the mainland in 1976. Subsequent construction of a predator-proof wall greatly increased the breeding success of *Haematopus moquini* (black oystercatcher). Similarly, in New Zealand, Veitch (1983) and King (1984) recorded increases in native bird populations following eradication of island populations of feral cats (see also Section 21.3.1). During the period 1984 to 1986 about 20000 *Trichosurus vulpecula* (Australian brush-tailed possum) were killed on Kapiti Island, almost eradicating the species. Lovegrove (1986) recorded that, as the number of possums decreased, the number of birds increased (about two-fold during the first 2 years of the campaign).

In Australia, comparisons of kangaroo population densities both historically and on either side of the NSW/Queensland dingo fence have led Caughley *et al.* (1980) to hypothesize that the past and present densities are directly attributable to predation by dingoes. Dingoes, an introduced species, can keep kangaroos and emus at low population densities provided that there is an abundant alternative prey species. Although direct predation on kangaroos is important in keeping their numbers low, Robertshaw and Harden (1986) also showed that the predator can disrupt the breeding cycle as a result of the loss of young in the pouch due to harassment of the mothers.

Once again these studies of predator control indicate that the herbivore community can recover after the predation pressure, exerted either by killing or by harassment, is either relieved or removed. However, the assessments are usually not quantified, although large increases in bird or kangaroo abundance have been reported. The question that is never addressed is whether the post-control community is the same as, or similar to, the pre-invasion community. One reason why this question is so difficult to answer is that there are often no accurate records of the pre-invasion communities. However, the question 'Does control lead either to a full or to a partial recovery of the ecosystem?' is an important one to be able to answer. The answer must be in terms of the ecological and genetical components of that ecosystem (e.g. diversity and genetical variability) and not only in terms of its landscape contribution.

21.3.3 Are there relationships with other introduced species?

There are a number of possible relationships that could be considered, but only three will be discussed in this review, namely

Alien 1 depends on Alien 2 entirely (Case 1),
Alien 1 eats Alien 2 (but not exclusively) (Case 2), and
Alien 1 facilitates Alien 2 (Case 3).

Case 1 is trivial since Alien 1 is unlikely to be thought of either as invasive or as damaging native species or ecosystems. Elimination of Alien 2 will automatically lead to eradication of Alien 1. This is often a goal of biological control, since Alien 1 is introduced either to control or eradicate Alien 2.

Case 2 is of more interest, since control of Alien 1 may allow Alien 2 to become far more abundant and, in its turn, require control. An example of this is the control of rabbits on Motunau Island (New Zealand); they were finally eradicated in 1963 (Taylor, 1967; Mason, 1967), after which a complete vegetation cover was re-created, mainly by *Disphyrna australe* (ice plant) and *Hordeum musinum* (barely grass). *Dactylis glomerata* (cocksfoot) and *Festuca arundinacea* (tall fescue), both non-native grasses, became established for the first time, and *Carduus tenuiflorus* (winged thistle) grew in great abundance. Subsequently *Lycium ferocissimum* (boxthorn) has become a major weed problem on the island. The rabbit clearly had had an impact on the non-native vegetation. This kind of argument has also been used in considering whether the control or eradication of feral goats is desirable (Daly and Goriup, 1986). Although on balance the decision is often to reduce, exclude or eradicate the goats, it must be remembered that this can have an important impact on releasing potentially invasive plants from grazing pressure.

As well as herbivore–plant relationships, predator–prey relationships should also be considered. In the Kinchega National Park (New South Wales, Australia) the rabbit was the main food of the fox in all seasons of the year, except the autumn (when insects, and especially centipedes, were eaten in greater quantities) (Ryan and Croft, 1974). A study of 899 foxes collected throughout New South

Wales (Croft and Hone, 1978) found that the major food items, in terms of both percentage occurrence and percentage volume, were rabbit, sheep and house mouse, all non-native species. Consumption of native mammal and bird species was small, varying with season and location. What neither of these studies is able to answer is the question 'what would happen to the rabbit (and house mouse) population if foxes were reduced in number or eradicated?' An interesting answer comes from the study of the control of the feral cat on Marion Island. As the number of cats decreased, their diet changed from one where native breeding birds predominated (van Aarde, 1980) to one in which the introduced house mouse predominated (van Rensburg, 1985b), the total mouse consumption not increasing. It would be an ideal world if the reduction in the numbers of an invasive predator always led to its feeding on other invasive species and not killing the native species!

Case 2, like Case 1, may arise from a biological control situation, especially where a predatory vertebrate (Alien 1) is introduced to control some other species (Alien 2); examples are the introduction of the giant toad to Queensland (see Section 21.1.3) to control arthropod pests of sugar cane (Floyd and Esteal, 1986) or the introduction of *Herpestes auropunctatus* (small Indian mongoose) to Maui, Hawaiian Islands, in the 1880s to control rats in sugar cane fields (Brockie *et al.*, 1988). Both are examples of biological control that has gone wrong; the control agent has become an invasive species in its own right, preying both on native species and on the introduced species that they were planned to have controlled. Attempts to control vertebrates with vertebrate predators have generally been unsucessful (J.H. Brown, personal communication), but pathogens have been much more successful biological control agents of vertebrates due to their greater specificity (Case 1 rather than Case 2 relationships).

Case 3 involves the possibility of Alien 1 facilitating Alien 2. There is relatively little information on this possibility in more or less natural ecosystems, but one example is of *Cervus nippon* (sika deer) introduced into the Irish oakwoods (Cross, 1981). Overgrazing and disturbance is thought to make the environment more suitable for the regeneration and establishment of seedlings of *Rhododendron ponticum* (rhododendron). There are a number of examples of feral stock (sheep, goats, cattle) facilitating introduced grasses; examples on island nature reserves are reviewed by Brockie *et al.* (1988). Unlike the feral cat/house mouse and fox/rabbit examples, where the introduced species have come from the same part of the world, the rhododendron/sika deer example involves an invasive plant from southern Europe and an invasive mammal from Japan. Although this is an isolated example, will there be many species pairs from different parts of the world where one introduction will facilitate another? For management purposes, control of the facilitator will have an effect on the facilitated species, though the magnitude of this effect will depend on the nature of the facilitation. If sika deer were to be controlled in Ireland, the oakwoods would become less accessible for *Rhododendron* colonization and establishment, though those already colonized would continue to have an invasive *Rhododendron* population. Facilitation at the colonization or establishment stage is probably most difficult for management, since control of both introduced species, by different methods, will be required.

21.3.4 Are there undesirable side-effects?

Any method of controlling one vertebrate species may lead to the accidental death of other species. But, to what extent does this actually happen in practice?

The Scottish muskrat population originated from nine animals (including five females) that escaped from captivity in Perthshire in 1927. A compaign to eradicate the species from Scotland started in 1932, and Munro (1935) recorded the number of trap deaths between the inception of the campagin and September 1934 (see Table 21.1). Although public opinion would not tolerate jaw traps in the 1980s as it did in the 1930s, it is nevertheless interesting to ask what were the side-effects of the successful muskrat eradication campaign. Besides the muskrat, the jaw traps caught at least 26 other species of vertebrates, and there was a death rate of 6.97 other vertebrates for every muskrat killed. Although the deaths of rats and rabbits (both invasive, non-native species) would probably be acceptable, the loss of otters and many of the species of birds would not now be acceptable on conservation grounds.

The Scottish muskrat example used traps which could have been predicted to kill many other species of wildlife. In Australia, there has been experimentation with appropriate traps for *Canis familiaris dingo* (dingo). Newsome *et al.* (1983) indicated that at least 20 species of protected wildlife were trapped at a rate of two to three individuals per dingo trapped. Their study showed that a smaller trap

Table 21.1. Number of animals caught during the programme to eradicate the muskrat in the Forth and Earn Valleys, Scotland (data from Munro, 1935)

Group and species trapped	Number killed
Ondatra zibethica (muskrat)	945
Mammals	
Arvicola terrestris (water vole)	2305
Rattus norvegicus (brown rat)	1745
Mustela nivalis (weasel)	57
Mustela erminea (stoat)	36
4 other species (hare, mole, otter, rabbit)	8
Birds	
Gallinula chloropus (moorhen)	2178
Duck (unspecified species)	101
Gallinago gallinago (snipe)	28
Seagull (unspecified species)	23
Ardea cinerea (heron)	18
12 other species	87
Fish	
Anguilla anguilla (eel)	1

caught three times less protected wildlife (and 15 times less large marsupials) than a larger trap, but that the efficiency of trapping dingoes was similar. Both trap design and trap placement are considerations in the reduction of undesirable side-effects.

So far the discussion has been on trapping, but poisoning can also have undesirable side-effects. Spurr (1979) assessed the accidental deaths following the use of 1080 (sodium monofluoroacetate), incorporated in chipped carrots, oats, etc., to control the invasive *Trichosurus vulpecula* (brush-tailed possum) in New Zealand. Native birds which were killed included *Gallirallus australis* (weka), *Nestor meridionalis* (kaka), *Nestor notabilis* (kea), *Mohoua albicilla* (whitehead) and *Petroica australis* (robin), as well as several introduced species.

It is probably true that no method of control using traps or poisons can be aimed solely at the target species. Live-trapping, as with the coypus in England (see Section 21.4.1), with subsequent shooting of trapped animals, offers a reasonable degree of specificity, reducing the chances of other species being killed in the traps. However, awareness not only of accidental deaths but of the effects of human disturbance whilst trapping was evident in the evidence presented to the Coypu Strategy Group by wildlife conservations (Morton *et al.*, 1978). The coypu lives in wetland habitats, and the conservationists were particularly concerned at possible disturbance, during the breeding season, to two rare bird species, *Botaurus stellaris* (bittern) and *Circus aeruginosus* (marsh harrier); and they were also concerned about three other species, *Panurus biarmicus* (bearded tit), *Cettia cetti* (Cetti's warbler), and *Locustella luscinioides* (Savi's warbler). Many of these difficulties have been overcome by close cooperation between the conservation organizations and the trappers.

All of the examples indicate that there are a few general principles in relation to the control of invasive vertebrates. First, a few accidental deaths of other species, or limited disturbance, cannot be avoided. Second, awareness of such undesirable side-effects before a control campaign begins allows the campaign to be planned so that these effects are minimized. Third, although attempts at biological control by the use of predatory vertebrates have usually been unsuccessful, the use of pathogens, which are much more specific, is likely to be far more successful. Fourth, before the campaign proceeds, an assessment must be made both of the long-term benefits of control and of the short-term disadvantages of the side-effects (unless, of course, the side-effects are so large that their effects will also be long-term). Fifth, when all parties are satisfied that control is beneficial, then it should proceed.

21.4 PROGNOSES FOR THE FUTURE

21.4.1 Is control possible?

There appear to be three primary factors that influence the answer to this question: the dispersal ability of the invasive species, the extent of the area over which control is required, and the stage in the establishment/invasion process when control begins.

Reviewing the effects of invasive alien species on nature reserves in Great Britain, Usher (1986a) compared the campaigns to control *Mustela vison* (mink) and *Myocastor coypus* (coypu). The campaign to control the former was largely unsuccessful, whereas that to eradicate coypu by 1990 appears to be heading for success. Mink have a lower rate of increase than coypu, but a greater dispersal ability. Although it is said that mink are relatively easy to trap (Anon., 1981), Gerell (1971) showed that it was the juvenile males that were particularly trappable. Where local campaigns against mink have stopped, R. Gerell (personal communication) has shown that the population rapidly increases to its pre-campaign level, and he concluded that the effects were only of short duration. Chanin (1981) concluded that eradication of mink from Britain would be extremely difficult and expensive. The comparison between mink and coypu is interesting since coypu does not disperse so far, can also be relatively easily trapped (Gosling, 1981a), and is being effectively controlled. Trapping studies with this species indicate many subtle effects, such as the fact that traps on rafts are more effective than traps on the banks of water bodies (Anon., 1984) and that weather has a major effect on trapping success (Gosling, 1981b). Comparing these two species with the successful eradication of the muskrat in Britain in the 1930s led Usher (1986a) to suggest that successful eradication was related to small dispersal rates rather than to small rates of increase.

Studies on other alien mammals point to the same conclusion. Rabbits are difficult to control and have one of the largest mean annual dispersal distances. Auld and Tisdell (1986) discussed the control of the *Sus scrofa* (feral pig) in Australia, where individuals are known to have moved 20 km in 48 hours. They argued that the only method of control that is likely to be successful is cooperative since, if an individual farmer controls pigs on his property, other farmers benefit as the destroyed pigs are replaced by other pigs moving from elsewhere. The dearth of examples of the control of invasive birds is due to their high mobility; this is admitted by Brown (1985) for the invasive bird species in South West Africa/Namibia (see Section 21.1.3) and is admitted by Ward (1979) when discussing the control of the native *Quelea quelea* (red-billed quelea) in the dryer regions of Africa. There seems to be increasing evidence to suggest that the probability that control will be successful is inversely related to the dispersal ability of the invasive species (see Figure 21.2a).

The examples quoted in the previous sections suggest a second factor in determining success of a campaign to control an invasive species: action early in the invasion process. The control of bulbuls in New Zealand or of the red-billed blue magpie in Hawaii (see Section 21.1.3) are both examples of species that can disperse widely, have become invasive in some areas of the world, but where eradication on individual islands was successful because it started early in the invasion process.

The third important factor relates to the isolation of the area in which the invasive species is to be managed. The success stories listed in Section 21.3 are generally located on islands; the control of feral cats on Marion Island (van Rensburg, 1985b), the control of sheep on Campbell Island (Meurk, 1982) and the series of successes on New Zealand's offshore islands (King, 1984) are examples. Not all of New Zealand's offshore islands have had introduced mammals successfully controlled or had a successful recovery of a damaged ecosystem; Mark and Baylis (1982) quoted the case of Secretary Island (8000 ha) on which the continuing effects of red deer impact on the vegetation could be observed even after an almost successful control campaign. The experience in South Africa is interesting since the natural ecosystems seem to be less prone to invasion by introduced mammals than ecosystems elsewhere in the world. Macdonald and Richardson (1986) indicated that attempts to control *Sciurus carolinensis* (grey squirrel) were futile, but that *Hemitragus jemlahicus* (Himalayan tahr) is contained on Table Mountain by shooting. In Europe, muskrat was eradicated in Scotland (cf. Munro, 1935), whereas in continental Europe it has spread and control campaigns have been unsuccessful of (cf. Verkaik, 1987). These various studies all indicate that the control of an invasive species on islands is likely to be more successful than control on continental areas.

However, isolation can also be achieved in an artificial manner. Cronk (1986b) discussed the decline of *Commidendrum robustum* (St Helena gumwood) on St Helena due to cutting for firewood, grazing of stock in the wooded areas, and, once again, the depredations of feral goat. The species will, however, regenerate freely, and new woodlands can be created in areas which are fenced against goats. The construction of a predator-proof wall (Cooper *et al.*, 1985), or of the dingo fence (Shepherd, 1981), or of fences in the Hawaiian national parks for goat control (Brockie *et al.*, 1988), effectively increases the isolation of an area within which the invasive species can be controlled or eradicated. Although the barriers quoted above are physical barriers that prevent entry of widely dispersing predators or herbivores, less tangible barriers can also be effective. Quarantine barriers are used in some places with reasonable success, whilst control of the giant toad in Australia (Floyd and Easteal, 1986) could be referred to as a legal barrier if ever legislation prohibited the movement of produce from toad-inhabited to toad-free areas.

Isolation of an area of land is difficult to define precisely, but it is nevertheless an intuitive concept that is useful when considering the probability that management to control or eradicate an invasive species will be successful. Isolation is, of course, not completely unrelated to dispersal ability, since a short distance of sea or a fence would present no barrier to a bird but may be an impermeable barrier to a mammal. The concept of isolation is shown in Figure 21.2b.

Two of these three factors, dispersal of alien species and isolation of management area, can be combined as in Figure 21.2c. In this diagram only three contours have been drawn and, because of the difficulty of giving precise definitions to dispersal and isolation, no points have been plotted. However,

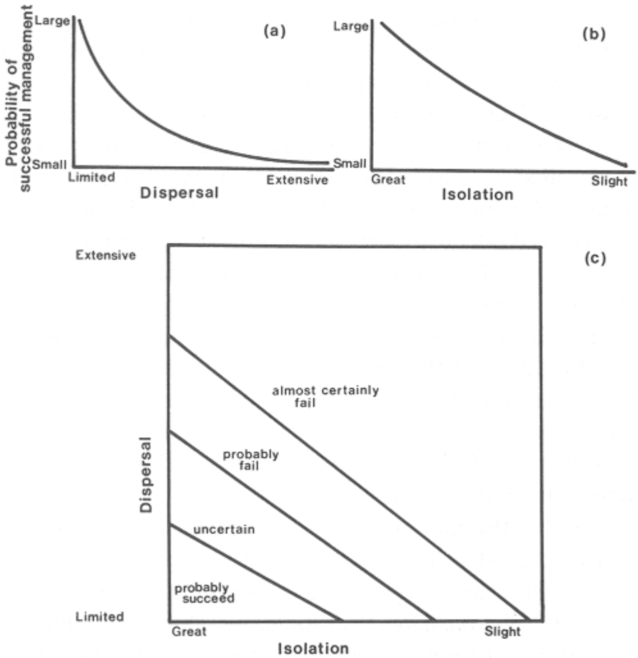

Figure 21.2. Diagrammatic representations of the possible relationships between the probability of successfully managing an invasive species and (a) its dispersal ability and (b) the isolation of the site being managed. These two factors are brought together in (c) to provide a 'picture model' to predict the probability that management will succeed. The real shapes of the curves in (a) and (b) are unknown, but both would be monotonically decreasing functions. The contours in (c) are drawn as straight lines; their precise shape would depend on the shape of the curves in (a) and (b). There is a discussion of the effects of the timing of control operations on the location of the contours in (c) in the text

within the very rough framework of these two factors, Figure 21.2c provides a picture model that could be used to predict how successful management to control an invasive species might be. If control begins early in the invasion process, then the contours in Figure 21.2c can be moved away from the origin towards the upper right-hand corner of the square. As the invasion process proceeds, the contours move closer towards the origin.

21.4.2 Is modelling helpful?

It could, perhaps, be argued that models are not yet able to predict sufficiently accurately the establishment and spread stages of a biological invasion

(Williamson, this volume), and hence that they are unlikely to be useful in designing control strategies.

The position with models is, however, not quite so bleak. In order to eradicate the coypu in Great Britain, the population not only needed to be censussed but estimates needed to be made of the population size in previous years. A simple, statistical modelling approach, estimating monthly frequencies of recruitment, was used to solve the problem of estimating retrospectively the census counts (Gosling *et al.*, 1981). Simple regression models were used by Gosling (1981c) to relate the proportions of female coypus littering in spring to the severity of the winter, and to relate the trap efficiency (number of adults killed per night of trapping) to the number of adults in the population. These simple, statistical models only address specific aspects of the overall control operation.

More sophisticated models have been developed by Anderson (1982) in relation to the fox and rabies interaction. Although his model of foxes under control by shooting and disease (rabies in this case) is applied in an area where the fox is native, the modelling approach adopted could well be used for non-native invasive species. In the fox/rabies model, the management objective was to reduce the size of the fox population below the threshold needed for rabies transmission; for introduced species the management objective would be to reduce the size of the population so that its effects on the native fauna and flora were perceived to be negligible. Anderson's (1982) model was deterministic; Mollison (1986) argued that for policy makers a stochastic modelling approach would be preferable. Whatever these advantages and disadvantages, there is clearly considerable scope for the development of suitable models for vertebrate control.

21.4.3 How is success measured?

The words success and failure have been used frequently both in the foregoing accounts and in the references cited. However, brief consideration should be given to the assessment of success. Holdgate (1986) said 'examples of successful elimination of an invader (like that of muskrat in Britain) will remain limited...success in most cases will be reflected in the reduction of the invader's population size to a level that is compatible with the perpetuation of the invaded ecosystem in only slightly altered form'. Note that, in this quotation, 'slightly altered form' is not defined and it could form the basis of an argument about how much constitutes 'slightly'. It highlights the need for an objective of control to be specified precisely before the control begins. The results of that control can then be compared with the specification; if they match the specification or exceed it then control is successful, whilst if they fall short of the *a priori* specification then management has been unsuccessful.

It may, however, be difficult to monitor the management sufficiently precisely to match results with the specification. As an example, the campaign against the coypu in Britain aimed to eradicate the species from the country (Morton *et al.*, 1978). However, as the population density has decreased, it is more and more difficult to estimate how many remain. This problem is discussed by Gosling (1985), who recently (in August 1986) expressed the opinion that there may only be 10 feral coypu females remaining in Britain (L. M. Gosling to S. Reeves, personal communication). Mark and Baylis (1982) highlighted this problem on Secretary Island (New Zealand), where, during a visit, they failed to sight red deer and only found two groups of pellets. If the aim of management is eradication, it is extremely difficult to be absolutely certain that eradication has been achieved; conversely, sighting an individual proves conclusively that eradication has not been achieved.

21.4.4 Are control and conservation compatible?

Perhaps the overwhelming reason for controlling an invasive vertebrate species is its effect on the native species and communities of its new environment. Macdonald *et al.* (this volume) have concentrated on aliens and conservation, and Loope and Mueller-Dombois (this volume) have stressed the effects of introduced species on the endemic species of the Hawaiian Islands. Frequently there can be different views as to the value of an alien species in conservation management; this was highlighted by Daly and Goriup (1986) who stated that control or eradication of feral goats was not always welcomed by conservations.

From a wildlife conservation point of view, many of the examples quoted in this paper are on the negative side of the non-native/native species interaction. Goats have grazed the native flora till only a few individuals of a native species remain (the St Helena ebony, for example) or foxes have killed the native marsupials so that only a few small, isolated populations remain (the rock wallaby, for example). Control of the non-native species is overtly beneficial to the native flora or fauna.

However, there are also examples that are on the positive side of the non-native/native species interaction. In Sweden, Danell (1979) reported that, if not too numerous, the presence of muskrats increased the waterfowl populations of well-vegetated lakes by expanding the area of open water and hence the feeding areas available to both adult and juvenile birds. Also in Sweden, the spread of the Canada goose has given wildfowlers another species to shoot, reducing the pressure on native species (Fabricius, 1983). In Western Australia the diet of the *Aquila audax* (wedge-tailed eagle) contains a large proportion of introduced species. In the dry Nullarbor Plain, Brooker and Ridpath (1980) recorded that 'rabbits were by far the major food item', whereas in other areas of Western Australia rabbits, sheep, foxes and cats all formed substantial proportions of the eagle's diet.

Even more complex interactions can occur. Christensen and Burrows (1986) explained the complicated management strategy to control foxes in Western

Australia, to encourage *Macropus eugenii* (tammar wallaby) and to burn the thickets of *Casuarina*, *Melaleuca* and *Gastrolobium*. To protect the tammar from excessive predation, the thickets require a fire of high intensity every 25 to 30 years. This leads to mass germination of the thicket species, but there are many management problems associated with small area fires, such as control of the fire, prevention of undue kangaroo and wallaby grazing during regeneration, etc. Management of an appropriate habitat for the tammer needs to consider the introduced species, balancing losses due to predation with losses due to habitat change if an appropriate form of management was not adopted.

21.4.5 Does control increase or decrease genetic diversity?

One of the main purposes of wildlife conservation is to retain as diverse a genetic resource as possible. If control of invasive species prevents the extinction of any native species, it could be argued that genetic diversity has been retained.

However, if a native species has been reduced to a very small population size, has the amount that it contributes to global genetic diversity already been irretrievably impaired? Miller (1979) catalogued some of the genetical problems that have to be thought about by conservationists; one of these is the 'bottleneck', which is particularly relevant in a study of invasive species. As an example, Cronk (1986a) documented the re-finding of *Trochetiopsis melanoxylon* (St Helena ebony). After being considered as extinct for more than a century, two individuals were recently found (see Section 21.3.1), both low bushes rather than shrubs or small trees as would have covered St Helena prior to the arrival of people and goats. Although genetical studies on this species have yet to be reported, Cronk (1986a) considered that these two remaining individuals represent a cliff ecotype and that the 'normal' ecotype is extinct.

Changes in genetic diversity can occur through interbreeding between native and feral populations. This has occurred around the world with the cats. In Britain, some rather bizarre animals, even recently suspected by amateurs and 'The Press' of being a new and undescribed cat species, have resulted from crosses between *Felis catus* (feral cat) and *Felis sylvestris* (wild cat) (D.D. French, personal communication). In southern Africa, the feral cat has hybridized with *Felis lybica* (the indigenous African wild cat) to such an extent that Griffin and Panagis (1985) considered that 'pure' *F. lybica* no longer existed. This raises the taxonomic problem of whether all *Felis* species are distinct, or whether they are essentially subspecies. With the feral cat in localities where there are wild cats it may not now be possible to eliminate the former, and indeed the genetic diversity of the wild population may have been increased with feral cat genes.

General features of the genetic aspects of the invasion process are considered by both Barrett and Richardson (1986) and Gray (1986). What appear not to have been studied are the genetic aspects of the control process. Studies of this are clearly needed.

21.5 CONCLUSION

There are three general points that emerge from a discussion of the control of invasive vertebrate species.

First, there is now much more awareness of the problems and of the need for management policies. The discussion of the need for control is moving from the scientific to more general literature (e.g. the book by Fitter, 1986), and there are lively debates when proposals are brought forward to introduce mammals, e.g. the discussions reported in Pinder (1981) concerning the re-introduction of *Castor fiber* (European beaver) into Britain. More awareness of the problems caused by invasive vertebrates will probably help in the solution of those problems.

Second, conservationists are beginning to recognize the importance of thinking about invasive species. In reviewing the criteria used for selecting nature reserves, Usher (1986b) listed 24 criteria that have been used in 17 evaluation studies around the world. Not one of these studies considered the presence or management consequences of non-native species. Usher (in press) has suggested that, in Africa, the potential problem posed by invasive species should be a criterion in the selection of nature reserves, national parks, etc. The search for the naturalness of reserves (see Brooke *et al.*, 1986) should be as much related to the impacts of invasive species as to the impact of human societies.

Third, to end on an optimistic note, control of invasive vertebrate species can frequently be achieved, as shown in the discussion by Wodzicki and Wright (1984) of the many invasive vertebrate species in New Zealand; the only species that they say is still unmanageable is *Trichosurus vulpecula* (brush-tail possum). Control, or eradication, is likely to be relatively easy for species/site pairs that are located towards the bottom left corner of the diagram (Figure 21.2c). Moving either to the right or upwards, control becomes more difficult. This, of course, is tempered by the timing of control operations; wherever one is in Figure 21.2c, the operation is likely to be easier the earlier control starts in the invasion process. Difficulty of control does not generally mean impossibility; it usually means that more effort is required, and this in turn requires more resources (people and money) and operations over a longer period of time or over a larger territorial area. If the management objectives are defined, and if the resources are available, invasive vertebrate species control or eradication has usually proved possible. Scientists have developed the methods; what is needed is the political will to use them.

21.6 SUMMARY

The chapter aims to investigate how frequently control measures have been attempted for invasive vertebrate species and to explore the factors that lead to successful control (or management). The review starts by asking how the control operations affect the invasive species itself; genetical aspects are little studied but

they may be tremendously important, as, for example, the development of warfarin resistance in rats.

Control is usually commenced due to damage either to individual native or endemic species, or to the structure of communities. It is seen that control operations are often successful when individual species are to be protected from invasive species, and that communities can often recover at least structurally if not to their full pre-invasion diversity. For future management, control is usually possible, there being relatively few examples where invasive vertebrates are considered to be unmanageable. Three factors are seen to predispose any campaign to success. First, campaigns that start at the establishment phase of an invasion, or very soon after establishment, have a much greater probability of success. Second, management success is inversely proportional to the dispersal ability of the species to be controlled. Third, success and isolation of the invaded habitat are correlated; thus campaigns to control an invasive vertebrate species are more likely to be successful on an island than on a part of a continent, and barriers (such as fences or even quarantine enforcement zones) increase isolation of continental areas, making control that much more possible.

ACKNOWLEDGMENTS

In preparing this review a number of people around the world have provided information and case histories. I should like to thank Dr R. H. Groves and Dr J. E. Kinnear (Australia); Dr V. Landa, Dr J. Lepš and Dr J. Rusek (Czechoslovakia); Professor R. H. Drent, Dr H. van Emden Dr W. Joenje and Mr. A. J. Verkaik (Netherlands); Dr R. E. Brockie and Professor A. F. Mark (New Zealand); Mr I. A. W. Macdonald (South Africa); Dr K. Danell, Professor E. Fabricius, Dr R. Gerell, Dr G. Görannson, Dr O. Liberg and Dr S. Ulfstrand (Sweden); Miss J. Barber, Dr L. M. Cook, Dr L. M. Gosling and Dr M. Rands (UK); and Dr J. H. Brown, Dr J. A. Drake, Professor P. R. Ehrlich and Dr S. L. Pimm (USA). I should like to thank Professor H. A. Mooney and SCOPE for financial assistance and Professor M. H. Williamson for reading through the manuscript.

REFERENCES

van Aarde, R. J. (1980). The diet and feeding behaviour of feral cats, *Felis catus*, at Marion Island. *S. Afr. J. Wildl. Res.*, **10**, 123–8.

van Aarde, R. J. (1984). Population biology and the control of feral cats on Marion Island. *Acta Zool. Fennica*, **172**, 107–10.

van Aarde, R. J., and Skinner, J. D. (1981). The feral cat population at Marion Island: characteristics, colonization and control. *Com. Nat. fr. Rech. Antarctiques*, **51**, 281–8.

Anderson, R. M. (1982). Fox rabies. In: Anderson, R. M. (Ed.), *Population Dynamics of Infectious Diseases: Theory and Applications*, pp. 242–61. Chapman & Hall, London, New York.

Anonymous (1981). *Feral mink.* Ministry of Agriculture, Fisheries and Food Leaflet No. 794. HMSO, London.

Anonymous (1984). Coypu Research Laboratory. *Agr. Dev. & Advisory Serv. Ann. Rep., 1983*, pp. 96–9. HMSO, London.

Atkinson, I. A. E. (1985). The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In: Moore, P. J. (Ed.), *Conservation of Island Birds*, pp. 35–81. ICBP Technical Publication No. 3.

Auld, B. A., and Tisdell, C. A. (1986). Impact assessment of biological invasions. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: an Australian Perspective*, pp. 79–88. Australian Academy of Science, Canberra.

Backhouse, G. N. (1987). Management of remnant habitat for conservation of the helmeted, *Lichenostomus melanops cassidix.* In: Saunders, D. A., Arnold, G. W., Burbidge, A. A., and Hopkins, A. J. M. (Eds), *Nature Conservation: the Role of Remnants of Native Vegetation*, pp. 287–94. Surrey-Beatty, Sydney.

Barrett, S. C. H., and Richardson, B. J. (1986). Genetic attributes of invading species. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: an Australian Perspective*, pp. 21–33. Australian Academy of Science, Canberra.

Berger, A. J. (1981). *Hawaiian Bird Life.* University of Hawaii Press, Honolulu.

Berry, R. J. (1977). *Inheritance and Natural History.* Collins, London.

Bishop, J. A., Hartley, D. J., and Partridge, G. G. (1977). The population dynamics of genetically determined resistance to warfarin in *Rattus norvegicus* from mid Wales. *Heredity*, **39**, 389–98.

Bourne, W. R. P., and David, A. C. F. (1983). Henderson Island, central South Pacific, and its birds, *Notornis*, **30**, 233–52.

Bourne, W. R. P., and David, A. C. F. (1985). Henderson Island. *Notornis*, **32**, 83.

Bourne, W. R. P., and David, A. C. F. (1986). Henderson Island. *Nature*, **322**, 302.

Brockie, R. E., Loope, L. L., Usher, M. B., and Hamman, O. (1988). Biological invasions of island nature reserves. *Biological Conservation*, **44**, 9–36.

Brooke, R. K., Lloyd, P. H., and Villiers, A. L. de (1986). Alien and translocated terrestrial vertebrates in South Africa. In: Macdonald, I. A. W., Kruger, F. J., and Ferrar, A. A. (Eds), *The Ecology and Management of Biological Invasions in Southern Africa*, pp. 63–74. Oxford University Press, Cape Town.

Brooker, M. G., and Ridpath, M. G. (1980). The diet of the wedge-tailed eagle, *Aquila audax*, in Western Australia. *Aust. Wildl. Res.*, **7**, 433–52.

Brown, C. J. (1985). Invasive alien birds in South West Africa/Namibia. In: Brown, C. J., Macdonald, I. A. W., and Brown, S. E. (Eds), *Invasive Alien Organisms in South West Africa/Namibia*, pp. 41–3. South African National Scientific Programmes Report, 119.

Butler, W. H. (1970). A summary of the vertebrate fauna of Barrow Island, W. A. *West. Aust. Nat.*, **11**, 149–60.

Butler, W. H. (1987). Management of disturbance in an arid remnant: the Barrow Island experience. In: Saunders, D. A., Arnold, G. W., Burbidge, A. A., and Hopkins, A. J. M. (Eds), *Nature Conservation: the Role of Remnants of Native Vegetation*, pp. 279–85. Surrey-Beatty, Sydney.

Caughley, G., Grigg, G. C., Caughley, J., and Hill, G. J. E. (1980). Does dingo predation control the densities of kangaroos and emu? *Aust. Wildl. Res.*, **7**, 1–12.

Chanin, P. (1981). The feral mink—natural history, movements and control. *Nature in Devon*, **2**, 33–54.

Christensen, P. E., and Burrowns, N. D. (1986). Fire: an old tool with a new use. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: an Australian Perspective*, pp. 97–105. Australian Academy of Science, Canberra.

Cooper, J., Hockey, P. A. R., and Brooke, R. K. (1985). Introduced mammals on South and

South West African islands: history, effects on birds and control. *Proceedings of Symposium on Birds and Man, Johannesburg, 1983*, pp. 179–203.
Croft, J. D., and Hone, L. J. (1978). The stomach contents of foxes, *Vulpes vulpes*, collected in New South Wales. *Aust. Wildl. Res.*, **5**, 85–92.
Cronk, Q. C. B. (1986a). The decline of the St. Helena ebony *Trochetiopsis melanoxylon*. *Biol. Conserv.*, **35**, 159–72.
Cronk, Q. C. B. (1986b). The decline of the St Helena gumwood *Commidendrum robustum*. *Biol. Conserv.*, **35**, 173–86.
Cross, J. R. (1981). The establishment of *Rhododendron ponticum* in the Killarney oakwoods, S. W. Ireland. *J. Ecol.*, **69**, 807–24.
Cunningham, A. (1979). A century of change in the forests of the Ruahine Range, North Island, New Zealand, 1870–1970. *New Zealand J. Ecol.*, **2**, 11–21.
Daly, K., and Goriup, P. (1986). *Eradication of Feral Goats from Small Islands*. Report of the International Council for Bird Preservation and of the Fauna and Flora Preservation Society. 44 pp.
Danell, K. (1979). Reduction of aquatic vegetation following the colonization of a northern Swedish lake by the muskrat, *Ondatra zibethica*. *Oecologia*, **38**, 101–6.
Diamond, J. (1985). Rats as agents of extermination. *Nature*, **318**, 602–3.
Ehrlich, P. R. (1986). Which animal will invade? In: Mooney, H. A., and Drake, J. A. (Eds), *The Ecology of Biological Invasions of North America and Hawaii*, pp. 79–95. Springer-Verlag, New York.
Evans, G. R., Payton, I. J., Burrows, L. E., Parkes, J. P., and Batchelor, G. L. (1976). *Summary Report on a Vegetation Resurvey of Part of Fiordland National Park*. New Zealand For. Serv. Prot. For. Rep., No. 141.
Fabricius, E. (1983). *Kanadagasen i Sverige*. Naturvardsverket Rapport, 1678.
Falla, R. A., Sibson, R. B., and Turbott, E. G. (1966). *A Field Guide to the Birds of New Zealand and Outlying Islands*. Collins, London.
Fenner, F. (1983). The Florey Lecture, 1983. Biological control as exemplified by smallpox eradication and myxomatosis. *Proc. R. Soc. Lond. B*, **218**, 259–85.
Fitter, R. (1986). *Wildlife for Man: How and Why we should Conserve our Species*. Collins, London.
Floyd, R. B., and Easteal, S. (1986). The giant toad (*Bufo marinus*): introduction and spread in Australia. In: Groves, R. H., and Burdon, J. J. (Eds.), *Ecology of Biological Invasions: an Australian Perspective*, p. 151. Australian Academy of Science, Canberra.
Gerell, R. (1971). Population studies on mink, *Mustela vison* Schreber, in southern Sweden. *Viltrevy*, **8**, 83–114.
Gerell, R. (1985). Habitat selection and nest predation in a common eider population in southern Sweden. *Ornis Scand.*, **16**, 129–39.
Gosling, L. M. (1981a). The coypu. In: Boyle, C. L. (Ed.), *RSPCA Book of British Mammals*, pp. 129–35. Collins, London.
Gosling, L. M. (1981b). The effect of cold weather on success in trapping feral coypus (*Myocastor coypus*). *J. Appl. Ecol.*, **18**, 467–70.
Gosling, L. M. (1981c). The dynamics and control of a feral coypu population. In: Chapman, J. A., and Pursley, D. (Eds), *Proceedings of Worldwide Furbearer Conference*, pp. 1806–25.
Gosling, L. M. (1985). Coypus in East Anglia (1970 to 1984). *Trans. Norfolk & Norwich Nat. Soc.*, **27**, 151–3.
Gosling, L. M., Watt, A. D., and Baker, S. J. (1981). Continuous retrospective census of the East Anglian coypu population between 1970 and 1979. *J. Anim. Ecol.*, **50**, 885–901.
Gray, A. J. (1986). Do invading species have definable genetic characteristics? *Phil. Trans. R. Soc. Lond. B*, **314**, 655–74.

Griffin, M., and Panagis, K. (1985). Invasive alien mammals, reptiles and amphibians in South West Africa/Namibia. In: Brown, C. J., Macdonald, I. A. W., and Brown, S. E. (Eds), *Invasive Alien Organisms in South West Africa/Namibia*, pp. 44–7. South African National Scientific Programmes 119.

Holdgate, M. W. (1986). Summary and conclusions: characteristics and consequences of biological invasions. *Phil. Trans. R. Soc. Lond. B*, **314**, 733–42.

Howell, P. G. (1984). An evaluation of the biological control of the feral cat *Felis catus* (Linnaeus, 1758). *Acta Zool. Fennica*, **172**, 111–3.

King, C. (1984). *Immigrant Killers: Introduced Predators and the Conservation of Birds in New Zealand*. Oxford University Press, Auckland.

Kinnear, J., Onus, M., and Bromilow, B. (1984). Foxes, feral cats and rock wallabys. *Swans*, **14**, 3–8.

Lockley, R. M. (1970). *Man Against Nature*. Andre Deutsch, London.

Lovegrove, T. (1986). *Counts of Forest Birds on Three Transects on Kapiti Island 1982–1986*. New Zealand For. Serv. Rep. 17 pp.

Macdonald, I. A. W., and Richardson, D. M. (1986). Alien species in terrestrial ecosystems of the fynbos biome. In Macdonald, I. A. W., Kruger, F. J., and Ferrar, A. A. (Eds), *The Ecology and Management of Biological Invasions in Southern Africa*, pp. 77–91. Oxford University Press, Cape Town.

Mark, A. F., and Baylis, G. T. S. (1982). Further studies on the impact of deer on Secretary Island, Fiordland, New Zealand. *New Zealand J. Ecol.*, **5**, 67–75.

Mason, R. (1967). Motunau Island, Canterbury, New Zealand: vegetation. *New Zealand Dep. Sci. Ind. Res. Bull.*, **178**, 68–92.

Meurk, C. D. (1982). Regeneration of subantarctic plants on Campbell Island following exclusion of sheep. *New Zealand J. Ecol.*, **5**, 57–8.

Miller, R. I. (1979). Conserving the genetic integrity of faunal populations and communities. *Environm. Conserv.*, **6**, 297–304.

Mollison, D. (1986). Modelling biological invasions: chance, explanation, prediction. *Phil. Trans. R. Soc. Lond. B*, **314**, 675–93.

Mooney, H. A., Hamburg, S. P., and Drake, J. A. (1986). The invasions of plants and animals into California. In: Mooney, H. A., and Drake, J. A. (Eds), *The Ecology of Biological Invasions of North America and Hawaii*, pp. 250–72. Springer-Verlag, New York.

Morton, J., Calver, J., Jefferies, D. J., Norris, J. H. M., Roberts, K. E., and Southern, H. N. (1978). *Coypu: Report of the Coypu Strategy Group*. HMSO (Ministry of Agriculture, Fisheries and Food), London.

Moulton, M. P., and Pimm, S. L. (1986). Species introductions to Hawaii. In: Mooney, H. A., and Drake, J. A. (Eds), *The Ecology of Biological Invasions of North America and Hawaii*, pp. 231–49. Springer-Verlag, New York.

Munro, T. (1935). Note on musk-rats and other animals killed since the inception of the campaign against musk-rats in October 1932. *Scot. Nat.*, (1935), 11–6.

Myers, K. (1986). Introduced vertebrates in Australia, with emphasis on the mammals. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: an Australian Perspective*, pp. 120–36. Australian Academy of Science, Canberra.

Newsome, A. E., and Noble, I. R. (1986). Ecological and physiological characters of invading species. In: Groves, R. H., and Burdon, J. J. (Eds), *Ecology of Biological Invasions: an Australian Perspective*, pp. 1–20. Australian Academy of Science, Canberra.

Newsome, A. E., Corbett, L. K., Catling, P. C., and Burt, R. J. (1983). The feeding ecology of the dingo. I. Stomach contents from trapping in south-eastern Australia, and the non-target wildlife also caught in dingo traps. *Aust. Wildl. Res.*, **10**, 477–86.

North, S. G., and Bullock, D. J. (1986). Changes in the vegetation and populations of introduced mammals of Round Island and Gunner's Quoin, Mauritius. *Biol. Conserv.*, **37**, 99–117.

Parkes, J. P. (1984). Feral goats on Raoul Island, II. Diet and notes on the flora. *New Zealand J. Ecol.*, **7**, 95–101.

Pinder, N. (Ed.) (1981). *Conservation and Introduced Species.* University College London Discussion Papers in Conservation No. 30.

Rensburg, P. J. J. van (1985a). Feral cats and sub-Antarctic skuas on Marion Island: competition or co-existence? *S. Afr. J. Sciences*, **81**, 691.

Rensburg, P. J. J. van (1985b). The feeding ecology of a decreasing feral house cat, *Felis catus*, population at Marion Island. In: Siegfried, W. R., Condy, P. R., and Laws, R. M. (Eds), *Antarctic Nutrient Cycles and Food Webs*, pp. 620–4. Springer-Verlag, Berlin.

Ritchie, I. M. (1970). A preliminary report on a recent botanical survey of the Chatham Islands. *Proc. New Zealand Ecol. Soc.*, **17**, 52–6.

Robertshaw, J. D., and Harden, R. H. (1986). The ecology of the dingo in north-eastern New South Wales, IV. Prey selection by dingoes, and its effect on the major prey species, the swamp wallaby, *Wallabia bicolor* (Desmarest). *Aust. Wildl. Res.*, **13**, 141–63.

Ross, J., and Tittensor, A. M. (1986). The establishment and spread of myxomatosis and its effect on rabbit populations. *Phil. Trans. R. Soc. Lond. B*, **314**, 599–606.

Ryan, G. E., and Croft, J. D. (1974). Observations on the food of the fox, *Vulpes vulpes* (L.), in Kinchega National Park, Menindee, N. S. W. *Aust. Wildl. Res.*, **1**, 89–94.

Shepherd, N. C. (1981). Predation of red kangaroos, *Macropus rufus*, by the dingo, *Canis familiaris dingo* (Blumenbach), in north-western New South Wales. *Aust. Wild. Res.*, **8**, 255–62.

Spurr, E. B. (1979). A theoretical assessment of the ability of bird species to recover from an imposed reduction in numbers, with particular reference to 1080 poisoning. *New Zealand J. Ecol.*, **2**, 46–63.

Taylor, R. H. (1967). Motunau Island, Canterbury, New Zealand: an ecological survey. *New Zealand Dep. Sci. Ind. Res. Bull.*, **178**, 42–67.

Usher, M. B. (1986a). Invasibility and wildlife conservation: invasive species on nature reserves. *Phil. Trans. R. Soc. Lond. B*, **314**, 695–710.

Usher, M. B. (1986b). Wildlife conservation evaluation: attributes, criteria and values. In: Usher, M. B. (Ed.), *Wildlife Conservation Evaluation*, pp. 3–44. Chapman & Hall, London, New York.

Usher, M. B. (1987a). Modelling successional processes in ecosystems. In: Gray, A. J., Edwards, P. J., and Crawley, M. J. (Eds), *Colonization, Succession and Stability*, pp. 31–55. Blackwell, Oxford.

Usher, M. B. (1987b). Effects of fragmentation on communities and populations: a review with applications to wildlife conservation. In: Saunders, D. A., Arnold, G. W., Burbidge, A. A., and Hopkins, A. J. M. (Eds), *Nature Conservation: the Role of Remnants of Native Vegetation*, pp. 103–21. Surrey-Beatty, Sydney.

Usher, M. B. (1988). Biological invasions of nature reserves. *Biol. Conserv.*, **44**, 1–35.

Usher, M. B. (1987). The evaluation of potential conservation locations in Africa. *Proc. Internat. Symp. African Wildlife, Mweya, Uganda, December 1986.*

Veitch, C. R. (1983). A cat problem removed. *Wildlife: a Review* (*New Zealand Wildl. Serv.*), **12**, 47–9.

Verkaik, A. J. (in press). The muskrat in the Netherlands. *Proc. Kon. Nederl. Akad. Wetens.* C, **90**, 67–72.

Ward, P. (1979). Rational strategies for the control of queleas and other migrant bird pests in Africa. *Phil. Trans. R. Soc. Lond. B*, **287**, 289–300.

Watt, A. S. (1957). The effects of excluding rabbits from grassland B (Mesobrometum) in Breckland. *J. Ecol.*, **45**, 861–78.

Wodzicki, K., and Wright, S. (1984). Introduced birds and mammals in New Zealand and their effect on the environment. *Tuatara*, **27**, 77–104.