Biol. Rev. (2003), **78**, pp. 347–383. © *Cambridge Philosophical Society*
DOI: 10.1017/S1464793102006061 *Printed in the United Kingdom*

Mammal invaders on islands: impact, control and control impact

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(*Received* 11 *January* 2002; *revised* 5 *July* 2002)

ABSTRACT

The invasion of ecosystems by exotic species is currently viewed as one of the most important sources of biodiversity loss. The largest part of this loss occurs on islands, where indigenous species have often evolved in the absence of strong competition, herbivory, parasitism or predation. As a result, introduced species thrive in those optimal insular ecosystems affecting their plant food, competitors or animal prey. As islands are characterised by a high rate of endemism, the impacted populations often correspond to local subspecies or even unique species. One of the most important taxa concerning biological invasions on islands is mammals. A small number of mammal species is responsible for most of the damage to invaded insular ecosystems: rats, cats, goats, rabbits, pigs and a few others. The effect of alien invasive species may be simple or very complex, especially since a large array of invasive species, mammals and others, can be present simultaneously and interact among themselves as well as with the indigenous species. In most cases, introduced species generally have a strong impact and they often are responsible for the impoverishment of the local flora and fauna. The best response to these effects is almost always to control the alien population, either by regularly reducing their numbers, or better still, by eradicating the population as a whole from the island. Several types of methods are currently used: physical (trapping, shooting), chemical (poisoning) and biological (e.g. directed use of diseases). Each has its own set of advantages and disadvantages, depending on the mammal species targeted. The best strategy is almost always to combine several methods. Whatever the strategy used, its long-term success is critically dependent on solid support from several different areas, including financial support, staff commitment, and public support, to name only a few. In many cases, the elimination of the alien invasive species is followed by a rapid and often spectacular recovery of the impacted local populations. However, in other cases, the removal of the alien is not sufficient for the damaged ecosystem to revert to its former state, and complementary actions, such as species re-introduction, are required. A third situation may be widespread: the sudden removal of the alien species may generate a further disequilibrium, resulting in further or greater damage to the ecosystem. Given the numerous and complex population interactions among island species, it is difficult to predict the outcome of the removal of key species, such as a top predator. This justifies careful pre-control study and preparation prior to initiating the eradication of an alien species, in order to avoid an ecological catastrophe. In addition, long-term monitoring of the post-eradication ecosystem is crucial to assess success and prevent reinvasion.

Key words: alien species, biological invasions, introduced species, island restoration.

CONTENTS

I. INTRODUCTION

(1) Biological invasions: a cause of major change

The invasion of species into naive ecosystems, a process known as biological invasion, has historically been overlooked not only by many scientists, but also by politicians and economists. It is now, however, considered the second most important cause of biodiversity loss, after habitat destruction and fragmentation (Vitousek *et al.*, 1997*b*). Thanks to human migration and commerce, the number of species colonising new habitats has increased by orders of magnitude in the last two centuries (di Castri, 1989; in Mack *et al.*, 2000). Not only do human activities promote biological invasions by being very effective dispersal agents, but they also facilitate the establishment of new immigrants through husbandry activities that protect small and vulnerable immigrant populations until they become larger and more resistant (Mack *et al.*, 2000). It has been estimated that the current rate of species extinction is between 50 and several hundred times greater than was estimated previously on the basis of geological data (Wall *et al.*, 2001). The ecological homogenisation caused by biological invasions is mainly due to the relatively recent increase in human travel around the globe leading to the erosion of geographical barriers and reduced isolation among ecosystems. For tens of millions of years, species not capable of long-range dispersal have diverged behind their sea barriers on separate land habitats (Holdgate, 1986). Recent accelerated influxes of previously separated species by human dispersal activities are now eliminating such isolation. Biological invasions currently constitute one of the main causes of major global ecological change (Vitousek *et al.*, 1997*a*), and could very well influence other agents of global change (Mack *et al.*, 2000). For the purpose of this review, we distinguish between natural and human-induced movement of species into ecosystems, with a focus on the latter.

(2) Islands: fragile and threatened ecosystems

Most introductions of species into new habitats are failures (deVos & Petrides, 1967). For example, of the 150 or so species of birds introduced to Hawaii, and of the 145 introduced to New Zealand, 'only' 30 and 36 have become established, respectively (Roots, 1976; Veitch & Clout, 2001). This relates to what has been termed the '10's rule': approximately 10% of introductions succeed and approximately 10% of these will be significantly ecologically disruptive (Williamson, 1996). However, with the sheer number of previous attempts, a small proportion of successful introductions translates into a very large number of cases, which concern virtually all major islands. In addition, some species, whose ecological equivalents are naturally lacking in the native ecosystem, may have a disproportionately greater impact and do not follow the 10% rule. For example, of the 55 mammal species introduced to New Zealand, 32 have become established, far more than the 10% (Veitch & Clout, 2001). A little more than a decade ago, Ebenhard recorded 644 mammal introductions on islands (Ebenhard, 1988). Few islands have escaped the problems caused by species introductions, and islands are the recipients of 80% of documented bird and mammal introductions (Ebenhard, 1988). Over 80% of all islands have been invaded by rats, *Rattus* sp. (Atkinson, 1985), and at least 65 major island groups have also been invaded by cats, *Felis catus* (Atkinson, 1989).

Oceanic islands are home to plant and animal communities with relatively little diversification, simplified trophic webs and high rates of endemism (Chapuis *et al.*, 1995). These three points partially explain the high susceptibility of island ecosystems to disturbances, and the observed high rate of extinction of species. Most of contemporary worldwide extinction events have indeed occurred or are currently occurring in insular ecosystems. For example, more than 90% of the 30 species of reptiles and amphibians reported as extinct since the 17th century were island forms (Honnegger, 1981). Similarly, 93% of 176 species or subspecies of bird extinctions that have occurred during this period, as well as 81% of the 65 mammal species, also occurred on islands (King, 1985; Ceballos & Brown, 1995). These include only the species that are known to have disappeared: the vertebrate fauna of mainland ecosystems is in many cases better known than for insular ecosystems predating human arrival, hence the extinction rates could be much higher. Similarly, it is likely that the smaller number of reptile and amphibian extinctions reported above only reflects the smaller number of studies on these taxa. Few data are available concerning extinct insular species of plants and of invertebrates, but the figure is undoubtedly proportional. The actual number of species extinctions is thus likely to be far greater than the currently accepted figures.

The successful introduction of alien species is the major cause of ecosystem perturbation and biodiversity losses on islands (Atkinson, 1985; Moors & Atkinson, 1984; Lever, 1994; Williamson, 1996). For example, predation by introduced animals has been a major cause of 42% of island bird extinctions in the past, and is a major factor endangering 40% of currently threatened island bird species (King, 1985). There is thus an urgent need to understand and counteract the processes by which biological invasions threaten biodiversity on insular ecosystems. For research on threatened species, resources and time are limited and are usually focused on a single species; there will never be sufficient time and resources to manage each taxon individually (Fitzgerald & Gibb, 2001; Saunders & Norton, 2001). Emerging from this is the concept of biodiversity hotspots: areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat (e.g. Reid, 1998; N. Myers *et al.*, 2000). Islands or island groups such as New Caledonia, New Zealand, the Caribbean, Polynesia/Micronesia, Madagascar and the Philippines have been defined as biodiversity hotspots (N. Myers *et al.*, 2000). No less than nine of the 25 hotspots defined by N. Myers *et al.* (2000) are entirely or mainly made up of islands, and almost all tropical islands fall into one or another hotspot (N. Myers *et al.*, 2000). Conservation of these insular ecosystems is not only among the most urgent, it might also be among the most feasible: in most cases, the biodiversity crisis taking place on islands is singularly the result of biological invasions, which is easier to fight in a closed and often remote area as compared to the same surface area on a continent.

(3) Nature and purpose of this review

Introduced mammals have reportedly caused more problems than any other vertebrate group (Ebenhard, 1988; Lever, 1994). Mammals also are responsible for the best documented and most spectacular of ecological disturbances resulting from biological invasions (Holdgate, 1967). This is certainly due in part to the general lack of naturally occurring terrestrial mammals on most remote islands (Atkinson, 2001). By themselves, introduced mammal species constitute a large subject, and thus we will focus only on them in this review, although we recognise that other taxa, including plants and insects, are also notoriously devastating invaders (e.g. Pimentel *et al.*, 2001).

In this paper, we will attempt to review the effects that can follow the introduction of one or several mammal species onto an island. In addition, we will outline the most utilised methods of control of introduced mammal populations. We will then discuss the main possible impacts, both positive and negative, of mammal control. Because exhaustiveness is not possible on this subject, we will instead provide an overview of the main effects of mammal introductions, of the main methods of their control and of the main consequences of such control, illustrating most cases with typical examples. By the nature of studies on biological invasions (often triggered by conservation problems following invasion events), and by our choice of giving striking examples of the effects of such invasions, this review may be biased towards reporting negative effects of introduced species.

Following the Invasive Species Specialist Group's (ISSG) definition of terms (I.U.C.N., 2001), alien, foreign, exogenous and exotic species will be used synonymously to qualify species occurring outside of their natural range of potential dispersal, by opposition to native, indigenous or autochthonous species. Alien invasive species will be used for an alien species that becomes established and is an agent of change in the invaded ecosystem, threatening the native biological diversity. Introduced species refers to a movement (unintentional or intentional) by human agency of a species outside its historically known natural range.

II. ECOLOGICAL CONSEQUENCES OF INTRODUCTIONS

(1) Impact assessment

The impact of alien species can be considered at five different levels: effects on individuals, on genetics, on population dynamics, on community composition and functioning and on ecosystem processes (Parker *et al.*, 1999). On islands, the successful establishment of introduced species can lead to dramatic changes at all five levels. As we will detail below, the presence of introduced species often causes significant changes of the abundance and/or spatial structure of the autochthonous species it interacts directly or indirectly with, and thereby can affect significantly the global functioning of the ecosystems concerned (Williamson, 1996, 1999).

It is generally very difficult to assess the impact of an introduced species on the ecosystem it has invaded (Parker *et al.*, 1999). In most cases, data are not available to compare communities before and after the invasion. The recovery of native flora and fauna following exotic mammal eradication is generally a good illustration of their real impact on invaded ecosystems (Newman, 1994; Taylor, Kaiser & Drever, 2000; Towns, Daugherty & Cree, 2001). An alternative approach is possible in the case of archipelagos, where several combinations of introduced species can occur on nearby islands. Such islands are similar in most biotic and abiotic aspects, which allows the estimation of single species effects (e.g. comparing islands with and without introduced goats, *Capra hircus*) or of combinations of introduced species (e.g. islands with rats and cats *versus* islands with cats only, islands with rats only and islands with no introduced species). Unfortunately, studies on the effects of alien control programmes based on comparison between areas with or without alien removal (or comparisons before/after removal) cannot always be considered as unconditional evidence. Indeed, the communities may not restore themselves to their former states, due to the deep modifications caused by the alien prior to its removal, to the presence of other aliens, or to other factors. Even evidence based on diet of invaders and correlated with shifts of abundance of native species can be rightly criticised, since a causative process is next to impossible to demonstrate in this context. In the absence of such evidence, there has even been doubt concerning the actual impact of species considered by most conservationists as the most notoriously harmful invading species (Norman, 1975). As stated by Ebenhard, 'The decision whether an introduction has had an ecological effect is often hard to make on the basis of published information only, and hence is open to criticism by people with first-hand experience of some particular situation' (Ebenhard, 1988). There is however a very long list of circumstantial evidence of the effects of introduced species, which, taken together, is a body of 'circumstantial proof' (Peabody, 1961) that can overpower even the slightest doubt about the dramatic impact of biological invasions on oceanic islands.

According to Ebenhard (1988), introduced animal species may affect native species in one or more of six different ways. They may: (*i*) affect plant populations and species living in the habitat structured by these plants; (*ii*) be predators of native prey; (*iii*) induce interference or resource exploitation competition; (*iv*) spread micro- and macroparasites into native populations; (*v*) induce genetic changes to native species through hybridisation; (*vi*) act as prey to native predators. The last two categories are probably relatively unimportant as far as islands are concerned. Effects through competition or release of pathogens are probably much more important, but there are few examples in the literature, as it is extremely difficult to demonstrate unambiguously such effects. The examples given in this review will be mostly restricted to the results of exploitation of native species by introduced species, as well as resulting indirect effects (habitat destruction and competition with other species).

(2) Reasons for high impact

Not only are most alien invasive species highly adaptable (e.g. Apps, 1986; van Aarde, 1986; Ebenhard, 1988, Flux, 1993), but they also encounter favourable conditions in the new environment, compared to their native environment. In fact, alien invasions can be facilitated by three factors: more (or better) resources, less (or less efficient) natural enemies, and advantageous physical environment (Shea & Chesson, 2002). Because of their long evolution in isolation from other species, insular species have not evolved traits to provide an adapted response to efficient interference and exploitation (van Aarde & Skinner, 1981; Moors & Atkinson, 1984; Atkinson, 1985, 2001; Burger & Gochfeld, 1994). For example, defensive traits against intense herbivory such as high fecundity, compensated growth, production of toxins or unpalatable substances, or physical deterrents such as spines, are generally absent in plants on oceanic islands (Atkinson, 1989). Rather, plant communities of oceanic islands are mainly composed of species that are highly palatable and vulnerable (Holdgate, 1967). Similarly, small vertebrates may not have learned to hide their sounds, odours, or their shelters from predators, and once discovered, they may not flee or defend their young. Flightless birds are a good example of this: dodos in Mauritius, moas and kiwis in New Zealand, kagus in New Caledonia. In addition to being behaviourally maladapted, these prey species lack the life-history traits associated with many continental species, such as an earlier age of first reproduction and high fecundity [some examples are given for New Zealand shorebirds in Dowding & Murphy (2001)]. These species constitute a major (sometimes unique) and easy trophic resource for the few founders of introduced predators. Introduced cats, rats and dogs *Canis familiaris*, have all participated in the extermination of the flightless birds of Tristan da Cunha, Amsterdam, Ascension and Saint Paul islands, among others (Lever, 1994). The main islands mentioned in the text are indicated on the map shown in Fig. 1.

In addition to a potentially great abundance of resources on islands, the lack of natural enemies also favours the successful establishment of introduced species. Introduced species generally suffer from a smaller subset of parasites that are often less virulent than on the mainland (Dobson, 1988), for two key reasons. First, the limited number of hosts involved in introduction processes results in fewer pathogenic parasites being transmitted to the new environment. Second, many introduced parasitic species may be lost because either the new environment is unsuitable, key species are lacking that prevent the completion of their life cycle, or because the density of the introduced population is initially too low to allow the maintenance of the parasite population (Keeling & Grenfell, 1997). Where potential insular predators exist, they are often relatively inefficient in preying upon introduced species. After more than a century, the skua *Catharacta skua* still does not prey very efficiently on rabbits *Oryctolagus cuniculus*, introduced to the Kerguelen islands, preying mostly on young and sick individuals (Moncorps *et al.*, 1998).

With an abundance of resources and a lack of pressure from natural enemies, invasive animals often build up numbers in an abnormally short period after introduction. Initially confronted with a closed (and often small) geographic area, and freed from the normal biotic pressures found on the mainland, introduced species often increase in population size beyond the limit of sustainability of the new environment (in terms of food resources as well as shelters). As a result, when these resources are depleted a population crash may follow a marked peak (Nugent, Fraser & Sweetapple, 2001). For example, the 29 reindeer *Rangifer tarandus*, introduced onto St Matthew Island initially responded so well to the high quality and quantity of forage that they increased in less than 20 years up to 6000 individuals. The huge impact of such a large population on a restricted environment led to a severe impoverishment of the flora, resulting in a dramatic population crash, down to 50 individuals (Klein, 1968). Such a reduction of the population can lead to an increase of the vegetation, which then may allow another build up of the herbivore population, sometimes leading to another crash. In 1957, a pair of mouflons (*Ovis musimon*) was introduced on a small island (650 ha) of the Kerguelen Archipelago. From those two individuals, a population developed that numbered around 700 individuals 20 years later. Between 1977 and 1995, at least five population crashes occurred, mainly because of insufficient food availability at high density. Each crash, concerning 400–450 individuals, was followed by a recovery of the flora, despite an increasing degradation of the environment by erosion, which in turn led to a rebuilding of the population. This cycle of events was broken in 1995,

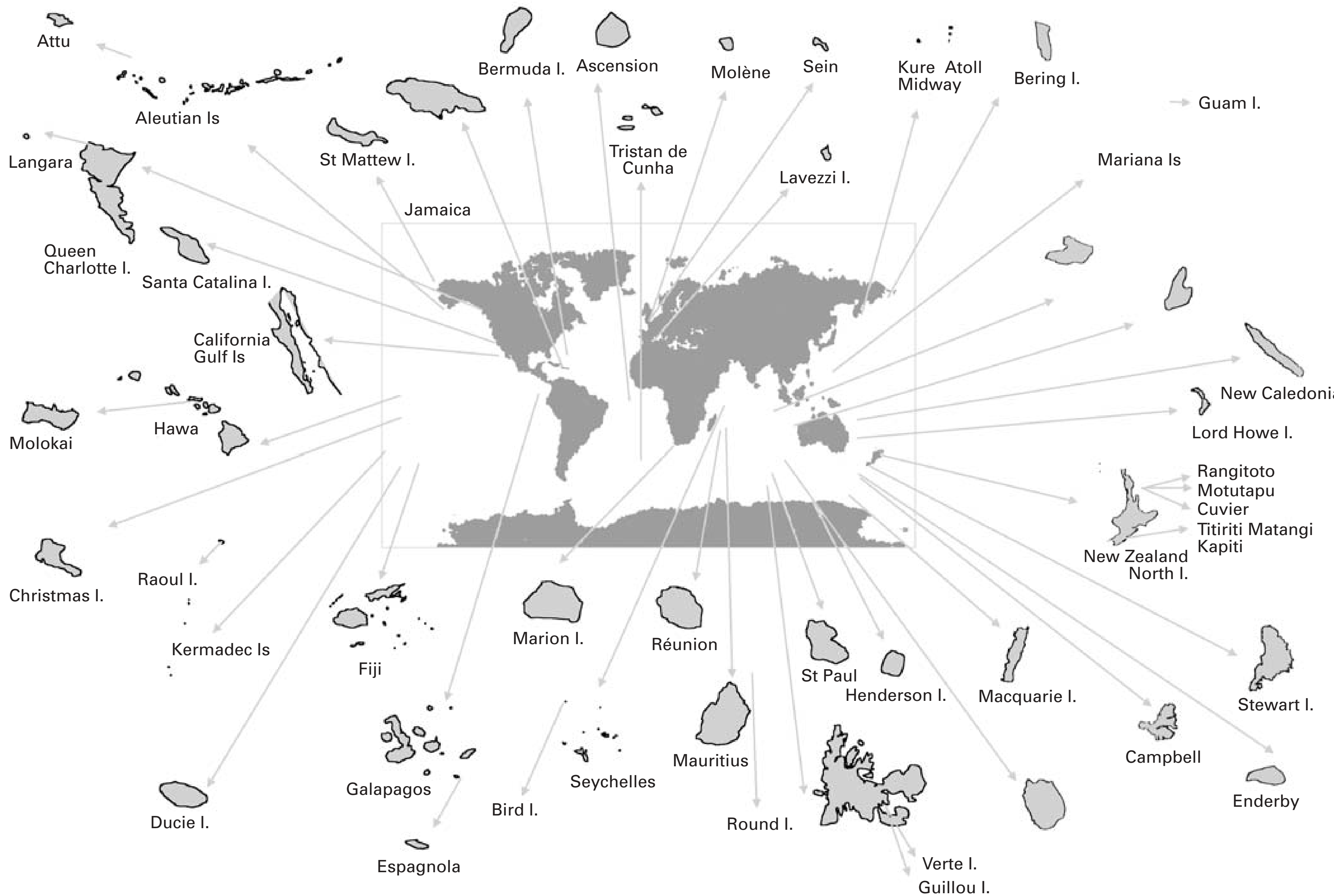

Fig. 1. World location of main islands mentioned in the text.

the date of the last population crash, since when the population has been kept small by a yearly shooting campaign (Boussès, Réale & Chapuis, 1994; Chapuis, Boussès & Barnaud, 1994*a*; Réale, Boussès & Chapuis, 1996).

Alternatively, the damage to the environment may be such that the habitat or the resources themselves can be totally destroyed, also resulting in the extinction of the introduced species. In the long term, such a natural extinction of introduced species (more likely to occur on small islands with simple ecosystems) may be more general than currently witnessed. For example, it has been reported that for the 607 islands where the fate of introduced rabbits is known, the population died out naturally in more than 10% of cases (Flux, 1993). However, following disappearance or removal of exotics, recolonisation by local species is not always possible, owing to the very high endemism of oceanic islands and the lack of neighbouring populations that can act as recolonisation sources, or because the alien invasive species caused irreversible modifications of the environment.

(3) Simple ecological effects

(*a*) *Simple effects due to single species introductions*

Ecological effects of introduced species may be better appreciated if one can disentangle the different effects of different species from the effects of species combinations. Because trophic webs on oceanic islands are often very simplified, with little ecological or taxonomical redundancy (Holdgate, 1967), dramatic increases of introduced species may lead to important imbalances in the whole ecosystem. The decline of endemic species that are victims of interference or exploitation from introduced species is often the first consequence, and may then lead to further damage at the ecosystem level. Three types of ecological effects can be distinguished: (*i*) shift of relative species abundances, without affecting the total number of species; (*ii*) disappearance of some species from parts of the habitat; (*iii*) extinction of some species. Some ecological effects, habitat changes or shifts of native abundance of plant or animal species caused by predation or competition have been reported in at least 40% of all mammal introductions (Ebenhard, 1988). These dramatic results are better appreciated when compared to the effects of bird introductions, which have resulted in observed ecological effects in only 5% of all cases (Ebenhard, 1988). The figure for mammals is much higher if only introductions onto oceanic islands are considered.

Ebenhard (1988) also calculated that 93 out of 95 introductions of strict herbivore species caused habitat change on oceanic islands, and the number of plant species affected by introduced herbivores is probably innumerable. Because there is little published information on the indirect effects of plant community changes on invertebrates, it is difficult to assess the direct and indirect effects of mammal introduction on local invertebrates. It is likely that they are considerable.

A single introduced species can also affect, directly and indirectly, a whole range of indigenous species, thereby affecting the whole invaded ecosystem. Nine Indian mongooses (*Herpestes auropunctatus*), introduced to Jamaica from Calcutta in 1872, seem to have been the source of all the populations on 29 Caribbean and four Hawaiian islands before the end of the 19th century (Lever, 1994). These mongooses eradicated many invertebrates, reptiles, amphibians, birds and mammals, mostly in the West Indies (Westermann, 1953; Nellis & Everard, 1983; Lever, 1994). Another good example of this is given by domestic goats, generally seen as one of the most destructive feral mammals to native vegetation (Turbott, 1948; Parkes, 1990; Keegan, Coblentz & Winchell, 1994). Introduced goats have a very large spectrum diet: they consumed at least 48 species of vascular plants on Raoul Island, mostly indigenous species, and several of them rare and endangered (Parkes, 1984). Within 35 years of overgrazing, over-browsing and trampling, introduced goats reduced the number of plant species from 143 to only 70 on Great Island, New Zealand (Turbott, 1948). Through direct competition, or by severely reducing the vegetation cover, goats introduced in the Galapagos archipelago also indirectly threatened several species of birds and reptiles (including the local race of the giant tortoise; Hamman, 1975). On Santa Catalina Island, they also almost wiped out the native sagebrush *Artemisia californica*, and the resulting reduced coverage seriously threatened the California quaii *Lophortyx californica*, as well as several native rodents; consequently, several species of reptilian and mammalian predators have decreased as well (Coblentz, 1978).

(*b*) *Effects of resource exploitation*

The main impact type is the result of exploitation of the invaded ecosystem resources by browsers, grazers and predators. In this section, we review the effects of consumption of native species by herbivores, omnivores and carnivores, focussing on three emblematic species. Other examples could easily have been used, as many other mammals have notoriously devastated populations and communities. Most of man's commensal species, and many domestic animals have been introduced onto islands. Some have been introduced inadvertently; for example, they went ashore from ships by themselves or they came from newly established human colonies (e.g. rats, mice *Mus musculus*, cats, dogs). Nevertheless, in contrast to plants and invertebrates, the majority of mammals were deliberately introduced, sometimes repeatedly and tenaciously. These were generally introduced either to control the spread of previously introduced rodents (e.g. cats, mongooses), for fur or stock farming or hunting (e.g. cattle *Bos taurus*, goats, pigs *Sus domestica*, wild boar *S. scrofa*, horses *Equus caballus*, donkeys *E. asinus*, foxes *Alopex lagopus* and *Vulpes vulpes*, possums, reindeer, mouflon, deer), or to provide a durable source of food for shipwrecked mariners (e.g. rabbits, goats, sheep *Ovis aries*, and the brown and Arctic hares *Lepus europaeus* and *L. arcticus*). A large part of research on biological invasion is focussed on characterising the biological attributes of successful invading species (Crawley, 1986; Williamson, 1996; Mack *et al.*, 2000; Kolar & Lodge, 2001; Sakai *et al.*, 2001). Some species are particularly more successful in this regard, both because they have been more often introduced and because such introductions have been more often followed by establishment. Among these, some are well known to conservation biologists because their establishment is almost invariably followed by rapid and important changes in the original communities. The most important introduced mammals, both in terms of numbers of introductions and resultant damages, are the rabbit, the cat, three commensal species of rats, the house mouse, the goat, the pig and cattle. Apart from cattle, all are in the ISSG list of 100 of the worst alien invasive species (http://www.issg.org/database/welcome/). Many of these invasive species have had a major impact, as illustrated by the number of species allegedly extirpated by their introduction. For example, (Jackson, 1977 cited in Ebenhard, 1988) estimated that 61 bird taxa have been exterminated by introduced predators, with cats (33 extinctions), rats (14 extinctions) and mongooses (nine extinctions) being the most important predators.

Specialists on several of these species share similar strong terms to describe the impact of these mammals when introduced into naive ecosystems:

'The domestic goat undoubtedly has been the most destructive feral mammal to native vegetation, particularly as it travels over all types of terrain and consumes all kinds of browse and herbaceous material' (deVos, Manville & Van Gelder, 1956).

'With the exception of man, the rat is the mammal that has undoubtedly had the greatest impact on the environment and economy of most Pacific islands …' (Storer, 1962).

'Of all the introduced pests, the rabbit is by far the worst. Its acclimatization in Australia was the greatest single tragedy that the economy and the native animals have ever suffered' (Frith, 1979).

'Cats are now ubiquitous on inhabited islands, and frequently present on those uninhabited. Probably no other alien predator has had such an universally damaging effect on seabirds' (Moors & Atkinson, 1984).

'The avifauna of some islands have suffered drastically from predation by rats. (…) On a few islands, the proportion of bird species that have declined or become extinct following the introduction of *R. rattus* is so great than the term catastrophe is appropriate' (Atkinson, 1985).

'Rats … have been implicated in the greatest number of extinctions due to predators (54 percent … Of the three species which have shared the blame for this record of predation, the Black Rat or Roof Rat (*Rattus rattus*) has been the most serious problem …' (King, 1985).

'Introduced predators have accounted for about half of island bird extinctions. Rats and cats are the most notorious killers and island birds the most notorious victims, in this regard' (Diamond, 1989*a*).

'… there can be little doubt that the mongoose in the West Indies … has helped to endanger or exterminate more species of mammals, birds and reptiles within a limited area than any other animal deliberately introduced by man anywhere in the world' (Lever, 1994).

This list of infamy could go on. Instead, we now provide a short view of the effects of the introduction of three of these species, in order to illustrate the effects of an herbivore, an omnivore and a predator.

(*i*) *Effects of herbivores: the rabbit as an example*

Because their impact is focused at the base of trophic webs, introduced herbivores can have a wide-ranging impact on invaded ecosystems. One of the most documented introduced mammal species, often referred to for its dramatic impact on endemic plant species, is the rabbit. This herbivore has been introduced (most of the time voluntarily) to more than 800 islands so far (Flux & Fullagar, 1992). Rabbits have a high ecological adaptability and introductions easily succeed (Flux, 1993). They can adapt to harsh conditions, eat a wide range of plant species (Thompson, 1953; Chapuis, 1981, 1990; Homolka, 1988), and have an exceptional growth rate for their body mass (Smith & Quin, 1996). The very rapid increase of their populations in ecosystems where indigenous grazers are in general much less numerous and competitive, leads to a dramatic impoverishment of the vegetation, both quantitatively and qualitatively

(Gillham, 1955; Costin & Moore, 1960; Holdgate & Wace, 1961; Norman, 1967; Selkirk *et al.*, 1983; Chapuis *et al.*, 1994*a*), and results in severe impacts on associated indigenous fauna.

Overgrazing by rabbits constitutes a reduction of the plant cover for terrestrial nesting birds, which often affects their reproductive success, as was seen on Meeuw Island (Gillham, 1963) or on the Kerguelen archipelago (Weimerskirch, Zotier & Jouventin, 1989). It also increases direct competition for food among birds depending directly (e.g. granivorous) or indirectly (e.g. insectivorous) on the terrestrial vegetation (Gillham, 1963). Overgrazing may lead to the exposure of larger proportions of soil surface to frost heaving, rain and wind erosion (Scott, 1988), resulting in dramatic denudation of the soil. Rabbits also compete directly for nesting burrows (or places to dig them) with many burrowing seabird species (e.g. Young, 1981). Furthermore, this burrowing can accelerate erosion (Norman, 1967; Chapuis, 1995). It is also believed that as much as 10% of Hooker's sea lion pups die annually by being trapped and suffocated in rabbit burrows on Enderby and Rose Islands (Sanson & Dingwall, 1995). Rabbit overgrazing also prevents any large-scale regeneration following natural catastrophes such as fire (Norman, 1967) or cyclones (Kirk & Racey, 1992). Rabbits may also have significant direct effects on other species, such as disturbance (Gillham, 1963), which could lead to colony desertion by seabirds. Lastly, and as we will see later on, rabbits often constitute an alternative prey for indigenous (e.g. skuas) or introduced predators (e.g. cats). By increasing the number of predators, or by allowing them to persist when and where local prey is scarce, they contribute to the decline of indigenous prey (Brothers & Copson, 1988). By one or several of these factors, rabbits are believed to have been ultimately responsible for the decline or extinction of several reptile and bird species (King, 1985; North, Bullock & Dulloo, 1994; Smith & Quin, 1996). One classic example concerns the extreme damage caused to Round Island, in Mauritius. Helped also by feral goats, introduced rabbits reduced the community of several endemic palm trees, which normally protected the island from hurricane damage, to 5–15 individuals depending on the species, with several having completely disappeared (Bullock, 1977). Of course, not only the plant species were directly affected, but also the animals depending on them disappeared as well, such as four species of endemic reptiles. As a result, this 151 ha island possessed the highest density of threatened plant and animal species in the world, before conservation efforts concentrated on eradicating both goats and rabbits (North & Bullock, 1986; North *et al.*, 1994).

Another example concerns Laysan Island in the Hawaiian chain, where rabbits alone were responsible for eliminating 26 species of plants between 1903 and 1923, a rate of loss exceeding one species per year (Christophersen & Caum, 1931 cited, in Atkinson, 1989). On that island, they have also led to the elimination of three bird species. A fourth, the Laysan duck, increased from seven individuals by one hundred-fold after the rabbit's removal (Warner, 1963). Rabbits are also believed to have been responsible for the decline or extinction of several other vertebrate species by the impact they have had on their habitat.

(*ii*) *Effects of omnivores: rats as an example*

The other main category of mammal pest invaders concerns omnivorous species. These have often been more present in the minds of conservation biologists because of their more direct and visible effect on indigenous wildlife. Three species of rats have become unequalled worldwide threats for small insular prey: the Kiore, Polynesian or Pacific rat *Rattus exulans*, the Black, Roof or Ship rat *R. rattus* and the Brown or Norwegian rat *R. norvegicus*. These three commensals are known to have colonised at least 82% of the 123 major island groups (Atkinson, 1985). Because they show important ecological differences, the three species have had a dissimilar impact, both quantitatively and qualitatively on insular wildlife (Atkinson, 1985; Lever, 1994).

The ecological impact of the Pacific rat is difficult to assess, but is it said to be the least harmful of all three species on vertebrates (although more destructive on insect and plant communities). Nevertheless, in addition to its impact on the native plant communities, this partly arboreal and partly terrestrial rodent (Atkinson, 1977) is believed to be responsible for the extinction of many invertebrate, amphibian, reptile and bird species (Atkinson, 1978; Crook, 1973). For example, on Kure Atoll, these rats are suspected of killing the translocated Laysan albatrosses (*Diomeda immutabilis*, Fig. 2), as well as sooty terns (*Sterna fuscata*), Noddy terns *Anous stolidus* and Bonin petrels *Pterodroma hypoleuca* (Kepler, 1967). Similarly, the impact of this rat on Murphy's petrel seems so great (100% of chicks killed within four days of hatching) on Henderson Islands, that the colony is believed to be subsisting only through immigration from the species' largest breeding site world-wide, located on two nearby islands, Oeno and Ducie (Lever, 1994).

The two other rat species have a much larger impact on the fauna of the islands they have invaded. The Norwegian rat has largely terrestrial habits, putting birds with similar habits at the highest risk, in particular seabirds: eggs, chicks or even brooding adults are regularly killed, often resulting in local extinction. Because it

Fig. 2. Introduced Polynesian rat attacking a Laysan Albatross behaviourally non-adapted to terrestrial predation. Photograph courtesy of Cameron Kepler.

is arboreal and therefore affects forest birds as well, the Black rat probably has had the largest impact of all three species (Lever, 1994). A well-known example of the important impact of black rats on native vertebrate communities is their establishment around 1964 on Big South Cape Island, New Zealand. There, they caused the local loss of three endemic birds, and the complete extinction of two other bird species and of one species of bat, in less than two years (Bell, 1978). The populations of many other native species were depleted, although not to complete extirpation. Another example illustrating the dramatic impact of introduced mammals on biodiversity concerns the emblematic tuatara *Sphenodon punctatus*, last of the Sphenodontida, an order of reptile present 225–80 million years ago in different parts of the world. This endangered species is endemic to New Zealand, but has been extirpated from the mainland and now occurs only on a few small islands. They are, however, not safe in those few restricted areas: the invasion of Whenuakura Island by Norway rats in 1982 led to the elimination of the entire local population of more than 130 tuatara (Newman, 1988). Rats have had an impact on most remaining tuatara populations as well as on other rare reptile species (Newman, 1988; Newman & McFadden, 1990; Cree, Daugherty & Hay, 1995; Towns *et al.*, 2001).

The impact of rats on the vegetation of the islands they have invaded is also extremely important. Rats eat leaves, seeds and fruits, flowers, bark and stems of many endangered species. By hindering regeneration and killing sapling and small adult trees, they modify entire plant communities, and thereby affect the associated fauna (Clark, 1981). By interference and/or exploitation, black rats that now occur on all vegetated habitat of the seven main islands of the Galapagos are said to be responsible for the extinction of four species of endemic rice rats *Oryzomys* sp. (Brosset, 1963). Black rats have an effect on the regeneration of maritime forest (Campbell, 1978) because they are major consumers of inland podocarp seeds, and also because they compete with and kill many species of birds that disperse seeds (Clark, 1981). Inversely, although examples are rare, introduced rodents may favour seed dispersion: black and Pacific rats are better seed dispersers than the native bats on Tonga (Drake & McConkey, 2001).

The Pacific rat has been documented killing at least 15 different bird species, predation by the black rat has been described in at least 39 bird species, while the brown rat has been recorded killing at least 53 bird species (Atkinson, 1985). Evidence of predation on small vertebrates by rats on remote islands is more difficult to obtain, therefore these numbers surely are an underestimation of the actual number of bird species killed by each rat species. Arthropods, snails, amphibians and reptiles are less studied than birds, and few data are available concerning the number of species under threat by introduced rats, but here again, there is little doubt that the number is very large (e.g. Clark, 1981; McKenzie, 1993).

As mentioned above, the impact of an introduced species on a remote oceanic island is very difficult to prove and even more difficult to quantify. Norman (1975) even suggests that the impact of introduced rats may have been overstated in some cases. That author argues that evidence of bird population decreases is often circumstantial, and that few data are available to conclude that rats are solely responsible for some bird extinction events. Norman (1975) suggests that the majority of the impact of introduced predators has been imputed to rats while the impact of cats on the same island may have been much higher. Although most specialists concur on the nearly invariable significant impact of introduced rats, it is true that untangling the effects of several introduced predators, such as rats and cats, is difficult at best. Cats are indeed a major problem on oceanic islands and are often present on islands where rats have been introduced.

(*iii*) *Effects of predators: the cat as an example*

Because they were the main means of controlling rodents on ships, domestic cats travelled around the world with explorers, sealers, whalers and other seafarers, and thus gained easy access to most remote oceanic islands (Todd, 1977). On those islands, in addition to all the cats that escaped ashore during a stopover, and those that stayed with colonies or lighthouse keepers, many cats were in fact introduced (as were mongooses) in an attempt to control growing populations of rodents near newly established human populations. Domestic cats are very adaptable (Konecny, 1983; Apps, 1986; van Aarde, 1986) and have survived in the most inhospitable conditions on many remote oceanic islands, both inhabited and uninhabited (Fitzgerald, 1988). They are found on most major island groups, from subantarctic islands to arid islands with no fresh water (Derenne, 1976; Pascal, 1980; Tabor, 1983; Atkinson, 1989).

Despite sometimes-harsh climatic conditions, these ecosystems were very favourable for domestic cats, being virtually exempt of natural enemies and often full of defenceless prey (as well as introduced prey such as rodents and rabbits, which may allow cats to survive the season when migratory birds are absent). The cat is an opportunistic predator, and its diet on oceanic islands may include a large proportion of reptiles (e.g. Konecny, 1987; Bamford, 1995), birds (e.g. Fitzgerald, 1988; Rodriguez-Estrella *et al.*, 1996), or mammals (Derenne & Mougin, 1976; Jones, 1977; Pascal, 1980), according to the prey's relative abundance in different seasons and regions.

As a consequence of the wide diet of this very efficient predator and the lack of adaptation of the local prey, introduced cats are known to be the direct cause of severe reductions or extinctions of numerous populations of insular vertebrate species (Iverson, 1978; Taylor, 1979*b*; Moors & Atkinson, 1984; King, 1985). As is the case for rats, to enumerate the exhaustive list of (suspected) victims of domestic cats would be too long and depressing. As Lever (1994) points out in the case of impacts of cats on birds, 'the list of species they have helped to exterminate or endanger reads like a roll-call of avian disaster'. Here we provide a few famous examples to help to illustrate the huge impact that a few individual cats introduced onto an island can have on the local fauna some decades later.

Cats have often been introduced in small numbers, but their ease in proliferation in such favourable conditions makes then a fearsome threat for local animal communities. For example, within 70 years of their introduction to the Fijian islands, cats increased so much in numbers on Viti Levu that they were hunted for food and sport (Gibbons, 1984). It has been estimated that 25 years after the introduction of five cats on Macquarie Island, the established population of 2000 cats killed nearly half a million burrowing petrels per year (van Aarde, 1980). Similarly, in the Kerguelen Archipelago, 30 years after the introduction of a cat and her three kittens, the population of 3500 cats destroyed 1.2 million birds per year (Pascal, 1980). Some predators kill more than their immediate need: foxes store surplus birds and eggs for use in winter when few birds are present, and single larders have been found with more than 100 seabirds of several species (Bailey, 1993). This may obviously unbalance the predator–prey dynamics if the prey population is not adapted to such behaviour. On small islands, the impact of such a population may result in the extinction of the prey species, especially if alternative prey are present to sustain the predator population (see Fig. 3).

In a few decades, cats introduced onto Herekopare islands destroyed all but a few thousand of the 400 000 birds living there, extirpating no less than six entire species of land birds, and large colonies of seabirds (Fitzgerald & Veitch, 1985). In addition to many local extinctions, introduced domestic cats are said to have caused more than half of the avian species extinctions due to introduced predators (Jackson, 1977 cited in Ebenhard, 1988). Here again, it is not unreasonable to suggest that since birds are far more studied than other animal taxa on oceanic islands, the lack of published data on the extinction by cats of indigenous invertebrates, amphibians and reptiles probably does not accurately reflect the actual widespread occurrence of such events.

(*iv*) *Other mammals*

Many other species have caused significant conservation problems all over the world, especially goats (Turbott, 1948; Parkes, 1984, 1990, 1993; Rudge, 1984), pigs (Hone, 1990, 1992, 1995; Sterner & Barrett, 1991), small Indian mongooses (Seaman, 1952), mice (Rowe-Rowe, Green & Crafford, 1989; Crafford, 1990; Newman, 1994; Le Roux *et al.*, 2002), foxes (arctic *Alopex lagopus* and red *Vulpes vulpes*, West & Rudd, 1983; Bailey, 1992, 1993) and domestic dogs (Iverson, 1978). For example, feral dogs in the vicinity of humans are reputed to hunt principally for 'sport', and can exceed other alien predators in exterminating species. A prime illustration of this is the individual dog that is said to have systematically hunted and killed more than half of the remaining 900 New Zealand brown kiwis, *Apteryx australis*, in less than three weeks (Taborsky, 1988; Diamond, 1989*b*).

Some mammals can have an important impact on multiple levels such as in the case of the brushtail possum *Trichosurus vulpecula* in New Zealand (Clout, 1999). The primary conservation impact of this invading marsupial is through the damage they cause to native forest through browsing. Possums also feed on flowers and fruits, reducing fruit crops of native plants and hence both forest regeneration and the food supplies of several native birds, which in turn may fail to reproduce

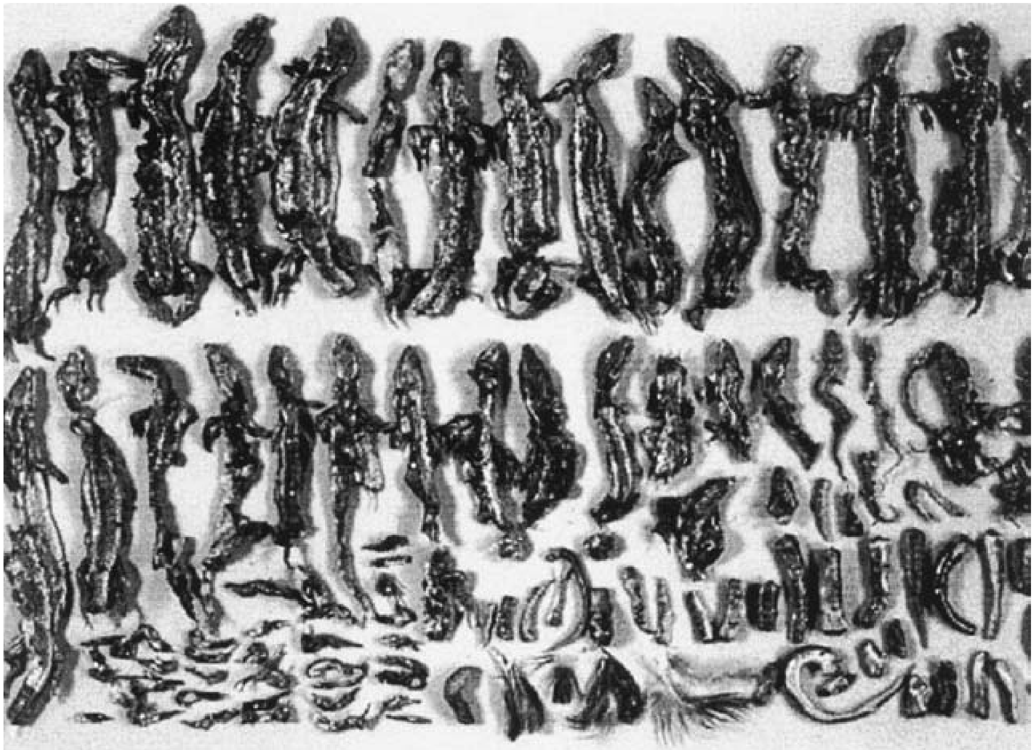

Fig. 3. Stomach content of a single feral cat caught in New Zealand, with at least 34 native skinks *Leiolopisma* spp. Photograph courtesy of John Dowding.

and even survive. They also compete for hollows with endemic hole-nesting species, such as kiwi (*Apteryx* spp.). Although mostly herbivorous, possums have recently been shown preying on the eggs and chicks of birds, including those of threatened species (Brown *et al*., 1998). Finally, they also have an economic impact, as they transmit the bovine tuberculosis virus to cattle and deer (Clout & Sarre, 1997). Because of their multiple ecological and economic effects as an invasive species, the introduction of possums to New Zealand is now recognized as 'an unmitigated disaster for the natural ecosystems and native biota of this archipelago' (Clout, 1999).

In addition to the above, several authors list mammal species reported to have been introduced onto islands (deVos *et al*., 1956; Holdgate, 1967; Ebenhard, 1988; Lever, 1994). There have been at least 80 mammal species introduced since 1700 (Atkinson, 1989), but some of them cause more damage than others. The other introduced mammals include mustelids (stoat *Mustela erminea*, weasel *M. nivalis*, ferret *M. furro*, North American mink *M. vison*, polecat *M. putorius*, Japanese weasel *M. sibirica itatsi*), wallabies (dama *Macropus eugenii*, parma *M. parma*, and brush-tailed rock *Petrogale penicillata*) and deer (axis *Cervus axis*, fallow *C. dama*, red *C. elaphus*, rusa *C. timorensis*, while-tailed *Odocoileus virginianus* and reindeer). Some species are introduced less often but may nonetheless be important, for example the Virginia opossum *Didelphis marsupialis*, the house shrew *Crocidura russula*, the musk shrew *Suncus murinus*, the crab-eating macaque *Macaca fascicularis*, the green monkey *Cercopithecus aethiops* and the water buffalo *Bubalus arno*.

(*c*) *Effects of competition and parasitism*

Apart from the classically studied direct effects of herbivores and predators, which we have detailed above, introductions may be deleterious for native populations through two other processes, both understudied but potentially very important: competition and spread of parasites.

Although competition is rather rare, when it occurs it often affects the abundance of the native species (Ebenhard, 1988). Competition can be of two types. It can be called interference competition, as is the case with grey-bellied squirrels (*Callosciurus caniceps*) introduced on the island of Oshima, which chase local birds away from the flowers they feed on and pollinate (Lever, 1994). It can also be a resource exploitation competition, a process both more likely to occur and more difficult to demonstrate. Examples of such interactions include the competition of rabbits and seabirds for nesting burrows

(Cooper & Brooke, 1982) or the competition of introduced ungulates (which often overgraze) for plants that constitute the basis of diet or shelter for native species (see Lever, 1994 for examples). These relationships can be complex, because some birds may benefit from rabbit burrowing, or from the vegetation opening. Direct competition for food with introduced goats is considered one of the direct reasons for the decline or even extinction of several populations of birds and reptiles, among which is the Galapagos giant tortoise *Geochelone elephantus* (Daly & Goriup, 1987). Obviously, strict herbivores are more likely to get involved in competitive relationships with native species than are omnivores or predators, especially since terrestrial predators are scarce on oceanic islands. However, some examples concern the competition for food with native predators, notably in the Kerguelen islands between cats and skuas: where cats are present, there are not enough petrels for the skua to reproduce, despite the presence of alternative prey such as mice and rabbits (Chapuis *et al.*, 2001).

The spread of new parasites with invading animals is probably the least studied of the major effects of species introductions on native ecosystems and only a few examples exist concerning mammal pathogens. These include the introduction of unidentified pathogens by black rats on Christmas Island, that seems to have led to the extinction of the endemic bulldog rat (*Rattus nativitatis*; Day, 1981) and the introduction by the Northern red-backed vole (*Clethrionomys rutilus*) to Bering Islands of the cestod *Echinococcus multilocularis* which affected native foxes (deVos *et al.*, 1956).

(*d*) *Simple ecological effects due to multi-species introductions*

Unfortunately, there are many well-known examples of coincident introduction of several species, leading to more complex, and often detrimental, effects on the original trophic webs. For example, the construction of a tourist hotel on Caicos Islands led within three years to the near extirpation of the 5500 endemic West Indian rock iguanas *Cyclura carinata* that were hunted by introduced cats and dogs (Iverson, 1978). On Stewart Island, cats and three species of rats have exterminated five species of birds, three of which were endemic (Karl & Best, 1982). Similarly, in the Marianas Islands, Rota Island numbered no more than 121 adult trees of the endangered Micronesian *Serianthes nelsonii*, while the neighbour Guam had only one, these trees being mostly threatened by introduced red deer, pigs and granivorous insects (Wiles *et al.*, 1996).

In many cases, several invaders belonging to distinct trophic levels have been introduced into naive ecosystems, leading to some of the most complete cases of community disruptions. The effects of mammal introductions on Lord Howe Island, off Australia, are a good example of this. The endemic forest of *Howea forsterana* now contains very few small individuals, due to the combination of grazing by goats and seed consuming by rats (Pickard, 1982). In addition, in less than 20 years, rats eradicated at least five endemic bird species (which account for more than 40 % of all the indigenous species of land birds) and three endemic invertebrates on this island. They also extirpated all the seabird colonies and greatly reduced the numbers of lizards, land snails, and other invertebrates of the island (Recher & Clark, 1974; Atkinson, 1985). These two introduced mammals have had many other indirect effects, including changes to the structure of the habitat and removal of native species. One can easily imagine how profound changes can be following the introduction of even more mammal species, as is the case for many other islands. In addition to increased effects owing to increased numbers of actors, there are many cases of interactions between introduced species having a synergistic effect in the damage suffered by the local species. These are what we term complex interactions.

(4) Complex interactions

On most islands, several introduced mammal species interact to modify trophic webs greatly. Most islands that have been inhabited by humans, even for a short time, also shelter a great number of alien species, many of which are mammals. A great number of alien mammals were introduced, even on the most remote islands, as long as they were in a useful location for ships, or worse, had a permanent colony, often deliberately. For example, the Kerguelen Archipelago is one of the most remote island groups, in the subantarctic zone of the Indian Ocean, 4000 km off the coast of Africa and 3000 km away from Australia, Nevertheless, rats, mice, cats and dogs rapidly followed sealers and whalers. In addition, rabbits, pigs and sheep were introduced to constitute self-maintaining reserves of food, while American mink were introduced for their fur, reindeer to serve as draught animals, and Corsican mouflon for hunting purposes (Pascal, 1983). Apart from pigs, dogs and American mink, all these species are still currently present in the wild in these islands (Chapuis *et al.*, 1994 *a*). Islands that are inhabited or that have been heavily used for their resources may be even more heavily impacted. For example, the islands of Hawaii now shelter one of the most complete arrays of alien species, with many mammals, including the three species of commensal rats, mice, cats, mongooses, dogs, pigs, goats, cattle, sheep, rabbits, axis deer and even brush-tailed rock wallabies. The very complex interactions between indigenous and one or several introduced species make it very difficult to characterise the impact of introduced species on the indigenous flora and fauna.

The simplest example of interaction is when a previously introduced species facilitates the invasion of a second invasive species, usually by modifying the habitat. For example, some exotic birds need the forest to be modified by browsing herbivores and are unable to colonise undisturbed native forest in the absence of alien mammals. After the removal of introduced browsers (and predators) from Cuvier Island, the indigenous forest was able to regenerate, and the exotic bird species disappeared (Diamond & Veitch, 1981). A comparison of Pacific islands with and without introduced ungulates suggests that many island species of plant can 'resist' alien plant invasions in the absence of ungulates (Merlin & Juvik, 1992, cited in Cabin *et al.*, 2000).

There are also many cases of direct interactions between several established alien species. For example, if a predator is introduced into a trophic web where two prey species are competing for a resource, the complexity of its effects may increase if one of the prey is preferred over the other. An exacerbation of this is when both a prey species and its predator are introduced into a naive ecosystem. In this case, the introduced prey is well adapted to the predation and has an indirect competitive advantage over the native prey. Worse, the introduced prey's adaptation to predation may be such that they are less favoured (i.e. more difficult to catch), but at the same time this allows an increase of the predator population without suffering from it (because only the population surplus is killed), leading to hyperpredation (see below). In this context, it is interesting to compare the effect of introduced cats on seabird communities, with and without alternative prey.

Impacts of the presence of alternative prey are well illustrated by the example of rabbits, whose effects on endemic vertebrate species can be more complex than the ones presented above, especially when predators have also been introduced. In this case, rabbits are only a secondary prey item in months when seabirds are present, but appear to enable predators (mostly domestic cats) to subsist over winter, when seabirds are absent or rare (Pascal, 1980; Brothers, Skira & Copson, 1985; Chapuis *et al.*, 1994*a*). They also allow predator populations to reach remote colonies or populations of indigenous prey on islands with heterogeneous indigenous prey distribution (Brothers & Copson, 1988). In addition, they can exacerbate the predation pressure on indigenous species through what has been termed hyperpredation (Smith & Quin, 1996). This process is well illustrated by the example of Macquarie Island, where predation by introduced cats caused the decline of burrow-nesting petrels (Brothers, 1984) and the extinction of an endemic parakeet *Cyanoramphus novaezelandiae erythrotis* and a banded rail *Rallus philippensis* (Taylor, 1979*a*). Cats were introduced to this island 60 years before the introduction of rabbits. However, the dramatic impact of cat predation on bird populations dates back to just ten years following the introduction of rabbits (Taylor, 1979*a*). It is believed that the rabbit population allowed not only the maintenance of the cat population in winter (when seabirds are absent from the island), but also a significant increase, therefore resulting in increased predation pressure on the land bird species. The rabbit population, which was more adapted to predation by cats supported such an increase. It was, however, fatal to the bird population, which on its own could support a small cat population, but was extirpated by an over-sized cat population that no longer depended on the presence of birds to survive (Courchamp, Langlais & Sugihara, 1999*b*; Courchamp, Langlais & Sugihara, 2000). Since a great many islands harbour both populations of introduced predators and their natural prey, this hyperpredation process could be a widespread cause of further threat to small indigenous vertebrate populations.

A fascinating example of complex interactions through single species introduction comes from the California Gulf Islands. There, an endemic fox species, *Urocyon littoralis*, has dangerously declined more than 90% over the past decade. In parallel, its only competitor, an endemic skunk *Spilogale gracilis amphiala*, has been increasing. The reason for this decline was far from obvious. Careful studies showed that skunks were not responsible: they are largely dominated by foxes in a competitive relationship, and their increase was a consequence of the fox decline. Pathogens were not the cause either, and prey was plentiful and indeed increasing, following the relaxation of fox predation. The only remaining explanation was a top predator whose presence, or effect, was new to the ecosystem (since foxes were known to be the top predators on these islands, and their decline was recent). Researchers on these islands pointed out that the decline in foxes was linked to a coincident increase in golden eagle (*Aquila chrysaetos*) predation (Roemer, 1999; Roemer *et al.*, 2001). A combination of field data and mathematical modelling suggested a hyperpredation process, engendered by the introduced population of pigs (Roemer, Donlan & Courchamp, 2002). On these islands, golden eagles are not able to survive as a population on the local prey only, but piglets now constitute year round sources of abundant food, which allows eagles to breed. Pigs have thus facilitated the colonisation of the islands by eagles;

while the pig population does not suffer too much from predation (only the surplus of piglets is taken by eagles), they represented a threat to foxes. The endangerment of this endemic fox is directly linked to a significant increase of an endemic skunk, its natural competitor, and is caused by a predator whose survival is threatened in other places, thus complicating conservation measures.

Some other interesting complex effects of mammal introductions include the displacement of native species from preferred habitat by introduced predators, or habitat destruction by introduced herbivores, both of which lead to increased exposure to predators. Both have been documented. On Bermuda islands, introduced rats have forced cahows (*Pterodroma cahow*) to nest in suboptimal habitat where chicks are threatened by the white-tailed tropicbird *Phaethon lepturus* (Jackson, 1977, cited in Ebenhard, 1988). In the Galapagos Islands, goat browsing has destroyed the cover of land iguanas *Conolophus pallidus* and thereby increased their susceptibility to predation by Galapagos hawks, *Buteo galapagoensis* (Dowling, 1964; Gibbons, 1984).

There are also mutualist interactions between introduced species, which can act in synergy to inflict damage to local communities. An interesting illustration concerns the facilitation of access of introduced brush-tailed possums to forests. In the northern forests of New Zealand, introduced deer destroy the understorey, which causes the forests to become drier. This makes the habitat more suitable for introduced possums. The possums in turn cause a partial elimination of the tree canopy, which facilitates understorey regeneration, and thereby benefits red deer (Wallis & James, 1972).

These examples illustrate the near-impossibility of accurately predicting the ecological consequences of relationships among several introduced and native species. Nevertheless, conservationists generally agree about the need to control mammals introduced on oceanic islands. We will see that such complex interactions necessitate a deeper understanding of the system in order to predict properly the result of drastic management actions such as the removal of one species from the ecosystem.

III. CONTROL: TRADITIONAL *VERSUS* BIOLOGICAL METHODS

The first and best course of action is to prevent species introduction in the first place (I.U.C.N., 2001). Unfortunately, a great number of introductions already exist, forcing a response after the fact. There are three strategies to alleviate problems caused by introduced species: exclusion, control and eradication (see, e.g. Bomford & O'Brien, 1995). All three involve a reduction of the numbers of the animals causing problems. Exclusion is only a local solution, as it concerns a spatially delimited zone of effort from which the alien species will be removed. Control can have two meanings: it can be a general term of action against an alien species ranging from simple reduction up to eradication, and it can more specifically mean lowering of the introduced population numbers, that is mitigation or reduction. In this review, we use control as a general term, and use reduction or mitigation for partial population elimination. Control in the sense of mitigation is the reduction of the size of the pest population, down to acceptable levels, in ecological or economic terms. As such it is opposed to eradication (see below). Since it is not complete, such a removal strategy involves constant and/or repeated actions, to keep the population at low density after the initial decline. Although it is generally more feasible than eradication, the gains achieved by control are temporary. Many pest mammals have a density-dependent reproductive rate with higher reproductive levels at low density, leading to faster recovery rates for controlled populations. For example, after an 80% reduction, a goat population returned to previous levels within four years, the doubling time of a controlled goat population being around 20 months (Parkes, 1984).

Eradication is the complete removal of all the individuals of the population, down to the last potentially reproducing individual, or the reduction of their population density below sustainable levels (J. H. Myers *et al.*, 2000). This is generally, although not always, the best strategy for islands, but it is often limited by its high cost, logistically as well as economically. There are a number of factors that make some islands more difficult to free from alien species, or some alien species more difficult to remove from islands. Some factors are related to the island, for example area, ecosystem accessibility (field ruggedness, ecosystem penetrability, mooring possibilities, …) and isolation (distance to continent or other source). Some other factors are related to the alien species, for example dispersal abilities, diet width and ecological plasticity. Some species are said to be particularly robust and difficult to eliminate from large remote surfaces. In addition, when pushed down to a very low density, the last individuals of the populations of most species are generally very difficult to remove, for two reasons. First, the few remaining individuals are simply more difficult to find, and second, because of the density dependence that characterises most populations of invaders, these last individuals will quickly reproduce, which is a force that the control programme will have to fight against. An amazing example concerns the last remaining mule deer on San Clemente Island, USA. During a pig eradication programme in 1991, hunting dogs turned up an old male mule deer, which was shot. This was the first sighting of a deer on the island since the Navy's Natural Resources Office 'completed' deer eradication in 1977. Of course, being a single male, eradication had been essentially achieved, but this illustrates well how even large animals can remain undetected for quite a long time (14 years in this case; R. Brand Phillips, personal communication). For the pig eradication programme on Santiago Island, Galapagos, 450 times more effort was required to remove a pig in 2000 than in 1998; the actual cost per pig removed increased by approximately 2000% between 1997 and 2000 (Patry, 2001).

However, unless the island has a high likelihood of repeated invasions, the eradication should have to be implemented only once, as opposed to regulative control. It may be initially more expensive, but will be more cost effective than repeated (or continuous) population reductions because it is permanent (Veitch & Bell, 1990; Rice, 1991). For example, the cost of rat mitigation for the Mediterranean Lavezzi islands was estimated at around 3000 euros per year while its eradication cost five times that amount (M. Pascal, unpublished data). Although the larger amount is more difficult to obtain, it is more cost-efficient in the long term when compared to a 5+ year population reduction programme. In addition, if poisoning is one of the chosen action methods, eradication requires lesser amounts to be used than would be necessary for sustained control efforts. Similarly, fewer animals will have to be killed during an eradication campaign than would be for a long-term mitigation, which may be more acceptable to animal rights campaigners.

(1) Traditional methods

We will here compare two main types of control: traditional and biological. Each method comes with its own set of advantages and disadvantages and often these depend on the species to be controlled, resulting in some control methods being very well adapted to a given species. We provide in Table 1 a summary of method types, with the associated main advantages, disadvantages and typical target species.

Rather than describe all existing traditional control methods for introduced mammals, we will now provide a few typical examples of the techniques often used to control the main mammal invaders. Table 1 summarises the main advantages and disadvantages for each type of control method (physical, chemical and biological).

(*a*) *Fencing*

Because of their large size, ungulates are among the easiest mammals to exclude using fences. This solution is most appropriate when the area to be controlled is too large for an eradication programme, or if the herd is not to be entirely destroyed. An example of this is the feral cattle of Amsterdam Island (55 km^2) in the Indian Ocean (Micol & Jouventin, 1995). In 1871, a farmer gave up his livestock attempt on this island because of the harsh conditions, abandoning five cattle. These individuals adapted well enough, and bred rapidly to form a population reaching 2000 individuals in 1988. Owing to the grazing and trampling of this large population, as well as several major fires since the eighteenth century (1792, 1853, 1899, 1974), the native vegetation regressed in favour of introduced species. From the 1980s, introduced cattle started to colonise high elevation zones, which are especially sensitive to trampling and which shelter a relic population of Amsterdam albatross (*Diomedea amsterdamensis*). This species was discovered in the early 1980s and at that time numbered only 12 breeding pairs (Jouventin & Roux, 1983). Despite their impact, eradication of the cattle was not initiated because they represented one of the very few feral herds of this species anywhere in the world, a large herd that had evolved in total isolation for more than a century. The restoration strategy adopted was to divide the island into two sectors with a fence, and the cattle were eliminated from the main and most sensitive part of the island while the herd was regulated on a smaller sector with no birds. Fences are also used to exclude smaller animals, such as foxes, cats, rabbits, rats or even mice, in conjunction with other control methods, to clear the fenced area of the unwanted species. An impressive example is the Karori Wildlife Sanctuary, near Wellington, New Zealand (Saunders & Norton, 2001). It is a mammal-proof enclosure of 252 ha from which all introduced animals (including black rats, mice, possums, stoats and ferrets) have been eliminated in order to restore the local hardwood forest and to reintroduce extirpated species.

(*b*) *Shooting*

Large mammals will evidently be more easily shot, and therefore hunting has historically been used to control them. This is also linked to the associated gain in meat, and sometimes to the recreational aspect of hunting. The main disadvantage of this method is the poor accessibility of many oceanic islands, which makes it costly and logistically difficult to maintain enough manpower for a sufficient task force. This problem may be at one or both of two scales: accessibility to the island itself, and accessibility to some parts of the island. For example, it

Table 1. *Advantages and disadvantages of different control methods*

Method type	Typical target species	Advantages	Disadvantages
Physical methods			
Shooting	Ungulates	Very efficient for large animals Very selective Environmentally clean More ethical method (but usual targets have a high public profile)	Requires good accessibility for hunters in the field Requires experienced and dedicated staff May be costly and logistically difficult to maintain enough manpower for a sufficient amount of time Requires public information and sensibilisation May require special authorisation for guns May imply additional techniques: dogs, Judas technique, helicopters, etc.
Trapping	Small carnivores, possums	Efficient for small populations of small and medium-sized species in accessible and small areas Can be selective Environmentally clean	Certain traps may pose ethical problems Requires a limited infested area Requires a limited population Requires good accessibility to carry traps on the field May be expensive to buy sufficient traps May require good trapping experience to be efficient Requires attractive baits for target species that are non attractive (or repulsive) for non-targets May be selective (age or sex) Rarely achieves eradication unless used with another method
Chemical methods			
Poisoning	Rodents, carnivores, small herbivores	Very efficient for small rodents	Requires special authorisation May affect non-target species (protection measures may be expensive and not fully efficient) Implies complete coverage of the whole infested area Targets can develop bait aversion Implies the use of adequate baits and often of bait stations May cause secondary poisoning (accumulation in animal tissues) Some toxins are only slowly degraded Can be costly, especially for large islands Requires public information and sensibilisation
Biological methods			
Predator introduction	Rodents, small herbivores	Environmentally clean Very low cost	Great risk of specificity loss, causing further ecological disequilibria Historical reason for the existence of alien cat and mongoose populations Add a species and its parasites to the ecosystem

Table 1. (*Cont.*)

Method type	Typical target species	Advantages	Disadvantages
Competitor introduction	Carnivores	Can be very efficient if well planned	Released individuals must to be removed or die off without reproducing Very little information available Add a species and its parasites to the ecosystem
Pathogen introduction	Carnivores, small herbivores	Environmentally clean Very low cost Can be very specific	Poor efficiency at low density Ethical problems (may induce suffering) Sanitary risks Requires good knowledge of host-parasite system Requires absence of risk for non-target species Potential for host adaptation (evolution of immunity)
Virus vectored immuno-contraception	Rodents, carnivores, small herbivores	Most ethical method Low cost (when self-dissemination) Can be very specific Environmentally clean	Not yet operational Concerns for loss of control Very slow Irreversible process Low public acceptance of release of genetically engineered organisms Potential for development of host resistance

takes more than twenty days round trip by ship to access the Kerguelen islands, with a limited number of trips each year. In addition, the main area of this archipelago is extremely rugged: it has an area of approximately 6500 km^2 and a coastal length of more than 1000 km (i.e. between three and four times more than a perfect circle of the same area). Most parts of the island are reachable only by foot, requiring several days of trekking. This precludes the use of many control methods, and it seriously hinders others such as hunting. Yet, when accessibility can be dealt with, hunting is one of the most efficient ways of controlling or even eradicating a herd of ungulates, especially if large incentives are made available for hunters (Gosling & Baker, 1989). Using helicopters, it would be possible to eliminate the reindeer population from Kerguelen, but this would incur a high cost.

The most difficult part of large mammal control by hunting is the localisation of the last few individuals, since the very low density may seriously hinder the elimination of these few survivors, thereby threatening the whole control programme. Two main methods are used to overcome this problem. In many cases, dogs can be trained to assist hunters with rifles, and their help in detecting isolated individuals may make the difference (Cowan, 1992). Another, very clever method, especially designed to eradicate goats, is what has been called the Judas goat method (Parkes, 1984, 1990; Keegan *et al.*, 1994). It consists of fitting one individual, preferably a female in oestrus, with a radio collar. Goats are highly gregarious animals, and this female will be very efficient at finding isolated groups throughout the island. At regular times, the radio signal will be used to localise the female, and the hunters will have little difficulty in reaching the group, either by foot or by helicopter. Once in view, the whole group will be shot, except for the 'Judas', which will be spared so that it can find another group, thus involuntarily leading the hunters to it. When the 'Judas' is regularly found alone, the population is considered eliminated and that last goat is removed.

(*c*) *Trapping*

Trapping has historically been used for medium-sized mammals, such as small carnivores and large rodents, because they are less easy to shoot, but still valuable to collect either for fur or for meat. Trapping is mostly used for rodents, cats, mustelids, mongooses, rabbits and hares, but only for population reduction, since their eradication is not feasible by trapping alone (except for carnivores). Trapping has also been very efficient for possums (Cowan, 1992). Leg-hold traps are more rarely used now for ethical reasons, rather live door-traps are routinely used. However, in some cases leg-hold trapping may be the only efficient method, especially for cats (Veitch, 2001). The control methods based on trapping are very similar to those based on poisons: both will generally need to cover a substantial area and to develop attractive baits. However, traps may be of limited use if the area to control is too large, with limited accessibility, if the population is too large, or if the animals are trap shy. The eradication of a small population of cats can be considered by trapping on a small island if the terrain is not too irregular, but populations on large and/or rugged islands cannot be eradicated, since it is simply impossible to carry and set enough traps on very large or poorly accessible areas. However, traps do have the advantage of selectivity, because they can be designed to exclude or reduce accidental capture of native animals.

(*d*) *Poisoning*

Poisoning is the other major control method for medium and small mammals. Poisoning programmes often attempt to avoid non-target species kills with baits targeted for the pest species. However, discrimination can be difficult to achieve when native and alien species are taxonomically or ecologically close, and the impact of poisoned bait on native species can sometimes be important. Losses of non-target individuals to poisoning must thus be assessed with respect to losses caused by the uncontrolled introduced species (I.U.C.N., 2001). In fact, research consistently suggests that the harmful effects of introduced mammals are greater (and longer lasting) than those of the toxin used to remove these mammals. Even if many non-target individuals die from poisoning, populations of these individuals often recover rapidly once the pressure from the introduced species is removed (Merton, 1987). As an example, Pukekos (*Porphyrio porphyrio*) have re-populated Tiritiri Matangi and Motuihe Islands, New Zealand, after an initial reduction of around 90% due to a poisoning campaign with brodifacoum (Dowding, Murphy & Veitch, 1999). In some cases, elimination of non-target species through poisoning has been deemed unavoidable, and the eradication programme has been designed so that the native species could be reintroduced, once the alien species was eliminated. This was the case for the burrowing bettong *Bettongia lesueur*, which was eliminated during the poisoning of black rats on Boodie Island, off Australia. However, this had been foreseen by the programme leaders, who thus designed their programme such that once the rat was eradicated, bettongs could be reintroduced from a nearby island used as a reservoir (Morris, 2001).

Another possibility is to capture at-risk non-target endemics in order to protect them from poison during the eradication programme and then to release them once the invasive population is eradicated and the poison removed or degraded. This has been done for several programmes in New Zealand. In 1996 Pacific and Norway rats were eradicated from Kapiti Island (2000 ha), New Zealand (Empson & Miskelly, 1999). During the operation three pairs of takahe *Porphyrio mantelli*, a giant flightless rail, were held in captivity on the island for just over two months. In addition approximately 200 weka, *Gallirallus australis*, a large flightless rail, were removed from the island, 50 of which were held in pens in a mainland reserve and the remainder released in a remote former part of the species mainland range. The captive birds were held for around three months then returned to the island. During the period 1996–2000, the eradication of five introduced mammal species (feral cat, rabbit, black rat, Norway rat and house mouse), was attempted on four inhabited islands in the Seychelles. Since no rat-free island was available to which native animals at risk from poisoning might be transferred, it was necessary to maintain approximately 560 individuals of three threatened animal species in captivity for the three months duration of the eradication programme. Very low mortality was detected during captivity, and all captive animals were released in their former, now safe habitat, once the rats were eradicated (Merton *et al.*, 2001). The brown rat eradication programme for Fregate Island, Seychelles, included the capture and captivity of the entire population of the critically endangered Seychelles Magpie-robin *Copsychus sechellarum* (accounting for 50% of the world's population) and over 300 Seychelles Fodies *Foudia sechellarum* in 20 large aviaries for several months (Millet & Shah, 2001).

Paralleling the increased interest in mammal pest control and island restoration, there has been some technical progress in the development of mammal attractants and lures (e.g. Clapperton *et al.*, 1994; Saunders & Harris, 2000) and further research is currently under way. There has also been much progress to prevent aversion development in animals exposed to previously used poison (Cook, 1999; Hickling, Henderson & Thomas, 1999). Much effort has also been devoted to the development of baits that do not attract non-target species, by diminishing both hazard and exposure (e.g. McDonald *et al.*, 1999; Morgan, 1999).

Several toxins are routinely used for the control of small introduced mammals, mostly in Australia and New Zealand: sodium monofluoroacetate (or 1080), pindone, cholecalciferal, brodifacoum, cyanide, strychnine. Of these, 1080 and brodifacoum are currently the most widely used, with brodifacoum, an anticoagulant, being the most common used toxin (Innes & Barker, 1999). For example, brodifacoum was used in 28 of 33 mammal eradication programmes undertaken by the New Zealand Department of Conservation (DOC) in the last decade (Innes & Barker, 1999). Although 1080 is usually rapidly eliminated from live animals and rapidly broken down by microbial activity in baits, water and soil, it is still highly toxic to a wide range of animals and may pose problems for non-target species (Innes & Barker, 1999). By contrast, brodifacoum shows a greater persistence: it accumulates in vertebrate tissues, it is insoluble in water and only slowly broken down by microbial action (Dowding *et al.*, 1999; Eason *et al.*, 1999). It is however less toxic for non-target species (Godfrey, Reid & McAllum, 1981). Although it is often known for the control of brushtail possums in New Zealand, brodifacoum has also been used in successful mammal eradication programmes on islands for both rats (Buckle & Fenn, 1992; Taylor & Thomas, 1993; Brown, 1997; Empson & Miskelly, 1999) and rabbits (Godfrey *et al.*, 1981; Merton, 1987).

During control programmes, poisoned animals (alive or dead) may be eaten by carnivores or scavengers, potentially resulting in secondary poisoning. This may provide conservation managers with an efficient multispecies tool for controlling mammalian pests on offshore islands where their re-invasion is unlikely (Gillies & Pierce, 1999). Indeed, it is now known that mammal predator numbers can be effectively reduced by secondary poisoning with both brodifacoum and 1080 following rat control (McIlroy & McIlroy, 1992; Heyward & Norbury, 1998; Gillies & Pierce, 1999; Murphy *et al.*, 1999), to such a point that deliberate secondary poisoning has been suggested as a potentially cost-effective predator eradication tool (Alterio, 1996).

There is also a risk that pest species surviving a poison operation aimed at other pest species in the same area may subsequently develop an aversion to the poisoned baits and become exceedingly resistant to further toxin-based control (Hickling *et al.*, 1999). This not only can induce a learned aversion to the chemical used in the poisoned paste but also can cause animals to exhibit 'enhanced neophobia', as seen in possums following rabbit control (Hickling *et al.*, 1999). All these points highlight the need for developing medium and long-term strategies for the use of poisoning for mammal pest control.

(*e*) *Advantages and disadvantages of traditional methods*

Despite improved efficiency, especially concerning the recent progress for the eradication of rodents from larger islands, traditional methods remain logistically difficult, are costly in material, manpower and time, and generally have little specificity. These methods can have a low cost-efficiency on large and/or poorly accessible islands. This has led several biodiversity managers to look for alternative strategies, among which biological methods have an interesting potential (see Table 1).

(2) Biological methods

Biological control is the control of pest species by an enhancement of a different species that decreases the reproduction or survival of the target pest species. Several categories of natural enemies are used in this context, but predators and pathogens have historically been the most used for mammals.

(*a*) *Decreasing the survival of alien mammals*

The main biological control strategy is the introduction of natural enemies of the target species, with the aim of decreasing the survival of the target species. Parasitism, predation and competition are the three possible processes involved, although the former is the most common: the natural enemies most used for mammal pests are microparasites (viruses and bacteria). Concerning pathogen introductions, the best-known example is the myxoma virus, introduced in Australia and then on several islands to control rabbit populations (Brothers *et al.*, 1982; Chapuis, Chantal & Bijlenga, 1994*b*; Fenner & Ross, 1994; Chekchak *et al.*, 2000). Despite problems linked with virulence and immunity evolutions in large populations, this virus was successful at removing entire populations in many cases (Flux, 1993). More recently, the introduction of the rabbit haemorrhagic disease (RHD) in New Zealand and Australia has led to mass mortality in rabbit populations, but these were not scientifically planned eradications for conservation biology purposes and are extremely contentious. Regarding RHD in Australia, the disease has now been established in Australia for over five years and has reduced the abundance of rabbits across Australia, most spectacularly in arid, inland Australia (Brian Cooke, personal communication). Another example is the eradication of feral cats from Marion island, using the feline panleucopenia virus (van Rensburg, Skinner & van Aarde, 1987). In this case, a combination of biological control (the virus) and traditional control (hunting) was required to complete the eradication of cats, as neither technique alone would have been successful.

Generally, biological control by predator introduction has been disastrous. The presence of mongoose and or domestic cats on most islands is the result of failed attempts to control rodents, rabbits or snakes. Most of the time, these mammalian predators ignored the target prey and instead turned to native prey, which were often easier to locate and/or kill because they evolved in the absence of these terrestrial predators (Atkinson, 2001). The consequences of predator introductions for biological control of rodents are sometimes more subtle or unpredictable. For example, in the West Indies, rat control has often been attempted by mongoose introduction. But mongooses are typically terrestrial, and their presence often caused the rats to shift habitats in favour of arboreal niches (Seaman, 1952). As a result, not only have rats become less available to mongooses, which started preying on many species of ground birds, but also the introduction of mongooses led to an increased predation on tree nesting birds by the now more arboreal rats.

One of the rare attempts at controlling a mammal pest through competitive processes concerns a successful programme to eradicate arctic foxes from the Aleutian islands. This programme used the competitive superiority of red foxes: some sterilised individuals were introduced, and then removed once the arctic foxes were extirpated (West & Rudd, 1983; Bailey, 1992, 1993). This original method was highly efficient and, although very costly, certainly deserves more interest.

(*b*) *Decreasing the reproduction of alien mammals*

The common goal of control methods, either traditional or biological, is to decrease the survival of individuals of the target species. In some species with a short generation time and high reproduction rate (typically rodents and most other pest species), decreasing survival may not be as efficient as decreasing reproduction. During the last decade, a significant impetus of research effort has been devoted to the development of techniques lowering the fertility of mammal species. Notably, as an alternative to increasing the death rate, immunocontraception aims to reduce birth rates (Tyndale-Biscoe, 1994). Immunocontraception is a process by which the immune system of an individual is induced to attack its own reproductive cells, leading to sterility (Tyndale-Biscoe, 1994). This is achieved by infecting individuals with a protein derived from the follicular layers, which activates the production of antibodies against its own gametes, thereby blocking fertilisation (Bradley, Hinds & Bird, 1997). Depending on the size of the animal and the level of control desired for its population, infection is achieved by injection, as for large mammals (Kirkpatrick *et al.*, 1997) or by bait, typically for small carnivores (Bradley *et al.*, 1997). More recently, attention has been focussed on new methods that would allow infection through living vectors, typically genetically engineered viruses, bacteria or macroparasites. Virus-vectored immunocontraception (VVIC), for example, utilises a species-specific virus to disseminate this vaccine through a pest population by placing the gene encoding the reproductive protein into the genome of the virus (Tyndale-Biscoe, 1994). This potentially powerful new technique would be used mainly for rodents and small herbivores, such as rabbits and possums (Cowan, 1996; Rodger, 1997; Smith, Walmsley & Polkinghorne, 1997), but also could be very efficient for small carnivores as well (Bradley *et al.*, 1997; Pech *et al.*, 1997; Verdier *et al.*, 1999; Courchamp & Cornell, 2000).

Control by VVIC presents numerous advantages over traditional control methods based on increases in mortality. Because it does not result in animal suffering, the general public, ethics committees, and animal rights organisations are more likely to accept this method (Loague, 1993; Cowan, 1996). Moreover, unlike chemical control, this method is less harmful to the environment. It also shares the advantages of biological control over traditional methods: being self-disseminating, VVIC can be used to control large areas (even where accessibility is limited), for a minimal cost (Chambers, Singleton & Hood, 1997). Finally, it seems to be the most host-specific of current methods (Tyndale-Biscoe, 1994). Although genetic engineering of a pathogen is a prerequisite, preliminary studies are very encouraging (Moodie, 1995), and suggest a possibility of a durable sterilisation of the host without modifying its social behaviour. The main disadvantages of this emerging method include the irreversibility of the process once the vector is released (Nettles, 1997), the potential for development of host resistance, the need for the engineering of a genetically modified vector (Bradley *et al.*, 1997), a slow response time for definitive results as well as for monitoring progress (McCallum, 1996) and a low public acceptance of the release of genetically engineered organisms.

We cannot overemphasise that biodiversity conservation planners must be cautious and responsible with respect to the use of control through release of pathogens in general, and of genetically modified pathogens in particular. VVIC methods should only be used once they are deemed truly reliable and only in conditions of maximum security for the wild or domestic non-target populations inside and outside the target ecosystem. In this context, the application of VVIC methods, if the local biotic and abiotic conditions are favourable, should be first (and perhaps only) used in remote uninhabited islands, where potential unforeseen effects could be naturally and more easily circumvented (Courchamp & Cornell, 2000).

(*c*) *Advantages and disadvantages of biological methods*

The main advantages of biological control are a potentially very good specificity, and a higher cost efficiency since it corresponds to a self-disseminating control method, or what could be characterised as 'release and watch' effort. This can be crucial when large areas, low accessibility or low density prevent the use of traditional methods, as is often the case on islands (Courchamp & Sugihara, 1999).

However, there are also a number of disadvantages with this type of method, which have precluded the generalisation of its use. One drawback is the poor specificity of some of the species that have been used to control pest species. Although it could be argued that most failed attempts at introducing natural enemies to control exotic mammals could have been foreseen with a minimal scientific pre-release survey, the history of island restoration is dominated by catastrophic failures.

It is important to stress that biological control meets with growing success as programmes are scientifically established and implemented. The main criticisms of biological control concern programmes that have been conducted without adequate preliminary study of the ecosystem (see below). One must keep in mind that biological control, at least in the case of remote oceanic islands, is nothing less than the introduction of an alien species in order to solve a problem of a previous alien introduction. History has shown us that often more harm is generated from such interventions. In the case of attempted control of rodents in sugarcane fields in Jamaica, cane growers introduced ants (*Formica omnivora*), which did not reduce rat numbers but soon became a problem themselves. To remove rats and ants together, it was then decided to introduce venomous Marine toads (*Bufo marinus*). But toads still did not control rats, and became a pest themselves. Finally, small Indian mongooses were introduced to control rats and toads. Mongooses failed to control either, and began preying on native birds, posing new threats to wildlife (Lever, 1994).

The other main disadvantage of biological control is the lack of control once the natural enemy population is released. The advantage of a self-disseminating system may become a problem if the control method is not working properly, which it rarely does. Having no control over the released population also implies difficulties for the monitoring of the efficiency of the operation. Introduced species and their new environment interact in ways that are hard to predict even if we know all the details, which is seldom the case. Since we know little in most cases, accurate predictions are extremely difficult and entail unknown risks to every single introduction, including those for restoration purposes. This has led some authors to describe scientifically controlled introductions as 'a serious fallacy' (Ebenhard, 1988).

The third important problem in using biological methods to reduce mammal pest species is of an ethical nature. Because pathogens are more often used for the biocontrol of mammals, there are more concerns about safety and ethics than in classical biocontrol programmes in agricultural ecosystems. Most pathogens, for example, induce diseases that cause suffering before killing the individual host, which can be difficult to justify. Even though some animal rights association representatives agree that the death of a few individuals by control is more acceptable than the loss of hundreds of individuals, either by direct or indirect actions of invasive species, they rarely accept methods that induce suffering. The use of pathogens also generates concerns for the security of other populations and other species, including humans.

The risk of the control organism making its way back to the ecosystem from which the pest originated is a potential disaster. As has been shown with the introduction of the myxoma virus in France to reduce rabbit numbers, and more recently with the introduction of RHD in New Zealand for the same goal, it may be difficult to control fully the intentional introduction of micro-organisms by persons who are not fully aware of (and/or interested by) the potential ecological effects of such actions. It is particularly relevant to the case of the possums invading New Zealand, and native to Australia. Biological control of alien possums has been considered (Barlow, 1994; Cowan, 1996), but the risk such a programme represents for the native Australian population is a major drawback.

It is also often stated that biological control is more efficient at controlling than eradicating populations. One argument is that because of a long co-evolution, and the associated evolutionary 'arms race' of both the target species and its natural enemy (generally the host and its pathogen), the natural enemy has lost the ability to eliminate completely the host population (for it would disappear too). One point that is not taken into account in this reasoning is that the conditions may be very different from those where the two species have coevolved. In particular, the pathogen may rarely, if ever, have had to cope with a single population in complete isolation. It is conceivable that many pathogens have maintained characteristics that cannot eliminate a host population in contact with others, but which would eliminate a hypothetical population with no immigrants. Similarly, because of the founder effect, the genotype diversity of alien host populations may be reduced relative to mainland populations, and thus may not encompass enough variability to allow immunity of a fraction of the host population. A mammal population that would normally survive in presence of a virus may not do so if no immune individuals are present. Another argument is that some pathogens can be used in conditions that are not encountered naturally, for example if the virus is genetically modified.

A general question has been whether the advantages of biological control outweigh its risks (Simberloff & Stiling, 1996*a*, *b*; Thomas & Willis, 1998). Without entering a long debate that lies outside the purpose of this review, it is worth emphasising two points. Firstly, even though it is true that there have been more failures or semi-successes than complete successes with biological control, one should bear in mind that most of the programmes involving biological control have been carried out at a time when careful feasibility and impact assessments were not the rule. Thus past failures mostly reflect that these programmes were not optimised, but they do not rule out the possibility of using the same tools to get better results. It is conceivable that the small number of studies concerning biological control of vertebrates is due more to a lack of confidence and of effort than to a lack of potential (Wood, 1985). Secondly, even in the days when scientists and conservation managers did not benefit as we do from the hard learned lessons of initial failures or partial success, there were nevertheless interesting cases of impressive achievements through biological control. For example, the eradication of the cats from Marion Island would not have succeeded without the initial elimination of some 80% of the population by the introduction of feline panleucopenia virus. Biological control thus remains a potentially powerful method that merits future investigations.

Despite all the positive and negative examples given above, it should be recognised that neither biological control nor traditional methods are a universal panacea. Each method has specific disadvantages and each particular case of invasion should be managed with an adapted and specific plan of action. The most appropriate strategy will be more often the simultaneous use of biological, chemical and mechanical control methods. It is commonly accepted that a combination of strategies, that is, integrated pest management, is the best response to mammal introductions.

(3) Strategies

The dynamics of invasion can be divided into four stages: (*i*) the transport of organisms to a new location; (*ii*) the establishment of the invading species at this location; (*iii*) the consequences of the growth in numbers of the invading species for other species in the invaded community (interspecific interactions); (*iv*) the spatial spread of the invading species from the initial successful population (Hastings, 1996; Shea & Chesson, 2002). Although the best option is to act at stage (*i*) (I.U.C.N., 2001), many organisms have already been introduced and the strategies for invasive species control will differ according to the stage of invasion.

(*a*) *Eradication of established populations*

Many authors have insisted on investing time in optimising the strategy used to reduce or eradicate an alien species from an island. In particular, to ensure the best chances of success, an investigation of the historical, ecological, social and economic situation of the island must be completed. Moreover, the aim of the programme must be clearly defined in order to identify the available options and their respective likelihood of success.

Applying methods that were successful elsewhere, even if the same alien species is concerned or other aspects seem identical, is not necessarily a guarantee of success. Each case must be thoroughly studied independently, with careful planning of the protocol and how to institute it.

Many authors have given rather precise guidelines based on their experience with certain species, and much relevant information can be found either in published studies or from the national agencies that led or financed the programmes (e.g. the DOC). There are, however, a number of basic points that can be cited as important for the success of a programme. To be successful a control programme requires (but is not guaranteed by): (1) good planning (on all aspects, from logistics to ecology); (2) a good pre-control study of the situation (see below); (3) careful choice of the selected method or suite of methods (including good timing); (4) sufficient and lasting financial and political support to complete eradication (even if it takes time); (5) public support (e.g. Veitch & Clout, 2001).

It is outside the scope of this review to expand on each of these points. We provide a summary of the most important recommendations for a control programme (Fig. 4), but each aspect certainly deserves more detailed exposition. As an example, a few words can be said concerning the timing of the programme. This point is crucial for the success of the programme on several

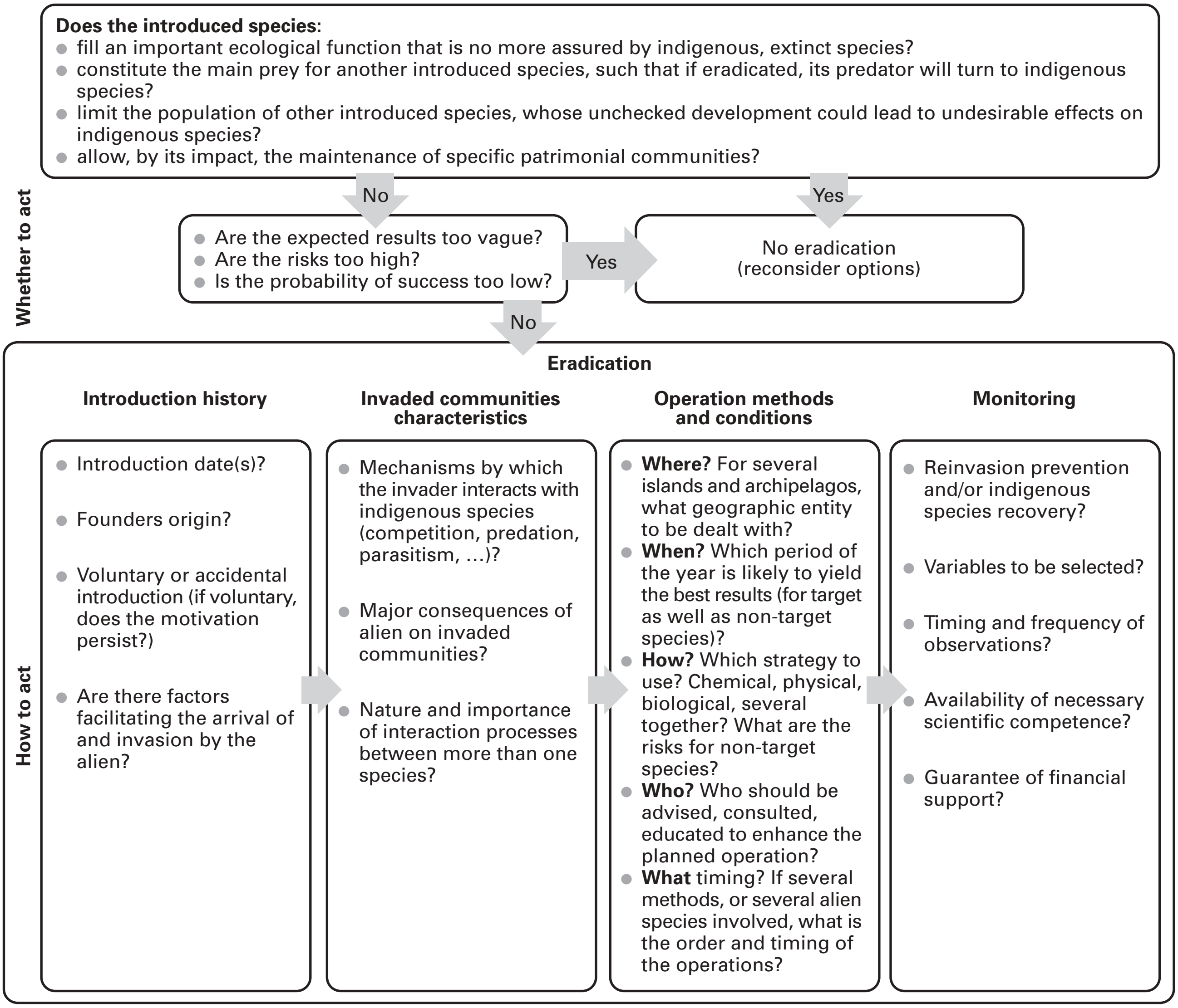

Fig. 4. Decision diagram for the eradication of mammal species from islands.

grounds, depending on the type of alien population i.e. whether it is an established or new incursion. For the former, the timing of the operation is of major importance because biotic and abiotic conditions play a role in the population dynamics of alien invasive and indigenous species (Innes & Barker, 1999). These conditions (climate, fluctuating dynamics of other species, etc …) can promote or hinder the growth of the target population, and it is better to have these forces acting with the protocol rather than against it. For example, it may make a difference to launch an eradication programme on a species when the food resource of that species (either plant or prey) is lacking, e.g. in winter or during migratory bird absence (Chapuis *et al.*, 2001). It may be also judicious to act when the target species is more vulnerable because it has less cover (e.g. vegetation cover is lacking in winter on many islands) or because it has a restricted home range (e.g. arctic foxes avoid the inner parts of the Aleutian islands in winter, restricting their movement to a coastal strip, and they are therefore more readily removed from those islands during this period, Steve Ebbert, personal communication). If several introduced mammals are present, careful thought must be dedicated to the strategy to be implemented. There is no currently admitted prioritisation scheme, but any such system would have to consider, among others, the known effect(s) of the alien invasives, the probability and rate of spread of the alien invasives and probability and cost of achievable eradication, and the interactions among the alien invasive species as well as with native communities. It is, however, our deep conviction that often all should be done to remove each introduced species, and that prioritisation schemes should equate to eradication timing not to a choice of which species to remove and which to leave. We describe in the fourth part of this review why and how the timing of such programmes is crucial for the restoration of the ecosystem.

(*b*) *Eradication of new incursions*

Eradication of new incursions also needs good planning, careful selection of methods, financial backing, and public support, but the reaction time is fundamentally different. Indeed, one needs to react rapidly when an invasion is first documented, because it almost invariably starts with few individuals in a localised place and this is easier to deal with than a large and expanding (or even established) population. Launching a control operation as close as possible to the beginning of the invasion, and if possible before the species is established, is by far the best option for success. Thus, the best approach is to have in place a strategy/policy that allows for rapid action. In this regard, it is crucial that a legal mechanism should exist that allows action to be taken swiftly by an appropriate authority or institution that is prepared for such situations. Similarly, public support must exist beforehand for the fact that rapid action may be needed at some stage. Accordingly, public consultation should be focussed on a general strategy for emergencies, rather than on a particular case. The 1999 exemplary case of the mussel-invaded marina near Darwin (Kaiser, 1999), immediately dealt with by Australia's Northern Territory government and the CSIRO was a great success and provides a model example for quick decision and rapid response in future cases.

IV. CONSEQUENCES OF ALIEN MAMMAL CONTROL

(1) An increased number of successful control programmes

Control or eradication programmes have been increasing in number in the last few decades. This is partly because of a shift in ecologists' interests, with an increased interest in conservation biology and restoration ecology (Young, 2000) in general, and by biological invasions and alien species in particular (there were more published articles with 'Biological Invasion' as key words for the first trimester of 2002 than for all years between 1981 and 1990). It is also because new protocols have allowed successful eradication of mammals from islands in conditions that were previously judged impossible to overcome (Dingwall, Atkinson & Hay, 1978). For example, it was admitted as late as 1976 that islands of more than 1 ha could not be freed of rats (Atkinson, 2001). However, improved protocols led to their eradication from the 3253 ha Langara Island (Bertram & Nagorsen, 1995; Drever & Harestad, 1998; Taylor *et al.*, 2000). This was made possible by both the availability of the 'one shot' anticoagulants in baits that are attractive to rodents and the development of a successful technique of dispensing poison baits from fixed stations spaced such that at least one station lies within the home range of each rat (Taylor & Thomas, 1989; Taylor & Thomas, 1993; Clout, 1999). This has been recently replaced by aerial poisoning using the Global Positioning System (GPS) to distribute baits accurately and evenly, a method less time-consuming than fixed bait stations. This innovative method has created a new impetus both to research on control protocols and to eradication campaigns on new (large) threatened insular ecosystems. Similarly, the use of the GPS and Geographic Information System can assist hunters in covering more efficiently the ground without leaving huge gaps and in coordinating their movements with extreme precision, thereby much improving overall hunting effectiveness (Patry, 2001).

Eradication programmes are hard to quantify in terms of their success or failure. Data are difficult to trace for many parts of the world and such programmes are not systematically reported in the classical scientific literature. This is especially the case concerning failures, which are more rarely reported. One good counter example of this is New Zealand, for which such data have been carefully recorded. The total number of completed mammal eradications was 153 at the end of 2001, with a further 24 ongoing operations, as compared with three stopped and nine failed programmes (C. R. Veitch, personal communication). In total, failures or discontinuation of programmes account for a mere 7.3 % of programmes not currently in progress. In total, these eradication programmes concern 144 islands, three quarters of which are now successfully completed, 2.8 % were stopped midway in the operation, and 7 % were considered failures (C. R. Veitch, personal communication).

Table 2 shows the largest islands from which 14 of the most notorious mammal island invaders have been successfully eradicated. This Table may lack completed programmes that are larger that those mentioned: not all programmes are presented in classical scientific literature, and, in most cases programmes need time in order for the managers to claim with success confidence. For example, rabbits have very probably been eradicated from the 8 km^2 St Paul Island, France, but the programme has only recently been completed, and several

Table 2. *Largest islands where eradication was achieved for 14 introduced mammals.* [1]*Eradication on part of the island, managed population on the rest;* [2]*Terres Australes et Antarctiques Françaises;* [3]*Galapagos National Park Services;* [4]*Charles Darwin Foundation;* [5]*23 years of control and four years of eradication*

Mammal species	Island and country	Size (km^2)	Method	Supervising institution	Estimated number eradicated	Date of completion	Operation duration (years)
Arctic fox	Attu, Alaska, USA	905.8	Shooting & trapping	US Fish & Wildl. Service	373	1999	?
Black rat	St Paul, F	8	Poison	TAAF	8–12 000	1999	3
Brushtail possum	Rangitoto-Motutapu, NZ	38.5	Poison, trapping, dogs	NZ Dpt Cons. (DOC)	21 000	1997	8
Brush-tailed rock wallaby	Rangitoto-Motutapu, NZ	38.5	Poison, trapping, dogs	NZ DOC	12 500	1997	8
Cat	Marion, SA	190	Biocontrol, trapping & shooting	S. Afr. Dpt Envir. Affairs	2790 + 1124	1990	4
Cattle	Amsterdam, Indian Ocean, F	55[1]	Shooting	TAAF	1059	1989	2
Goat	San Clemente, USA	148	Shooting, trapping	US Navy	30 000	1992	19
Mouse	Enderby, NZ	7.1	Poison	NZ DOC	?	1995	3
Norway rat	Langara, Can	32.5	Poison	Can. Wildl. Service	3000	1995	< 1
Pig	Santiago, Galapagos, Equator	584.6	Shooting, dogs, poison	GNPS[2] CDF[3]	19 210	2000	27[4]
Pacific rat	Kapiti, NZ	19.7	Poison	NZ DOC	?	1996	< 1
Rabbit	Enderby, NZ	7.1	Poison	NZ DOC	?	1995	3
Red fox	Dolphin, Aust	32.8	Poison	Aust. Dpt Cons. & Land Managt.	30	1980	10
Sheep	Campbell, NZ	112.2	Shooting	NZ DOC	?	1991	21

additional years of checking for recovering populations will be required before it is classified as a definitive success (T. Micol, personal communication). Similarly, the Norway rat may have been eradicated from the 113 km^2 Campbell Island, NZ, which would make it the world's largest successful rat eradication project. As is the case for St Paul Island, time is needed to assess the real state of the population and the population cannot be officially declared eradicated until the island has been confirmed rat-free after two years. It seems however that this major operation, which included an aerial poisoning campaign by the DOC, involving the airdrop of 120 tonnes of anticoagulant baits, is already a great success. A forthcoming project also aims to eradicate goats, from the 2100 km^2 of Isabela Island, Galapagos (Kaiser, 2001), which would make it the largest eradication project involving this species. A further problem of this table is the eradication of mammals living on small portions of very large islands. For example, the feral goats eradicated from the 460 km^2 Auckland Island, NZ, actually lived in only approximately 40 km^2 (Chimera, Coleman & Parkes, 1995). This poses problem for the definition of islands. In this review, we do not consider Great Britain, Australia or New Zealand as islands, although they are geographically defined as such. Therefore, we did not include cases such as the coypu, *Myocastor coypus*, eradicated from England, considered one of the most impressive achievements to date in this context (Gosling & Baker, 1989).

Some countries have been leaders both in research and implementation, most notably New Zealand and Australia. This is probably because they are countries with many islands, with a flora and fauna that evolved in the absence of many mammals (there is an absence of indigenous terrestrial mammals in NZ; Atkinson, 2001), and thus they have suffered more from species

Table 3. *Effort of mammal eradication for a few island groups. Data were obtained from Ian McFadden and John Parkes (NZ Is), Keith Morris (Western Australian Is), Steve Ebbert and Vernon Byrd (Aleutian Is), Fred Kraus (Hawaiian Is), Michel Pascal (French Is), Bernie Tershy and Josh Donlan (Mexican Is). *French islands include islands in different parts of the world: Brittany, Mediterranean, Caribbean, sub-Antarctic and Indian Ocean*

	Number of islands	Number of eradications	Species	Methods	Mean size (km^2) [min, max]
NZ Is	107	153	Mouse, cat, rabbit, brushtail possum, wallaby, ship rat, Norway rat, Pacific rat, stoat, ferret, pig, goat, cattle, sheep, red deer	Poison, shooting, dogs, traps	3.07 [1, 11 216]
W. Aus. Is	45	57	Mouse, Norway rat, fox, cat, rabbit, goat	Poison, shooting, traps	5.28 [0.01, 42.67]
Aleutian Is	34	36	Fox, cattle	Shooting, poison, traps, biological control	25.05 [0.25, 91.74]
Hawaiian Is	9	13	Cattle, sheep, goat, rabbit, Polynesian rat, ship rat	Poison, shooting, traps	50.55 [0.04, 18.85]
French Is*	39	46	Rabbit, goat, cattle, ship rat, Norway rat, mongoose	Poison, shooting, traps	27.3 [0.01, 55]
Mexican Is	24	32	Cat, rabbit, goat, sheep, mouse, ship rat, Norway rat	Poison, shooting, dogs, traps	3.3 [0.02, 20]

invasions than less isolated countries. Also undeniably important is the political will, the social maturity on environment-related matters and the economic ability to act to preserve the native fauna and flora. These three points unfortunately are not always present together in most other countries. The leadership of New Zealand and Australia in the restoration and management of invaded ecosystems is eloquently reflected in hard data showing the number of islands subject to mammal eradication programmes (see Table 3).

According to J. H. Myers *et al.* (2000), six factors contribute to successful eradication. First, financial support must be sufficient both in quantity and in duration. Second, all the necessary authority must be invested in the group in charge of the programme to ensure the protocol can be enacted. Third, the life history, reproductive biology, behaviour and dispersal ability of the invading species must make it susceptible to control procedures (implying that these parameters must be known before the implementation of the programme). Fourth, the programme should take into account the necessity of stopping the influx of individuals into the ecosystem. Elimination of mammals from islands might in this context be more successful because the probability of reintroduction can be easily reduced. Fifth, detection of the target species must be possible even at low densities, so that eradication can be best achieved and new introductions can be recognised before the species becomes widespread. Finally, complementary restoration actions might have to be taken to accompany the elimination of the pest species if it had assumed an important role in the ecosystem and if its removal can trigger further problems (Towns, 1997).

(2) On the definition of successful programmes

The increased number of successful control programmes must not mask the fact that in too many cases the so-called success is simply equated to achieving elimination of the target species, which cannot always be rightly called a success. As the term 'impact' requires definition (Parker *et al.*, 1999), it is also important to consider the meaning of 'successful' in the context of island restoration. The removal of the alien invasive species might be sufficient to restore the ecosystem if the invader did not have sufficient time to inflict irreversible damage to the normal functioning of the ecosystem. Often, the introduced mammal species will have had a quantitative impact on species it interacts with, and after its elimination, natural ecological processes will drive the interacting indigenous species back to their former equilibrium. However, unexpected changes may arise from the sudden removal of the alien species. Introduced species may have had an irreversible impact that requires further restoration actions. The simplest case is when an entire population or species has been eliminated from the considered islands and potential source populations are too far away to allow a rapid natural recolonisation. Another case is when the habitat has been degraded to a point where regeneration cannot be made rapidly enough to avoid the collapse of whole communities. In addition, the introduced species may have changed the local biotic and abiotic conditions in such a way that its sudden removal cannot facilitate the reestablishment of previous states, and sometimes may even lead to further threats to the native species. Dramatic changes to islands following the eradication of introduced species have been sometimes reported but less often quantified. The number of cases where an introduced species removal has led to even greater risks for the protected species is unfortunately high, and cases are still occurring with current restoration programmes. These situations, and recommended actions which help to reduce their occurrence, are discussed in the next section.

(3) Positive and negative effects of mammal eradication

There are a number of basic recommendations that can be made concerning the restoration of invaded islands (see Fig. 4, but also Parkes, 1990; Veitch & Bell, 1990; Towns & Ballantine, 1993; Towns, 1997; Atkinson, 2001; Saunders & Norton, 2001, for examples). Because removing a species from an ecosystem, even an alien species, can have diverse consequences, both desired and undesired, it is crucial to be able to quantify and to predict these effects. Indeed, quantification of the desired effects can lead to improvement of control methods as well as a better justification of the control programme for biodiversity conservation. Adequate knowledge can also help predict and thus prevent the undesired, and previously unexpected, effects.

Towards this end, one crucial point is to assess fully and precisely the current state of the ecosystem in order to establish a zero state qualification and quantification. As indicated in Fig. 4, it is necessary to assess the current state of invaded ecosystems prior to drastic interventions such as species removal, even if it is an introduced species (Thomas & Willis, 1998). This step is essential to allow a rigorous estimation of the effects of the invading species and of the expected effects following its removal. It is also fundamental to implement the best control strategies qualitatively as well as quantitatively (e.g. see Choquenot & Parkes, 2001), according to local conditions. Finally, it is indispensable to predict, and thereby avoid, the potential side effects of alien invasive removal. Researchers and managers are increasingly aware of community level interactions because pest control can have unforeseen repercussions such as mesopredator (or competitor) release and prey switching (Murphy & Bradfield, 1992; Dowding & Murphy, 2001). From some of the long-term pre-removal studies that have been conducted, it has been concluded that 10 years of study prior to an eradication may be required for post-eradication observations to be compared adequately (R. Veitch, personal communication). However, in many cases it is difficult to wait that long before acting on the invading population.

It may sometimes prove essential, however, in order to avoid the 'surprise effects' following eradications that are often mentioned by programme managers. The associated catastrophic chain reactions emphasise how crucial pre-control studies are for successful ecosystem restoration. Unexpected and undesired secondary effects are in general more likely to occur when ecosystems contain more than one invading species (that is, the great majority of islands), when invading species are in the late stages of invasion and when they have eliminated native species and replaced them functionally (Zavaleta, Hobbs & Mooney, 2001). In general, secondary effects following the sudden removal of alien species are very damaging to the ecosystem, and careful monitoring of the communities prior to any control action has the potential to prevent such catastrophic chain reactions. As we have seen in detail, exotics interact with native species as well as among themselves, creating a complex pattern of direct and indirect effects that can be extremely difficult to comprehend, let alone to predict. For example, the removal of one exotic species can favour the expansion of other exotics that were held in check by the removed species. This has been called the Sisyphus effect (Mack & Lonsdale, 2002).

The removal of herbivorous aliens such as rabbits and goats can lead to a release of exotic plants that, in the absence of browsing, are more competitive than native plants, leading to an explosion of such weeds. There are very few examples of islands on which the presence of feral goats or other browsers is more positive than negative (Daly & Goriup, 1987). But 'the immediate removal of introduced browsing mammals … may lead to unexpected and even undesired results' (Taylor, 1968). For example, a recent project was undertaken to remove goats and pigs from the Sarigan Island, one of the Mariana Islands, in order to stop and reverse the loss of forest and accompanying erosion, and thereby to protect the endangered native fauna (Kessler, 2001). In only two months, nearly 1000 animals were shot from this 500 ha tropical island, allowing rapid recovery of both plants and monitored vertebrates. The project was successful in reversing the trend of forest loss, and improving the habitat for local birds and bats. However, the removal of alien mammals has allowed the introduced vine *Operculina ventricosa* to thrive and spread, to such a point that part of the island is now covered by an almost uninterrupted carpet of vine, with unknown consequences for the future of the whole ecosystem (see Fig. 5). The introduced mammals had previously held the vine at a low density such that minimal pre-operation monitoring had not identified this threat.

A similar example, concerning predatory relationships, is what has been called the mesopredator release effect (Soulé *et al.*, 1988; Courchamp, Langlais & Sugihara, 1999*a*). This process predicts that once top predators are suppressed, a burst in growth of intermediate predators, or mesopredators, may follow that leads to prey extinction. A classic illustration of this is the removal of cats from islands where rats are also present: the elimination of feral cat populations from such ecosystems could lead to a severe negative impact on the endemic species, through a rapid growth of rodent populations following the removal of their predators. Attempted reduction of the cat population of Amsterdam Island is alleged to have caused a compensating increase in the number of rats and mice, and so has been abandoned (Holdgate & Wace, 1961). It is axiomatic that removal of cats (as well as similar predators) from islands must be accompanied by a control of their introduced prey (herbivores as well as omnivores or carnivores).

However, outcomes of changes of these already perturbed trophic webs are not intuitive and intervention as dramatic as species eradication should, when possible, be preceded by careful empirical and theoretical studies of the whole ecosystem. Sometimes, the presence of a few individuals of a species that may appear of minor importance can mask powerful interspecific interactions. Thus, avoiding unexpected changes may not be as simple as removing the most obvious introduced species: in this case, removing both cats and rats might not be sufficient. On Bird Island, in the Seychelles, eradication of the introduced rat population led to an explosion of the exotic crazy ant *Anoplolepis longipes*, now threatening colonies of Sooty terns and the endemic skink *Mabuya seychellensis* (Feare, 1999). Invertebrates are often overlooked in insular restoration programmes, perhaps because they are not as conspicuous as mammals, and may not be considered as harmful. However they are species anchoring the base of trophic pyramids. This implies that in some cases, anything but the most finely tuned intervention may lead to more damage than benefit to biodiversity, begging the question as to whether intervention should be done at all. Nevertheless, we can still gain from unwitting mistakes made in the past, since all results contribute to an understanding of island ecology and can be used in future conservation actions on other islands.

The other major aspect, also often overlooked in many control programmes, is post-eradication monitoring. This long-term surveillance is crucial for many aspects. First, it allows an assessment of the success of the proximate goal of the programme: durable elimination of the target species, with no further invasion. It also can quantify the ultimate goal of this elimination: the reversal of a decline of affected native species, their increase, or their recolonisation of the ecosystem. This part is not to be neglected: it may be surprising to learn that assessment of whether expected positive effects (restoration of initial ecological conditions) have been reached is still not systematically included in restoration programmes. Historically, the lack of assessment in control programmes may have led to a slower realisation that alien invasive elimination does not systematically lead to ecosystem restoration. Third, post-eradication monitoring allows the early detection of the increasingly described 'unexpected changes' that can be disastrous in closed and non-redundant ecosystems.

The before-after-control-impact study design, also called BACI, is used to assess the impact of some event on variables that measure the state of an ecosystem. The design involves repeated measures over time, made at one or more control sites and one or more impacted sites, both before and after the time of the event that may cause an impact (Manly, 2000).

The need for long-term monitoring is well illustrated by the famous case of Round Island, Mauritius, a unique ecosystem endangered by introduced species. This 151 ha island is an important refuge for several endemic plants and reptiles that have disappeared from the mainland of Mauritius (Bullock, 1977). The effects of goats and rabbits introduced in the early 19th century were so large that the main habitats were greatly modified and several native species were threatened with

Fig. 5. Landscape of Sarigan Island, before (1996) and after goat control (1999). In the presence of the goats, the destruction of the vegetation is very important (the scale is given by the goat in the centre, shown by the black arrow). Two years after goat eradication, the introduced vine has spread, eventually covering and asphyxiating the native vegetation that had already begun to recover. Photograph courtesy of Curt Kessler.

extinction (Bullock, 1986; North & Bullock, 1986). By 1986, rabbits and goats were eradicated from the island (Merton, 1987), and a programme was implemented to monitor the changes in the extent and composition of key elements of the biota, such as vegetation, invertebrates and reptiles (North *et al.*, 1994). Long-term monitoring now shows that a satisfactory regeneration and recolonisation of plant species formerly threatened by alien grazers is somewhat impeded by a new threat on native plants that is linked to the colonisation and rapid spread of several alien invasive plants (North *et al.*, 1994; Bullock *et al.*, 2001).

V. CONCLUSIONS

(1) There are many other aspects of the impact of mammal invaders and their control that are also important to discuss, and we hope that this review will trigger discussions on complementary elements of this theme. As a conclusion, two main points need to be especially stressed. First, despite the rather pessimistic image of the current situation depicted here, there is a growing number of successful control programmes, both because there are more programmes, indicating that researchers and conservationists are becoming more aware, interested and involved in the problems of biological invasions, and because programmes are better planned, with lessons learned from past experiences. Thus, some optimism is not unjustified and we foresee a sustained increase of successful restorations of insular ecosystems. The best strategy will always depend on the specific conditions and will often involve integrated pest management, combining the advantages of mechanical, chemical and biological methods, while avoiding their respective disadvantages through careful planning. As scientific and managing tools improve and become more available, we hope that other countries will follow the example of New Zealand and Australia with respect to their cogent political, financial and scientific resoluteness in controlling biological invasions and their effects.

(2) Second, if one lesson only were to be learned from past failures or semi-successes, it is that a restoration programme cannot be limited merely to eradication. A thorough pre-eradication assessment and long-term post-eradication monitoring (not limited to those communities directly linked to the eradicated species, as there can be unexpected indirect consequences) are both necessary. Only in this way will we ensure the best chances of success of full and durable ecosystem restoration. Moreover, these techniques will allow us to benefit fully from past experiences and enrich the knowledge of conservation biology as well as more general areas of modern ecology.

(3) We wish to conclude on the potential of insular ecosystem restoration programmes as sources of valuable knowledge for fundamental research. Experimentation in the epidemiology of biological invasions has been advocated as a way to obtain definitive synthesis, generalisation and prediction (Mack *et al.*, 2000). Future and ongoing eradication programmes also provide excellent research opportunities for ecologists to study the roles of species in communities, the impact of non-indigenous species, and the behaviour and population dynamics of exotics for which eradication is being considered (J. H. Myers *et al.*, 2000; Sakai *et al.*, 2001). In general, we advocate that eradication projects be viewed as ecological experiments in which the modification of trophic webs (by addition and subtraction of species) can expose community processes. This contributes to our understanding of biological invasion, but also more generally to many areas of population biology and general ecology (Shea & Chesson, 2002). As such, each alien control programme should be designed and implemented as a scientific experiment, with hypotheses, rigorous protocols, and control of expected (and unexpected) results (Pascal & Chapuis, 2000). This will allow researchers in conservation biology to establish a wider and stronger theoretical framework, which is much needed in this discipline (Caughley, 1994), and will also allow conservation managers to benefit from ensuing generalisations.

VI. ACKNOWLEDGEMENTS

The authors would like to acknowledge many colleagues who helped provide data, facts or comments on the manuscript, and without which this review would have been much poorer. We are especially grateful to Chris Buddenhagen, Vernon Byrd, Jenny Daltry, Josh Doolan, Steve Ebbert, Julie Geritzlehner, Fred Kraus, Jan Larson, Ian McFadden, Don Merton, Keith Morris, John Parkes, Mark Patry, Gad Perry, Brand Phillips, Dan Simberloff, Philip Thomas, David Towns, and Alvin Yoshinaga. Thank you to Matthew Godfrey who minimized the heavy French accent of the text. An earlier version of the review was improved by comments from Maj De Poorter, Mike Clout, Dick Veitch and two anonymous referees. This work is part of the two programmes IFB no. 209/01 and IPEV no. 276.

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