Review of negative effects of introduced rodents on small mammals on islands

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Abstract In this first comprehensive review of negative effects of introduced rodents on insular small mammals, the focal species *Rattus rattus*, *R. norvegicus*, *R. exulans* and *Mus musculus* are implicated in at least 11 extinctions. Furthermore, removal experiments, eradication campaigns and control programmes provide evidence for negative effects on extant populations. While data are currently insufficient for meaningful generalisation with regard to the most threatening rodents, the most threatened small mammals, and the true extent of the problem, it is interesting that *R. rattus* is implicated in the majority of impacts. This may be explained by its extensive distribution and ecological plasticity. I conclude with methodological recommendations to guide data collection for impact quantification and the study of impact mechanism. This information should facilitate the prioritisation and justification of eradication campaigns, control programmes and biosecurity measures while ensuring that much-needed attention is paid to the conservation of insular small mammals.

Keywords Black rat (*Rattus rattus*) · House mouse (*Mus musculus*) · Impact · Invasive alien species · Norway rat (*Rattus norvegicus*) · Pacific rat (*Rattus exulans*)

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Introduction

Of a documented 88 mammal extinctions since 1500, 57 (65%) have involved insular small mammals (MacPhee and Flemming 1999). Of extant species, the majority of mammals currently threatened with extinction are small and inconspicuous, such as rodents and bats (IUCN 2007). Although the extinction and endangerment of insular small mammals may be caused by a variety of factors including habitat destruction, over-hunting and the devastating impacts of introduced predators, the purpose of this paper is to examine the evidence supporting a contribution of introduced rodents. By 'introduced' I refer to a species that has been accidentally or deliberately transported, by human activity, to a location outside its natural range. Although various rodent species have been introduced onto islands (Musser and Carleton 2005; Simberloff 2008), four species are commonly considered conservation problems and are the focus of this review: the black rat *Rattus rattus*, Norway rat *R. norvegicus* and Pacific rat *R. exulans* and the house mouse *Mus musculus*.

Of the three rats, *R. rattus* was the first to be introduced to islands. It is thought to have been transported along trade routes from India (where it is native) to reach Mediterranean Europe by 6,000–4,300 years ago. Neolithic human population expansion and migration facilitated the dispersal of *M. musculus* (also native to the Indian subcontinent) so that it too had arrived in Europe by 6,000 years

ago. Both species have since been introduced to islands throughout the world. Of the three well-known subspecies of *M. musculus*: *domesticus*, *musculus* and *castaneus*, *domesticus* is the one that has been widely spread to numerous islands by European colonisation (Musser and Carleton 2005; Global Invasive Species Database 2006, 2007). The next important event probably began more than 3,000 years ago with the movement of *R. exulans* from mainland SE Asia, where it may have originated, into the Pacific basin, probably aboard the vessels of the proto-Polynesian Lapita people (Atkinson 1985; Musser and Carleton 2005). By 1100 BC *R. exulans* may have reached Samoa, Tonga and Fiji. The later, more rapid spread of Polynesians ensured that by about 700 years ago *R. exulans* had been introduced to most major island groups in the Pacific (Atkinson 1985; Wilmshurst and Higham 2004). The anthropogenic dispersion of *R. rattus* continued much later (although it may have been introduced to Madagascar by about 2,000 years ago) between approximately 1500 and 1700 AD when it was carried by trading vessels to various islands of the Indian and Atlantic Oceans (Atkinson 1985; Musser and Carleton 2005). However, this spread came to a virtual halt when *R. norvegicus* (originating in south-east Siberia, northern China and the Hondo region of Japan) displaced *R. rattus*, becoming the dominant species in European and eastern North American ports and the main species to invade oceanic islands during the eighteenth and into the nineteenth century (Atkinson 1985; Musser and Carleton 2005). By 1850 *R. rattus* had made a mysterious reappearance on ships and its introduction to Pacific islands ensued (Atkinson 1985). Over the last 180 years both *R. rattus* and *R. norvegicus* have been transported aboard ships so that many Atlantic and Indian island groups have been invaded by both species and many Pacific island groups host all three species of *Rattus* discussed in this review (Atkinson 1985). The taxonomy and nomenclature of *R. rattus* is controversial. However, current taxonomy recognises '*R. rattus*' as two species—*R. tanezumi* (the Asian type) and *R. rattus* (the Oceanian or European type). Hence, whenever I refer to "*R. rattus*" I shall be referring to members of the *R. rattus/tanezumi* species–complex (Musser and Carleton 2005). The Asian type (*R. tanezumi*) is apparently indigenous to

south-east Asia, generally north and east of peninsular India, with an introduced range extending from the Nicobar Islands in the west to Fiji in the east (Musser and Carleton 2005).

Today, over 80% of the world's major island groups host at least one of the rat trio reviewed here and rodent invasions are continuing (Atkinson 1985; Russell et al. 2008). This poses a major threat to native biota throughout the world (reviewed in Atkinson 1985; Courchamp et al. 2003; Atkinson and Towns 2005; Innes 2005a, b; Towns et al. 2006; Jones et al. 2008; and in this issue). Yet, there has been no attempt, to my knowledge, to quantify the global involvement of introduced rodents in small mammal extinctions and although their effects on insular birds have been widely studied (Atkinson 1985; Towns et al. 2006; Jones et al. 2008), significantly less attention has been paid to their effects on insular small mammals (although Towns et al. (2006) review some of the evidence). It is surprising that this subject has received such light coverage when we consider that the majority of modern era mammalian extinctions have occurred on islands, introduced rodents are ubiquitous but the vast majority of rodent species on islands are native or endemic, and there exists a voluminous literature on interspecific competition in native small mammal communities (Connell 1983; Schoener 1983; Atkinson 1985; MacPhee and Flemming 1999; Eccard and Ylönen 2003; Amori et al. 2008; Russell et al. 2008). The obvious potential for competition as well as disease/parasite transmission adds an extra dimension to introduced rodent impacts that is rarely discussed (although see Angel et al. 2008).

In this paper, I examine the support, from circumstantial evidence to replicated experiment, for the involvement of introduced rodents in extinction of and deleterious impacts on insular small mammals. Although I doubt that my coverage is exhaustive at the circumstantial end of the evidence scale, I have reviewed all studies, to my knowledge, that have involved monitoring during species manipulations (eradication, control and experiment). Where information is sufficient I discuss probable mechanisms of rodent impact. I conclude with recommendations to improve the quality and quantity of impact evidence, information that should help to prioritise and justify eradication or control programmes and biosecurity measures.

Introduced rodent involvement in insular small mammal extinctions

For this initial section of the review I used the CREO (the Committee on Recently Extinct Organisms) database "CREO list of mammal extinctions since AD 1500" (MacPhee and Flemming 2001), in conjunction with the literature to compile a list of insular small mammal species for which I could find some information to support a contribution of introduced rodents (*R. rattus*, *R. norvegicus*, *R. exulans* or *M. musculus*) to their extinction. This circumstantial 'evidence' is derived from fossil records, human observation and scientific collections. Purely speculative cases—i.e. those species for which I could find neither fossil nor observational evidence to support an impact of introduced rodents—have not been included in the list (Table 1). When counting the number of modern era, small mammal extinctions in the CREO database I included only resolved cases (50 species) plus cases that were categorised as unresolved because the species had not been formally described (10 species). A small mammal was defined as a species weighing less than 10 kg (MacPhee and Flemming 1999).

Of these 60 modern era extinctions of small mammals, 44 (73.3%) have occurred on islands. Of these insular extinctions introduced rodents were nominated by CREO as the sole "alleged extinction cause" in seven cases and as a possible contributing influence to the extinction of one other (*Nesophontes hypomicrus*). Of these eight cases I could find supporting 'evidence' in the literature for all species except *Oryzomys antillarum* of Jamaica, *Noronhomys vespuccii* of Noronha Island, Brazil and *N. hypomicrus* of Hispaniola (I categorise the former two as unknown in Fig. 1). This information is presented in Table 1. I also added two species listed by CREO with an alternative proposed extinction cause (two undescribed species of *Nesoryzomys* from Isabela Island, Galápagos Archipelago, Ecuador) to Table 1. So, of the 44 modern insular extinctions listed by CREO, I could find 'evidence' suggesting that introduced rodents (all *R. rattus*) were the main cause of extinction in 15.9% of cases (seven species including the two *Nesoryzomys* species of Isabela Island) (Table 1; Fig. 1). Of the cases with a known or suspected extinction cause, this represents 38.9% of cases. However, the extinction cause in most cases

is not known (Fig. 1). In addition to these seven species, *R. rattus* appears to have caused the modern era extinction of *Nesoryzomys indefessus* of Santa Cruz Island and Baltra Island, Galápagos and likely contributed to the pre-modern era extinction of *Rhagamys orthodon* of Corsica and Sardinia, Mediterranean Sea. Of the other introduced rodent species reviewed here, *R. exulans* is considered responsible for the pre-modern era extirpation of bat *Mystacina robusta* from the North and South Island of New Zealand, a species finally eliminated by *R. rattus* in the 1960s, and was probably at least partly involved in the pre-modern era extinction of *R. sanila* on New Ireland in the Bismarck Archipelago. The introduced *M. musculus* is convincingly implicated in just one (possibly pre-modern era) extinction: that of *Malpaisomys insularis* in the Canary Islands, Atlantic Ocean (Table 1).

I should emphasise that when I discuss extinction cause I refer only to ultimate, deterministic not proximate, stochastic drivers (e.g. inbreeding depression) although the latter may play an important role in small mammal declines and extinctions on islands, especially where introduced rodent impacts are chronic (see recent forum beginning with Jamieson 2007).

From Table 1 it is evident that the introduced black rat *R. rattus* has been the most often implicated in extinctions of native species. Despite the circumstantial and equivocal nature of most evidence the cause of extinction, in some cases, seems clear. The *R. rattus*-caused extinction of the Christmas Island (Indian Ocean) rodents, along with the proposed mechanism, is best supported. The observation that *R. rattus* had not spread across the entire island favours the theory of parasite or disease transmission over direct competitive or predatory impact (Andrews 1909 in Pickering and Norris 1996). The proposed involvement of *R. rattus* in the loss of the endemic Galápagos rodent fauna and a suite of Corsican mammals is less well evidenced. However, convincing cases exist within these groups (Clark 1984; Vigne and Valladas 1996; Harris 2006). Of seven endemic Galápagos rodent species extinctions, the evidence for *R. rattus* involvement is most convincing for the *Nesoryzomys* species of Santa Cruz Island, less persuasive for the *Nesoryzomys* of Isabela Island and debatable for the remaining three (Table 1; Patton et al. 1975; Steadman and Ray 1982; Clark 1984; Steadman et al. 1991;

Table 1 Evidence to support the contribution of introduced rodents to insular small mammal extinctions

Native species	Island(s)	Introduced species[a]	Candidate mechanism(s)	Supporting information
Malpaisomys insularis (Lava mouse)	Canary Islands (Fuertaventura, Lanzarote, and Graciosa), Atlantic Ocean	MM	Disease (Boye et al. 1992). Competition or disease (Hutterer et al. 1988)	Since the arrival (shortly before 2000 BP) of *M. musculus* on Fuerteventura, an increase in this species has coincided with a population decline in *M. insularis*. By 1730 BP *M. insularis* = 58.9% and *M. musculus* = 2.2% of the mammals and by 800 BP the percentages were 10.9 and 60.7%, respectively. *Rattus* species were not present during the extinction process (Boye et al. 1992)
Mystacina robusta (Greater short-tailed bat)	North Island, South Island and Stewart Island, New Zealand	RE	Predation and/or competition for food (Daniel 1979 in Daniel and Williams 1984)	Simultaneous disappearance of *M. robusta* and appearance of *R. exulans* in laughing owl middens (Lloyd 2005a)
				Fossil material dated prior to rat introduction contained short-tailed bats *Mystacina* spp. but remains are absent in post-rat age material (Worthy and Holdaway 1995)
	Big South Cape Island and Solomon Island, New Zealand	RR	Predation, competition for food or disturbance of nursery roosts (Daniel and Williams 1984)	Following arrival in the early 1960s, *R. rattus* reached plague numbers between 1964 and 1967. There was a rapid decline in bat numbers: very few flying bats were seen by 1965 and none were reported in 1966 (Lloyd 2005a)
Nesoryzomys darwini (Darwin's nesoryzomys)	Santa Cruz Island, Galápagos Archipelago, Ecuador	RR	Parasites/disease** (Clark 1984)	Between 1926 to 1930 an early settler observed that native rats were abundant from coast to summit but he saw no *R. rattus*. He left but returned in 1934 when he found *R. rattus* across the island but never saw native rats again (Clark 1984)
				J. P Chapin collected 14 *N. darwini* in the highlands in 1930. He caught only *R. rattus* in 1935 at a coastal site where both *N. darwini* and *N. indefessus* had been caught in 1929 (Clark 1984)
Nesoryzomys indefessus (Santa Cruz nesoryzomys)	Santa Cruz Island and Baltra Island, Galápagos Archipelago, Ecuador	RR	Parasites/disease** (Clark 1984)	See entry for *N. darwini* (above)
				Concurrent introduction of *R. rattus* to Santa Cruz and Baltra islands (Patton et al. 1975)
				Last collected in 1934 on Santa Cruz Island (Clark 1984)
Nesoryzomys sp. 2[b] (Undescribed species)	Isabela Island, Galápagos Archipelago, Ecuador	RR	None proposed	Became extinct post-1535 (Steadman et al. 1991) but known only from fossils which suggests early colonisation by *R. rattus* and resultant extinction prior to thorough scientific surveys (Steadman and Ray 1982; Steadman et al. 1991)
				Introduction of *R. rattus* during the 1800s (Patton et al. 1975)
Nesoryzomys sp. 3[b] (Undescribed species)	Isabela Island, Galápagos Archipelago, Ecuador	RR	None proposed	See above

Table 1 continued

Native species	Island(s)	Introduced species[a]	Candidate mechanism(s)	Supporting information
Oryzomys nelsoni (Nelson's oryzomys)	María Madre Island, Tres Marías Islands, Mexico	RR	Competition (Wilson 1991)	Found only in a limited area of small springs near the summit of the island in 1897. This area was revisited in 1976 but only *Rattus rattus* was found there and the latter was abundant and widespread on the island (Wilson 1991)
Rattus macleari (Maclear's rat)	Christmas Island, Indian Ocean	RR	Parasites/disease** (Andrews 1909 in Pickering and Norris 1996)	1897-1898 *R. macleari* is the most common mammal on the island and is present island wide
				1899 *R. rattus* introduced in a cargo of hay
				1901–1902 *R. rattus* abundant
				Specimens of *R. macleari* from around the settlement, where *R. rattus* is concentrated, are heavily infected with a trypanosome also found in the *R. rattus* specimens. Specimens of *R. macleari* away from the settlement are not infected
				1902–1903 Sick and dying rats observed around the island
				1904 No specimens of *R. macleari* found
				1908 Andrews pronounces the species extinct. (Pickering and Norris 1996 and references therein)
Rattus nativitatis (Bulldog rat)	Christmas Island, Indian Ocean	RR	Parasites/disease** (Andrews 1909 in Pickering and Norris 1996)	1897–1898 *R. nativitatis* is moderately abundant with a patchy distribution
				1899 *R. rattus* introduced in a cargo of hay
				1901–1902 *R. rattus* abundant
				R. nativitatis extremely rare
				1904 No specimens of *R. nativitatis* found
				1908 Andrews pronounces the species extinct. (Pickering and Norris 1996 and references therein)
				See also evidence for *R. macleari* above
Rattus sanila (New Ireland forest rat)	New Ireland, Bismarck Archipelago, Papua New Guinea	RE (and RP)	None proposed	Stratigraphic data from New Ireland reveals that the first remains of introduced *R. exulans* and *R. praetor* overlap with the last remains of *R. sanila* in a level dated at 3120 years ago, the approximate time that the latter became extinct. No other domestic animals were introduced at that time (Flannery 1995)

Table 1 continued

Native species	Island(s)	Introduced species[a]	Candidate mechanism(s)	Supporting information
Rhagamys orthodon (Tyrrhenian field rat)	Corsica and Sardinia, Mediterranean Sea	RR	Competition (Vigne and Marinval-Vigne 1991 in Vigne and Valladas 1996)	Stratigraphic data from Corsica shows a significant decrease in the frequency of *Rhagamys* at the level where *R. rattus* appeared (between the 4th and 2nd centuries BC). This event is separated, by 60 cm of sediments, from the extinction of *R. orthodon* suggesting that *R. rattus* may have contributed to, but not caused the extinction (Vigne and Valladas 1996) Late Roman or Medieval habitat destruction (deforestation) is thought to have caused the extinction. Yet, deforestation during the Neolithic agricultural expansion, in the absence of *R. rattus*, did not cause any small mammal extinctions (Vigne and Valladas 1996)

* Included within a sub-set of the CREO database composed of resolved extinctions and extinctions classified as unresolved because the species had not been formally described

** Evidence-based

[a] MM, *Mus musculus*; RE, *Rattus exulans*; RP, *Rattus praetor*; RR, *Rattus rattus*

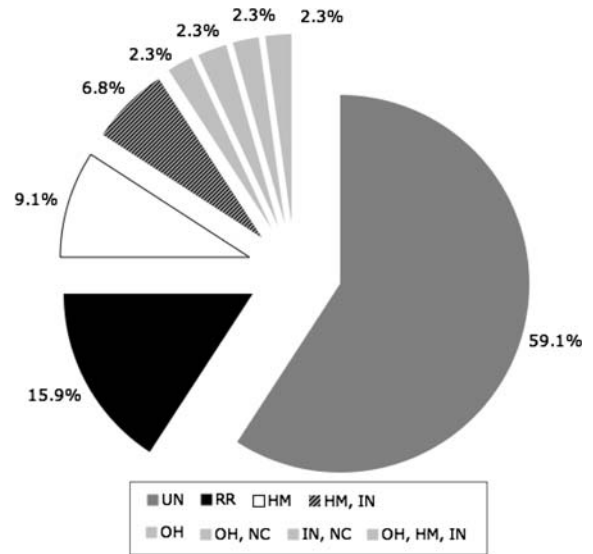[b] Name as listed in CREO (*Nesoryzomys* sp. 2 and 3)

Fig. 1 Percentage of insular small mammal extinctions since 1500 ($n = 44$) attributed to any or a combination of the following causes: UN, unknown; RR, *Rattus rattus*; HM, habitat modification (including eradication of food supplies); IN, introduced species other than rodents; OH, over-hunting; NC, natural cause. Data from MacPhee and Flemming (2001) with slight modification of alleged extinction cause categories and re-allocation of two species from RR to UN and two species from HM to RR

Hutterer and Oromí 1993; Dowler et al. 2000a). The rate with which the *Nesoryzomys* species were displaced on Santa Cruz Island favours disease transmission over competition (or predation) as the primary mechanism of displacement (Table 1). This hypothesis is further supported by an intriguing anecdote from Brosset (1963), who transferred 14 individuals of *Aegialomys galapagoensis bauri* (originally "*Oryzomys bauri*" but recently renamed by Weksler et al. 2006) from Santa Fe Island to Santa Cruz Island, where they were placed in an enclosure. They were observed in contact with *R. rattus* and all 14 *A. g. bauri* succumbed to a mystery illness within a week of their arrival. The involvement of *R. rattus* in the extinction of the bat *M. robusta* from its last island refuges off the south coast of New Zealand is also supported by strong circumstantial evidence (Table 1). These five cases: *M. robusta* (Big South Cape and Solomon islands), *R. macleari* and *R. nativitatis* (Christmas Island) and *Nesoryzomys darwini* and *N. indefessus* (Santa Cruz Island), detailed in Table 1 and summarised above are the most

convincing because the evidence involves direct observation in space and time. In all cases the establishment of *R. rattus* was quickly succeeded by the loss of the native species. The extinction of *M. robusta* followed the arrival and irruption of *R. rattus* and the Santa Cruz and Christmas island rodents also disappeared shortly after *R. rattus* introduction. In the latter case *R. macleari* were found to be heavily infected with a *R. rattus*-hosted trypanosome and sick and dying rats were found across the island shortly before their disappearance (details and references in Table 1). With the exception of the two Galápagos species and the two Christmas Island species, the mechanisms of displacement of the other species remain completely unresolved (Table 1).

Introduced rodents may also catalyse extinctions that are ultimately caused by other factors. Evidence suggests that the extinction of the endemic species *Prolagus sardus* (Lagomorpha, Ochotonidae), *Episoriculus corsicanus* (Soricidae), *R. orthodon* (Muridae) and *Tyrrhenicola henseli* (Microtidae) on the Mediterranean island of Corsica was caused, ultimately, by large scale deforestation during the Late Roman or Medieval period (Vigne and Valladas 1996). Yet, earlier anthropogenic deforestation on Corsica (during the Late Neolithic) involved no small mammal extinctions. This discrepancy may be explained by the absence of *R. rattus*, the introduction of which seems to have caused a decrease in the frequency of endemic species, especially *R. orthodon* (Table 1). It was concluded that if *R. rattus* did not cause the extinctions then it at least increased the sensitivity of these species to environmental change (Vigne and Valladas 1996). Introduced rodents may also indirectly facilitate small mammal extinctions through a process termed "hyperpredation". Patterns revealed in a study of the Australian mainland suggest that the principal cause of conilurine rodent decline is direct predation by foxes and cats in regions where predator abundance has been greatly elevated and sustained by the introduction and spread of rabbits and mice. It is also suggested that *R. rattus* may be responsible for increased cat impacts in sub coastal habitats. This theory of decline can be applied equally well to other endangered faunas including terrestrial marsupials which have undergone similar geographic patterns of decline (Smith and Quin 1996). This process may also occur on islands, where resources are often limited. For example, an introduced prey base of *R. rattus* may have enabled feral cats to push native golden bandicoots *Isoodon auratus* and hare-wallabies *Lagorchestes conspicillatus* to extinction on Hermite Island, Montebello Islands, Western Australia (K. Morris, pers. comm.).

The material presented in Table 1 and discussed in the preceding text demonstrates that introduced rodent impact may be inferred, convincingly in many cases, by circumstantial and observational accounts. More commonly, however, the cause of extinction simply cannot be isolated from a multitude of simultaneous threat factors that accompany human contact, colonisation and spread. For example, introduced *Rattus* may have contributed to the decline in diversity and abundance of rodents of the subfamily Capromyinae in Cuba, Hispaniola, Jamaica and Puerto Rico and the extinction of several endemic oryzomyine rodents as well as other small endemic mammals of the West Indies. However, other pressures include capture by man, habitat destruction and predation by feral cats, dogs and the mongoose (Pinchon 1967; Lescure 1979; Woods 1989; Alvarez and González 1991). Similarly, on Ambon Island in the Moluccas, Indonesia, introduced *R. rattus*, *R. exulans*, *M. musculus* and shrews may have displaced the native small mammal community that should be shared with Seram Island, to which Ambon Island had been historically joined. However, the extensive clearance of primary forest or the establishment of introduced predators may have driven these extinctions, alone or in concert with introduced rodents (Helgen 2003). Also unclear is the relative contribution of introduced *Rattus*, dogs and pigs to the extinction of two endemic terrestrial murids *Melomys spechti* and *Solomys spriggsarum* from Buka Island, Northern Solomon Islands, Papua New Guinea (Flannery 1995). In the Galápagos Archipelago, the historical distribution of extinct rodents is sympatric with that of feral cats while the extant species exist only on cat-free islands. Unfortunately the chronology of the cat introductions and spread is not known (Dowler et al. 2000a; Dexter et al. 2004).

Introduced rodent impact on extant insular small mammals—'correlative' evidence

While extinction cause is often indeterminable, the study of extant species obviously provides better

opportunities to link cause with population-level effect and explore the mechanisms of introduced rodent impacts. However, as for the extinct species, much of the available information is correlative which can again make it extremely difficult to tease apart rodent impacts from other factors. Nevertheless, compelling cases can be constructed from studies at multiple sites.

In Madagascar, *R. rattus* has penetrated remote, undisturbed, humid forest where it can be abundant while native rodent density and species richness are depressed (Goodman 1995; Goodman et al. 1996, 1997; Ganzhorn et al. 2003). Although the mechanism of displacement is uncertain, it is interesting to note the apparent absence of evidence for negative inter-specific impact at lower altitude sites relative to the distributional and abundance patterns observed at higher altitudes (Stephenson 1993, 1995; Stephenson et al. 1994; Goodman et al. 1996, 1997; Ramana-manjato and Ganzhorn 2001; Ganzhorn 2003; Ganzhorn et al. 2003). A mechanism that may help to explain this discrepancy and cast new light on the interactions between introduced and native rodents in Madagascar is disease transmission. With one exception, bubonic plague is known only at elevations above about 1,000 m. Within this zone there is evidence that the plague bacillus *Yersinia pestis* has transferred from introduced to native rodents via endemic fleas and then seems to have transferred to Tenrecinae. Experimental and serological evidence reveals that while about 30% of *Rattus* and 100% of tenrecids can survive an epizootic, plague is 100% fatal to native rodents (Duplantier and Duchemin 2003a, b; S. Goodman, pers. comm.). This could explain the mass mortality in *Brachytarsomys albicauda* (an endemic rodent) observed during an apparent plague epizootic in 1932 (Robic 1937 in Duplantier and Duchemin 2003b). This case clearly demonstrates the value of considering 'negative' as well as 'positive' evidence of introduced rodent impact because it was the altitude-dependence of interspecific impact that exposed this very plausible disease hypothesis.

In the Philippines, *R. rattus* and *R. exulans* are abundant in disturbed habitat but appear only able to establish in primary forests that support relatively depauperate small mammal faunas. For example, introduced rats are abundant in high-elevation, old-growth forest on the naturally species-poor islands of Negros (*R. exulans* and *R. rattus*) and Camiguin

(*R. exulans*) but they are absent or very rare in mature forest on Leyte, Luzon and Mindanao; islands with rich small mammal faunas (Heaney et al. 1989, 2003, 2006a, 2006b; Rickart et al. 1991). The effects of introduced rodents on native small mammals and the mechanisms by which the native exclude the intro-duced species are important research priorities in the Philippine Islands, a region with one of the highest concentrations of endemic mammals in the world (Heaney et al. 2003, 2006b; L. Heaney, pers. comm.). The Philippine research suggests that invasion resis-tance may be an important phenomenon in diverse native mammal communities. Unfortunately, habitat loss or modification is a real threat to the integrity of many native communities while introduced rodents may benefit from anthropogenic disturbance (e.g. Ganzhorn 2003). Habitat loss is not the only threat however, and even a healthy community in pristine habitat may be powerless in the face of a novel pathogen carried by an introduced rodent.

The introduction of trypanosome-infected *R. rattus* to Christmas Island may have led to the loss of the entire non-volant mammal community. The Christ-mas Island shrew *Crocidura trichura* was common in 1900, one year after the introduction of *R. rattus* but rare by 1909, shortly after the endemic *R. macleari* and *R. nativitatis* were declared extinct (Table 1). Although specimens were found in 1985, recent surveys to detect *C. trichura* were not successful. All three endemic species declined simultaneously fol-lowing the introduction of *R. rattus* (Hutterer 2005; Table 1) and this strengthens the argument for its involvement in their decline and extinction.

In other systems, presence/absence relationships for the same species at different sites might suggest introduced rodent-caused displacement. For example, in 1976, the Tres Marías deer mouse *Peromyscus madrensis* of the Tres Marías Islands, Mexico, was thriving on *R. rattus*-free María Cleofas Island. In contrast, it was only found away from human habita-tions, where *R. rattus* is common, on María Madre Island and had apparently disappeared from María Magdalena Island since the introduction of *R. rattus*, which was found across the island (Wilson 1991). However, alteration of the undergrowth by introduced herbivores on María Magdalena Island may have contributed to the extirpation (Wilson 1991). Also, the apparent absence or very low densities of the rare, endemic silver rice rat *Oryzomys palustris natator* on

Table 2 Insular small mammal species and sub-species considered threatened by introduced rodents in the IUCN Red List of Threatened Species

Species/sub-species and Red List category	Distribution	Relevant major threat type/s[a]	Information
Emballonura semicaudata[b] EN (Pacific sheath-tailed bat)	American Samoa; Fiji; Guam (regionally extinct); Micronesia, Federated States of; Palau; Samoa; Tonga; Vanuatu	2.2	Minor influence of introduced rats
Isoodon auratus barrowensis[c] VU (Golden bandicoot)	Hermite (extinct), Barrow and Middle islands off the Pilbara coast of Western Australia	2.1, 2.2	Competition with *R. rattus* may explain lower densities on Middle Island
Mesocapromys angelcabrerai[d] CR (Cabrera's hutia)	Cuba	2.1	Competition with introduced rats threatens survival
Mesocapromys auritus[e] CR (Eared hutia)	Cuba	2.1	Competition with introduced rats threatens survival
Neotoma floridana smalli[f] EN (Key Largo woodrat)	Key Largo, Florida, United States	2.1	Potential competition with *R. rattus*
Oryzomys galapagoensis[g] VU (Galápagos rice rat)	Santa Fe Island, Galápagos, Ecuador	2*	Possibility of alien rodent introduction is the primary threat to *O. g. bauri*
Nesoryzomys swarthi[h] VU (Santiago Galápagos mouse)	Santiago Island, Galápagos, Ecuador	2	Potential impact of introduced rodents (*R. rattus* and *M. musculus*)

[a] IUCN Red List—major threat types: 2, invasive alien species (directly affecting the species); 2.1, invasive alien species (directly affecting the species)—competitors; 2.2, invasive alien species (directly affecting the species)—predators

* Considered the only threat to this species. All other species are subject to multiple threats

[b] Chiroptera Specialist Group 2000

[c] Australasian Marsupial and Monotreme Specialist Group 1996

[d] Baillie 1996a

[e] Baillie 1996b

[f] Yensen and Kirkland 2000

[g] Gippoliti 2002

[h] Dowler et al. 2000b

islands in the Lower Florida Keys (e.g. Big Pine Key and Boca Chica Key) that contain apparently suitable habitat coincides with the presence of dense populations of *R. rattus* (Goodyear 1987; Forys et al. 1996; Mitchell 2000; Perry 2006).

More convincing evidence is, however, provided by rodent irruptions. Both the extinction of the greater short-tailed bat *M. robusta* (Table 1) and the extirpation of the endangered lesser short-tailed bat *M. tuberculata* followed an irruption of *R. rattus* on Big South Cape Island and Solomon Island, New Zealand. The mechanism of displacement is unclear but may involve one or more of predation, competition for food or disturbance of nursery roosts (Daniel and Williams 1984; Lloyd 2005a, b).

Similarly, increased local mortality of the New Zealand long-tailed bat *Chalinolobus tuberculatus* coincided with seed mast triggered irruptions of *R. rattus* in the Eglinton Valley in 1996 and 2000–2001 and resulted in population crashes in three separate colonies (O'Donnell 2005; Pryde et al. 2005; C. O'Donnell, pers. comm.). An impact of *R. rattus* on *C. tuberculatus* has now been confirmed via experimental rat control (C. O'Donnell, pers. comm.), the details of which are presented later in this review. Although the mechanism(s) of *R. rattus* impact on the New Zealand bat fauna remains unknown, rat predation is clearly a major threat to the endangered Mexican fishing bat *Myotis vivesi* on islands in the Gulf of California. The terrestrial

Table 3 Evidence for a negative effect of introduced rodents on insular small mammal populations from pre- and post-eradication monitoring and field experiments

Native species[a]	Introduced species[b]	Island(s)	Method of effect detection	Effect	Reference
Bettongia lesueur (Burrowing bettong)	RR	Boodie Island, Western Australia	Pre/post-eradication monitoring (post-eradication population from reintroduction)	Pre-eradication estimate of 20–50. This population became locally extinct during the baiting campaign but 36 individuals were reintroduced in 1993. The population is now (2002) believed to have reached 200–300 individuals	Morris 2002
Chalinolobus tuberculatus (New Zealand long-tailed bat)	RR	Eglinton Valley, Fiordland, South Island, New Zealand	Monitoring at two colonies treated with rat poison compared to a control colony	Pre-eradication distribution: limestone portion of the island. Post-eradication distribution: whole island	C. O'Donnell, pers. comm
				Intensive control programme conducted during a rat population irruption in 2006–2007. Preliminary analysis shows that survival was 20–30% higher in the 2 treatment colonies relative to the control colony that same year and 20–30% higher compared to survival during previous rat irruption years in the same colonies	
Crocidura russula (Greater white-toothed shrew)	RN	Tomé Island, English Channel Islands, French Atlantic	Pre/Post-Eradication Monitoring using live-traps	Abundance index (captures/trap night) increased by a factor of 9 and 17 at 1 and 2 years post-eradication	Pascal et al. 2005
Crocidura suaveolens (Lesser white-toothed shrew)	RN	Sept-Îles Archipelago[c], Brittany, France: Bono Island	Pre/Post-Eradication Monitoring using live-traps, with comparison to a control island	Pre-eradication distribution restricted to areas with less *R. norvegicus* compared to post-eradication spread across the island by 4 years after eradication. Abundance index (captures/trap night) increased by a factor of 15, 25 and 13 by 4, 5 and 10 years post-eradication.	Pascal et al. 2005
		Moines Island		Pre-eradication abundance index (captures/trap night) was zero. If it is presumed that the true value was the same as on Bono Island then the abundance index increased by a factor of 7 and 19 by 4 and 10 years post-eradication	
		Les Mottes Islets		Pre-eradication abundance index (captures/trap night) was zero. If it is presumed that the true value was the same as on Bono Island then the abundance index increased by a factor of 16 and 18 by 4 and 10 years post-eradication	
				Compared to maximum variation of the abundance index of 2.5 over 7 years on *R. norvegicus*-free Béniguet Island (Molène Archipelago)	
Crocidura suaveolens (Lesser white-toothed shrew)	RN	Trielen Island, Molène Archipelago, Brittany, France	Pre/Post-Eradication Monitoring using live-traps, with comparison to a control island	Abundance index (captures/trap night) increased by a factor of 32 by 8 years post-eradication.	Pascal et al. 2005

Table 3 continued

Native species[a]	Introduced species[b]	Island(s)	Method of effect detection	Effect	Reference
				Compared to maximum variation of the abundance index of 2.5 over 7 years on *R. norvegicus*-free Béniguet Island (Molène Archipelago)	
Isoodon auratus barrowensis (Golden bandicoot)	RR	Middle Island, Western Australia	Pre/Post-Eradication Monitoring using live-traps	Abundance index (trap success rate %) increased by a factor of 5 by 7 years post-eradication	Morris 2002
Leggadina lakedownensis (Lakeland Downs short-tailed mouse)	MM	Thevenard Island, Western Australia	Monitoring on trapping grids (two with selective poison bait stations at 10 m spacing, two with the bait stations at 20 m spacing and two unbaited control grids)	On one of the grids with selective poison bait stations spaced at 10 m the abundance of *M. musculus* decreased by 83% (the greatest decline on all the baited grids) and this was correlated with an 86% increase in the abundance of *L. lakedownensis* (the only grid to show a trend in abundance of *L. lakedownensis*) Survivorship of *L. lakedownensis* increased over time on the 10 m baited grids[d]	Moro 2001
Nesoryzomys swarthi (Santiago nesoryzomys)	RR	Santiago Island, Galápagos Archipelago, Ecuador	Removal Experiment—using a balanced, "randomized block" design (Hurlbert 1984). Three blocks of grids. Each block: a control grid and adjacent *R. rattus* removal grid	The immigration rate of female *N. swarthi* increased by 27.6% following initiation of *R. rattus* removal, relative to a decline in immigration onto control grids. This slowed the rate of seasonal population decline of *N. swarthi* on the removal relative to control grids	Harris and Macdonald 2007
Peromyscus maniculatus anacapae (Anacapa deer mouse)	RR	Anacapa Island (composed of East, Middle and West Anacapa islands), Southern California	Pre/Post-Eradication Monitoring (post-eradication population from reintroduction) using live traps (mark/recapture)	Density (mice/ha) increased by a factor of 2.3 by 2 years post-eradication on Middle Anacapa Island ($n = 2$ trap grids), 1.5 by 3 years post-eradication on East Anacapa Island ($n = 2$ trap grids) and 1.1 by 2 years post-eradication on West Anacapa Island ($n = 1$ trap grid)	Gellerman 2007
Sminthopsis griseoventer boullangerensis (Gray-bellied dunnart)	MM	Boullanger Island, Western Australia	Removal Experiment—Three *M. musculus* removal plots and three control plots. Monitored *S. g. boullangerensis* for 35 months with *M. musculus* removal starting at month 5	Abundance (pooled) of *S. g. boullangerensis* was initially similar on the removal and control plots but became consistently higher (up to a factor of 4) on the *M. musculus* removal plots after initiation of *M. musculus* removal	Dickman 1992

Table 3 continued

Native species[a]	Introduced species[b]	Island(s)	Method of effect detection	Effect	Reference
Sorex monticolus (Dusky shrew)	RN	Langara Island, British Columbia, Canada	Pre/Post-Eradication Monitoring on Langara Island using snap-traps	Abundance index (captures/100 trap nights) on Langara Island increased by a factor of 2.4 by 4 years post-eradication	Taylor et al. 2000; Drever 2002

[a] All species are native except C. russula that invaded continental France north of the Loire River and was introduced to the Channel and Atlantic French islands during the Holocene. C. suaveolens, native to the north of France, is presently considered cryptogenic to the French Atlantic and Channel Islands (Pascal et al. 2006; M. Pascal, pers. comm.)

[b] MM, Mus musculus domesticus; RN, Rattus norvegicus; RR, Rattus rattus

[c] Bono, Moines and Les Mottes islands are connected during low tide by a pebble isthmus

[d] Comparative data for the other grid types is unavailable

roosting habits (among rocks and in rock crevices) of this bat makes it particularly vulnerable. On some islands with introduced rats it is found only in relatively inaccessible rock crevices while on others it has completely disappeared (Villa 1979; Herrera-Montalvo and Flores-Martinez 2001). Observations of active hunting by large numbers of rats among the rock slides, observed attack and killing of two M. vivesi by R. norvegicus on San Esteban Island, and an individual R. norvegicus killing a specimen of M. vivesi while the latter was held in a collection sack further substantiates the rat predation hypothesis (Maya 1968 in Blood and Clark 1998; Villa 1979).

To complete this part of the review I searched the IUCN Red List of Threatened Species (IUCN 2006) for any insular small mammals that may be threatened, at least in part, by introduced rodents (any of the three Rattus or M. musculus). I used the following search criteria: Text search: MAMMALIA; Modifier: Exact phrase; Search in: Whole database; Major threat types: 2 (invasive alien species (directly affecting the species)); Systems: Terrestrial; Taxa: Species, Subspecies/varieties, Stocks/subpopulations and the default options were used for the other search terms. I also ran a second search identical to the first except for Major threat types: 1.5 (invasive alien species (directly impacting habitat)). After reviewing the species/sub-species information sheets for a specific mention of introduced rodents, I identified just five insular species and two insular sub-species (Table 2). Of these, evidence for an impact of R. rattus can be found for one species (Nesoryzomys swarthi) and one subspecies (Isoodon auratus barrowensis) later in this review. No additional species/sub-species were found in the second search.

Introduced rodent impact on extant insular small mammals—'experimental' evidence

So far in this review all evidence of introduced rodent impact on extinct and extant insular small mammals has been correlative. Although much of this evidence is compelling, for example, the disease transmission hypothesis in Madagascar and the circumstantial evidence deriving from rat irruptions in New Zealand, a population-level impact of introduced rodents is most reliably demonstrated by monitoring the response of a native species to introduced rodent

repression (species removal experiment or a control programme) or eradication. In this sense, control and eradication programmes can be viewed as experiments. Hence, in this section I compile 'experimental' evidence.

All of the reviewed studies provided evidence for a negative effect, at the population-level, of introduced rodents on insular small mammals. The evidence in Table 3 supports a strong interaction between *R. norvegicus* and shrews (*Crocidura suaveolens*, *C. russula* and *Sorex monticolus*). An increase in the abundance of *C. suaveolens* followed the eradication of *R. norvegicus* on four islands; three in the Sept–Îles Archipelago and one in the Molène Archipelago (Brittany, France). Furthermore, the response to eradication can be separated from any effects of environmental variation by comparison to the population dynamics on rat-free Béniguet Island (Molène Archipelago) illustrating the value of comparative 'control' data (Pascal et al. 2005). The repression of the dusky shrew *S. monticolus* was also lifted by the eradication of *R. norvegicus* on Langara Island, British Columbia (Canada). Despite some exposure to the poison bait the post-eradication abundance exceeded pre-eradication levels (Howald 1997; Taylor et al. 2000; Drever 2002). Pre- to post- eradication changes in abundance provided evidence of *R. rattus* repression of the two Western Australian marsupials *Bettongia lesueur* (Boodie Island) and *I. a. barrowensis* (Middle Island) as well as the Anacapa deer mouse *Peromyscus maniculatus anacapae* of Anacapa Island, Southern California (Morris 2002; Gellerman 2007). Post-eradication expansion across entire islands strongly suggested that two species (*C. suaveolens* and *B. lesueur*) had been locally displaced by introduced *Rattus* species (Morris 2002; Pascal et al. 2005). The possibility that *C. suaveolens* was actually absent from Les Mottes Islets (Brittany, France) and has recolonised from a neighbouring island since the eradication of *R. norvegicus* also supports this theory (Pascal et al. 2005). Introduced rodent control programmes may also provide useful data as illustrated by the greater survival of the New Zealand long-tailed bat *C. tuberculatus* in *R. rattus*-poisoned colonies versus a control colony during a *R. rattus* irruption year. Survival in the poison baited colonies also exceeded that of previous irruption years when rats were not controlled (C. O'Donnell, pers. comm.). In addition, a trial selective poisoning

programme revealed that *M. m. domesticus* represses the abundance and possibly the survival of the native mouse *Leggadina lakedownensis* on Thevenard Island, Western Australia (Moro 2001). Certainly, *M. m. domesticus* has a strong repressive effect on the abundance of the gray-bellied dunnart *Sminthopsis griseoventer boullangerensis* of Boullanger Island, Western Australia, as demonstrated during a replicated *M. m. domesticus* removal experiment (Dickman 1992). Finally, a 10 month replicated *R. rattus* removal experiment revealed evidence for a competitive impact of *R. rattus* on the endemic rice rat *N. swarthi* of Santiago Island, Galápagos (Harris and Macdonald 2007).

These studies provide clear demonstrations of introduced rodent impact on insular small mammals. However, the mechanism of impact is unknown in all cases except one. By monitoring the response of *N. swarthi* and *R. rattus* to a replicated resource supplementation experiment with patchy, scattered and no supplementary food (control) grids, Harris and Macdonald (2007) were able to identify the mechanism of impact as interference competition (by aggressive encounter). This is because despite gaining mass, the immigration and residency of female, relative to male *N. swarthi*, were repressed in response to an increase in *R. rattus* density regardless of the extra food and the dispersion of the food. Results from both this experiment and a *R. rattus* removal experiment permitted the elimination of alternative mechanisms (Harris and Macdonald 2007).

Discussion

Impact

Introduced rodents are often the prime suspects when hypothesising about probable causes of extinction and endangerment in small mammal species on islands (e.g. Clark 1984; Goodyear 1992; Carleton and Olson 1999). In support of such conjecture, I have reviewed some compelling circumstantial, correlative and experimental evidence. However, one of the main problems with much of the non-experimental data is the frustrating inability to eliminate alternative hypotheses such as habitat degradation or the impact of other introduced species (e.g. Helgen

2003). Even when confounding factors can be ruled out it is usually impossible to isolate the mechanism of introduced rodent impact because competition, predation, disease or all three may contribute to the observed patterns of decline and extinction in native mammals (e.g. Daniel and Williams 1984; Hutterer et al. 1988; Pascal et al. 2005). Nevertheless, in recent years, the opportunity to identify, quantify and explore introduced rodent impact has been exploited during eradication campaigns and by field experiment. This work, reviewed here, provides the most convincing support for a causal relationship between the presence of introduced rodents and the decline or extinction of native small mammals on islands because system manipulation allows the elimination of confounding factors. However, although all of the experimental studies of which I am aware demonstrated a negative effect of introduced rodents, studies that conclude no effect or are inconclusive may remain unpublished.

Of the four introduced rodents reviewed here, *R. rattus* has been linked to the vast majority of extinctions and current impacts on native insular small mammal species. This finding concords with two recent global impact reviews: Towns et al. (2006) found that of the three *Rattus* species, *R. rattus* is associated with declines or extinctions of the greatest number of native vertebrate species (60 species) and has recorded effects on the widest range of species. Similarly, Jones et al. (2008) found that *R. rattus* preyed on the most seabird species and had the largest mean seabird population impact of the three *Rattus* species. The extensive anthropogenic spread of *R. rattus* to islands across the globe in conjunction with its ecological plasticity may explain why it has accumulated recorded effects on the most native vertebrate species (Clark 1980; Towns et al. 2006; Global Invasive Species Database 2007). By comparison, *R. norvegicus* is also widespread but is more common at higher northern and southern latitudes and tends to be restricted to human-modified habitats in the warmer parts of its range (Musser and Carleton 2005; e.g. Traveset et al. 2008). Furthermore, it is mainly terrestrial while *R. rattus* and *R. exulans* are adapted for both terrestrial and arboreal activity (Musser and Carleton 2005). The latter has the most restricted distribution of the three *Rattus* species and its Pacific confinement (Musser and Carleton 2005) may explain the relative paucity of documented

impacts on small mammals by this rat. Finally, while the inter-island distribution of *M. musculus* may not be limited by introduced rats there is accumulating evidence that its density is repressed by the latter and interference competition has been demonstrated (Micol and Jouventin 2002; Russell and Clout 2004; Caut et al. 2007; Harris and Macdonald 2007; Witmer et al. 2007). An increase in reported mouse impacts could therefore be imminent as mice are proving difficult to eradicate and are being left behind as the last introduced mammal in an increasing number of island restoration projects. When freed from the constraints of competition and predation introduced mice may inflict substantial damage (Howald et al. 2007; Wanless et al. 2007; Angel et al. 2008; Simberloff 2008). For example, the summer density of *M. m. domesticus* reaches 700 mice per hectare on Boullanger Island, where it is the only introduced mammal (A. Burbidge, pers. comm.), and strong repression of the critically endangered marsupial *S. g. boullangerensis* has been demonstrated (Table 3; Dickman 1992). On this note, the competitive release of *M. musculus* following the eradication of introduced *Rattus* populations could result in underestimation of *Rattus* impact on native species as ascertained by pre-and post-eradication monitoring data.

In conclusion, the suggestion that *R. rattus* is the most detrimental of the introduced rodents per se has to be viewed with some caution. This hypothesis is yet to be tested through the provision of better evidence, from experiments and eradication/control programmes (e.g. Towns 2008).

Mechanism

It should be easier to elucidate mechanisms of biotic interaction in invaded relative to natural communities because of the limited opportunity for coevolution between the introduced and the native species (Mooney and Cleland 2001), yet only one study in this review has demonstrated a mechanism convincingly (interspecific interference competition—Harris and Macdonald 2007). While niche overlap between introduced rodents and insular small mammals has been identified by studies of resource and microhabitat use (Goodyear 1992; Goodman 1995; Gregory 2006; Harris et al. 2006) further investigation is required before resource competition can be confirmed. In contrast to our lack of knowledge

regarding the importance of interspecific competition between introduced rodents and native small mammals, a great deal is known about small mammal interactions in natural communities. Many experimental studies in rodent communities have provided evidence of competition (reviewed in Connell 1983; Schoener 1983; Eccard and Ylönen 2003). For example, 17 of 19 studies on rodents detected competition in a review by Schoener (1983). Although this manipulative field approach has been used to study competition between introduced and native rodents (mainland examples: Fox and Pople 1984; Stokes et al. 2006 and insular example: Harris and Macdonald 2007), case studies are rare. The reason for this discrepancy is unclear. Where it occurs, competition between introduced and native species should be more intense (than native—native competition) due to the limited time for character displacement and niche separation to evolve (e.g. Goodyear 1992; Petren and Case 1996 and references therein; Mooney and Cleland 2001). It seems that the lack of evidence for competition may well reflect a lack of experimental research in this field.

Disease transmission appears to have caused at least four of the 11 extinctions for which I could find evidence of introduced rodent involvement and may represent the main threat to the endemic Madagascan rodent fauna. This suggests that the transmission of novel parasites and diseases from introduced rodents to native small mammals (e.g. Pickering and Norris 1996; Goodman and Benstead 2003; Asakawa 2005; Smith and Carpenter 2006) should be a significant cause for concern. Rodent eradication may no longer be the silver bullet under such circumstances and conservation plans may need to be revised.

8The evidence for predation of insular small mammals by introduced rodents is limited. One problem is the inability to distinguish between predation of live animals and scavenging. For example, fragments of the bat *M. vivesi* were found in stomachs of *R. rattus* on Rasa Island, Gulf of California (J. Flores, pers. comm.) and *R. rattus* were observed in two fallen roost trees in Northland, New Zealand, in which 29 of 40 skeletons of the bat *M. tuberculata* were discovered with signs of rat predation (Lloyd 2005b). In neither case, however, can we conclude that the rats killed the bats. Long-term video surveillance reveals predation at colonial summer roosts of *M. tuberculata* to be rare (Lloyd 2005b). More convincing, however, is the

combination of reports of *R. norvegicus* killing *M. vivesi*, observations of rats hunting in rockslides and the disappearance of *M. vivesi* from rat-inhabited islands in the Gulf of California (Maya 1968 in Blood and Clark 1998; Villa 1979; Herrera-Montalvo and Flores-Martinez 2001). The evidence for predation of insular rodents is also limited: there have been observations of *R. rattus* preying on newborn *O. p. natator* in the Lower Florida Keys (Forys et al. 1996) and adult *P. m. anacapae* on Anacapa Island (Gellerman 2007) but the frequency and impact of this behaviour is unknown.

It is now recognised that an understanding of mechanism can increase the efficiency of management action (Park 2004). For example, by identifying the mechanism of competition as encounter interference competition, rather than indirect exploitation competition, El Niño episodes or wet years with their associated resource booms might be considered potential risk periods for *N. swarthi* on Santiago Island, Galápagos. This is because the predicted boom in *R. rattus* is likely to outweigh any advantage of the flourishing resource base to *N. swarthi*. Vegetation recovery following the recently completed eradication of introduced herbivores may similarly enhance resource levels, perhaps tipping the competitive advantage in favour of the *r*-selected *R. rattus* so the system should be closely monitored (Harris 2006; Harris and Macdonald 2007).

The importance of impact evidence

As our ability to eradicate rodents continues to improve we have greater capacity to protect threatened species and restore island ecosystems (Towns et al. 2006; Howald et al. 2007). However, evidence of negative impacts by introduced rodents is essential to enable us to prioritise and justify eradication campaigns and funds (Towns et al. 2006). Furthermore, while selective poisoning of introduced rodents is possible on smaller islands, eradication attempts on large islands with native small mammals are high-risk operations due to the necessity for aerial dispersal of bait and thus the high probability of non-target poisoning. In such situations, captive holding/breeding or translocation (followed by reintroduction) may be necessary to protect a viable subset of the native small mammal population. It is important in any eradication campaign but particularly where the risk of poisoning

non-target species is high, that we have evidence of the negative impacts of introduced rodents so that we can weigh up the projected benefits of eradication against the risks associated with ex-situ management and non-target in-situ loss. Reliable impact evidence should also help to convince opposition groups (Towns et al. 2006) who may be particularly concerned about poisoning campaigns involving non-target effects and who may even claim that there is no credible evidence of introduced rodent impacts on native flora and fauna (e.g. Craig 1986 in Towns et al. 2006). Where evidence is not available for a particular species or ecosystem, robust data for a similar species or ecosystem could potentially be used to illustrate the effects of introduced rodents.

Recommendations

The literature reviewed in the 'experimental' evidence section is a testament to the scientific potential of eradication programmes as large-scale experiments, especially where results can be compared to a 'control' island or islands. It is crucial, in this age of increasingly ambitious eradication campaigns, that the opportunities for pre- and post- eradication monitoring are seized so that we can quantify the impacts of introduced species (Lorvelec and Pascal 2005; Pascal et al. 2005; Towns et al. 2006; Howald et al. 2007; Jones et al. 2008). Where non-discriminatory baiting is the only option to achieve eradication it is important to ensure that good quality baseline data is collected prior to native species mitigation (translocation, captive holding etc.) for comparison to data from post-eradication/reintroduction monitoring. The post-eradication monitoring period must be of sufficient duration to detect an effect of rodent removal. This period will be determined by the life history of the native species and where appropriate the ex-situ mitigation measures employed (e.g. translocation and reintroduction) or the in-situ impact (e.g. non-target poisoning).

The benefits of an adaptive management or "research-by-management" (Innes et al. 1999) approach to tackling introduced species are becoming increasingly expounded upon in the scientific literature with an emphasis on management experimentation. This includes viewing control and eradication programmes as experiments, at an ecosystem level, with monitoring of native species before, during and after introduced species removal. Even better, a preliminary experimental approach involving localised replicated species removal can provide quantitative evidence of the impact of the introduced species on native species/ecosystems. Such an approach should allay ethical fears and uncertainty regarding the benefits of introduced species removal while simultaneously advising on feasibility and predicting consequences of control/eradication prior to the initiation of an expensive campaign (Courchamp et al. 2003; Park 2004; Towns et al. 2006).

A variety of techniques can be applied to explore the potential mechanisms driving the impacts of introduced rodents on native small mammals. Removal experiments, resource manipulation experiments and behavioural observation can all be used to investigate mechanisms of competition (e.g. Ovadia et al. 2005; Stokes et al. 2006; Harris and Macdonald 2007). Predation can be detected and quantified using one or more of direct observation (e.g. Gellerman 2007), filming nests (e.g. Wanless et al. 2007), radio tracking (e.g. Sommer 2000), spool and line tracking (see methods in Harris et al. 2006), fluorescent powder tracking (e.g. Fellers 2000) and dietary analysis techniques (e.g. Caut et al. 2008). The detection of introduced parasites could be greatly facilitated by conducting parasitological surveys of insular small mammal species and communities that may become exposed to introduced rodents. Alternatively, where baseline parasitological data are absent and introduced rodents are present, comparisons of parasite fauna of native populations in the presence and absence of the introduced rodent (e.g. on island archipelagos—Smith and Carpenter 2006) should be conducted. Rigorous tests can then be employed to assess the immunological, demographic, and ecological impacts of introduced parasites. As the removal of the introduced host may cause the impact of a shared, introduced parasite to intensify, the fate of shared parasites following rodent eradications is an important research priority (Smith and Carpenter 2006).

Increased research effort on the impacts of introduced rodents on insular small mammals should be part of a greater, global attempt to direct much-needed attention to the latter. If we fail to bring these less charismatic members of island communities into the conservation spotlight a large number of small mammal extinctions may be imminent (Amori et al.

2008). This review suggests that since 1500 the introduced rodents *R. rattus*, *R. norvegicus*, *R. exulans,* and *M. musculus* have together caused at least 16% of insular small mammal species extinctions. As the cause of insular small mammal extinctions remains unknown in 59% of cases, 16% is a minimum estimate that may, in reality, be much higher. Furthermore, based on the knowledge currently available, the threat of introduced rodents to extant insular small mammals seems low when we consider that just five species and two sub-species are believed to be affected by introduced rodents according to the IUCN Red List (IUCN 2006). Two factors suggest that the impact of introduced rodents has been underestimated: firstly rats have reached over 80% of the world's major island groups (Atkinson 1985) and secondly, whenever the interaction between introduced rodents and native, insular small mammals has been subject to experimental investigation a negative impact has been found.

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