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INVASIVE RODENTS ON ISLANDS

Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats?

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Abstract Research on the impacts of house mice *Mus musculus* introduced to islands is patchy across most of the species' global range, except on islands of the Southern Ocean. Here we review mouse impacts on Southern Ocean islands' plants, invertebrates, land birds and seabirds, and describe the kinds of effects that can be expected elsewhere. A key finding is that where mice occur as part of a complex of invasive mammals, especially other rodents, their densities appear to be suppressed and rat-like impacts have not been reported. Where mice are the only introduced mammal, a greater range of native biota is impacted and the impacts are most severe, and include the only examples of predation on seabird eggs and chicks. Thus mice can have devastating, irreversible and ecosystem-changing effects on islands, impacts typically associated with introduced rats *Rattus* spp. Island restoration projects should routinely include mouse eradication or manage mouse impacts.

Keywords Ecosystem impacts · Introduced mammals · Invasive alien species · Islands · *Mus musculus* · Southern Ocean

Introduction

The impacts of invasive alien mammals are most profound on insular fauna, flora and ecosystems (Diamond 1989; Williamson 1996). In particular, the predatory impacts of rats *Rattus rattus, R. norvegicus* and *R. exulans*, cats *Felis catus* and pigs *Sus scrofa* on insular ecology and charismatic fauna such as seabirds are such that their eradication from islands has progressed apace (Veitch and Clout 2002; Courchamp et al. 2003; Parkes and Murphy 2003; Towns and Broome 2003; Nogales et al. 2004; Howald et al. 2007; Jones et al. 2008). House mice *Mus musculus* are one of the most widespread invasive mammals on earth, and amongst vertebrates the breadth of their global distribution is second only to that of humans (Bronson 1979; Brooke and Hilton 2002). Despite this, there has been little island conservation action devoted to mice, relative to other introduced mammals (Wanless et al. 2007; Howald et al. 2007). Why has one of the most commonly introduced mammals

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on islands been so widely ignored by island conservation programmes? Two reasons are suggested. First is the relative paucity of described impacts on charismatic fauna (cf. Fritts and Rodda 1998), or lack of devastating herbivory, e.g. by goats *Capra hircus* (Campbell and Donlan 2005), especially relative to the impacts of other introduced mammals. Second, a higher percentage of mouse eradications has failed compared to *Rattus* spp. eradications (38 vs. 5–10%, Howald et al. 2007; MacKay et al. 2008), although the reasons for the higher rate of failed mouse campaigns remain unclear (MacKay et al. 2008). These factors have probably contributed to the slow development of technology for successful mouse eradications, and the patchy coverage of eradication attempts, relative to rat eradications.

Purpose of this review

The impacts of introduced mice on seabirds have only recently been assessed critically, in contrast to studies of their impacts on other biota from Southern Ocean islands; here we review all their described impacts. The impacts of mice preying on island-endemic invertebrates and causing extinctions, e.g. on Antipodes Island (Marris 2000) and Marion Island (Chown et al. 2002) or precipitating potentially irreversible changes to ecosystem functioning, e.g. Marion Island (Smith et al. 2002), have, to the best of our knowledge, failed to generate wide scientific, popular or conservation interest. By contrast, descriptions of conclusive proof that mice were preying on Gough Island's seabirds (Angel et al. 2005; Wanless et al. 2005) led to substantial media interest (e.g. Marris 2005; Dangerfield 2006; Pearce 2006), an unsolicited offer of support for eradication from the New Zealand Department of Conservation (G. M. Hilton, personal communication) and the establishment of an advisory group to raise funds for and oversee a process aimed at eradicating mice (Angel and Cooper 2006). The subsequent publication describing those impacts in a peer-reviewed, international journal (Wanless et al. 2007) led to renewed media interest (e.g. Millius 2007). The relative importance of conserving endemic invertebrates or plants is, in theory, the same as conserving charismatic fauna such as albatrosses. However, the evidence suggests that in reality, less visible fauna and flora tend not to generate sympathetic responses or to drive island conservation actions. It is our belief that negative impacts of mice on any insular systems, either direct or indirect (such as through changing nutrient cycles, synergy with other invasive species or changes to other major ecosystem processes) are sufficient grounds to merit remedial action as a high conservation priority. Demonstrating negative impacts on charismatic species such as seabirds should not be a pre-requisite for planning or securing funding for island conservation and restoration projects.

Here we summarise the impacts of mice on the plants, invertebrates and native birds of the islands of the Southern Ocean. The regional focus is chosen because various national Antarctic research programmes have facilitated the publishing of a substantive body of relevant research within the biogeographic setting. Special focus is given to those islands where mice are currently the only invasive mammal, some of which have been particularly well studied, and these studies describe the kinds of impacts that could be expected elsewhere, in more temperate and tropical systems where such studies are lacking. The aim of this review is to describe the distribution of introduced house mice on islands in the Southern Ocean and to draw attention to the importance of mouse impacts on island ecosystems, impacts that may be overlooked or (more probably) suppressed on islands where mice occur together with other introduced mammals. The long-term consequences of the impacts, both direct and indirect, of invasive house mice are as important to consider as the impacts of more widely studied invasive mammals on islands. Finally, we point to the importance of including the management of mouse impacts in island restoration programmes.

Regional distribution of mice

The house mouse is one of the most widely introduced mammals on oceanic islands, occurring on >200 islands where Red-listed birds are also found (Brooke and Hilton 2002; Brooke et al. 2007; G. M. Hilton, personal communication). However, it is seldom the only introduced species (Berry et al. 1978; Bronson 1979; Brooke et al. 2007). Thus, across most of their non-native range, the impacts of mice on island biota appear to be difficult to separate from those of other introduced mammal species.

For the purposes of this review, we have defined the Southern Ocean to include islands slightly to the north of the Subtropical Convergence (such as Tristan da Cunha, Amsterdam and St Paul) and islands well south of the Antarctic Convergence (Heard and McDonald) (Fig. 1). Only oceanic islands are considered. Antipodes and Gough islands have mice as the only introduced mammal (King 1990; Jones et al. 2003a; Angel and Cooper 2006). On Marion Island, mice have been present since the 1800s (Jansen van Vuuren and Chown 2007), whereas the domestic cat was introduced in the 1950s and eradicated in the early 1990s (Bester et al. 2000). On the French islands of St Paul and Australie (Kerguelen group), mice remain after successful eradications of ship rats *Rattus rattus* and rabbits *Oryctolagus cuniculus*, in both cases the only other introduced mammals (Micol and Jouventin 2002, T. Micol, in litt.). All other Southern Ocean islands/island groups either lack mice or currently have other mammals in addition to mice (Table 1).

Fig. 1 Islands of the Southern Ocean. Islands with house mice as the only introduced mammal currently present are indicated by arrows

Impacts on flora

On Antipodes Island, sedge species, in particular the native *Carex appressa*, attract large concentrations of mice that feed extensively on the inflorescences and seeds (Godley 1989). A more recent diet study found a large percentage of mouse diet on the Antipodes to consist of native sedges and plants in general (McIntosh 2001). On Gough Island at least 15 species of endemic or native as well as seven introduced plant species are consumed by mice (Jones et al. 2003a). The flower heads and fruiting bodies of the native tussock grasses *Spartina arundinacea* and *Parodiochloa flabellata* are chewed extensively by mice as are the seeds of the herbaceous *Acaena sarmentosa*, and endemic sedges *Carex* spp. and *Scirpus* spp. (Wace 1986; Jones et al. 2003a). On Macquarie Island mice consume a range of native plant species, some of which are available throughout the year (Copson 1986). Comparative studies between mouse-free Prince Edward Island and Marion Island are to date the most comprehensive with regards to the impacts that mice have on Southern Ocean island flora. The mice on Marion Island feed on the seeds and young shoots of at least five native and one introduced plant species. In the late 1960s the native sedge *Uncinia compacta* was abundant in mire vegetation (Huntley 1971) but has now almost been extirpated from this habitat on Marion due to seed predation by mice (Smith and Steenkamp 1990). Mice remove up to 75% of all the seed heads of this native plant, significantly reducing the population compared to the neighbouring mouse-free island of Prince Edward (Chown and Smith 1993). Given the long time that mice have been present on Marion Island and the relatively rapid decrease observed in this sedge species, it is possible that diet switches by mice caused similar impacts (or even extinctions) on other native/endemic species, before plant distributions and densities were mapped. Mice are also thought to be having a similar impact on the herbaceous *Acaena magellanica* (Avenant 1999) and damage the peat-forming *Azorella selago* (a disturbance-sensitive cushion plant) by burrowing into it (Chown and Cooper 1995). On Guillou Island (Kerguelen group), the seeds and flowers of the indigenous *Acaena magellanica* were among the main plant items consumed during summer (Le Roux et al. 2002). These studies all suggest a preference for

Table 1 Invasive mammal taxa extant and recently (since the start of large-scale, widespread eradications, *ca* mid-1970s) eradicated/died out from oceanic islands of the Southern Ocean

Main island - associated islands	Area (km^2)	Extant introduced mammals	Eradicated or died out in last 30 years	References
Tristan da Cunha	94	Rats, house mice, sheep, cattle	Cats	Richardson (1984), Angel and Cooper (2006)
Nightingale	4	None		Holdgate (1969)
Inaccessible	14	None		Ryan and Glass (2001), Ryan (2005)
Gough	64	House mice		Richardson (1984), Angel and Cooper (2006)
Bouvet	47	None		RMW (personal observation)
Marion	290	House mice	Cats	Bester et al. (2000), Jansen van Vuuren and Chown (2007)
Prince Edward	45	None		Crafford and Scholtz (1987), Anon (2006)
Crozet	352			
Possession	150	Rats		Chapuis et al. (1994), Frenot et al. (2004)
Cochons	67	House mice, cats, rabbits		Chapuis et al. (1994), Micol and Jouventin (2002)
Est	130	Rabbits		
Kerguelen (>20 large islands)	7200	Rats, house mice, cats, mouflon, sheep, reindeer, rabbits	Rats, rabbits from some islands	Chapuis et al. (1994), Frenot et al. (2004)
Australie	21	House mice	Rats, rabbits	
Amsterdam	55	Rats, house mice, cats, cattle		Chapuis et al. (1994), Micol and Jouventin (2002)
St. Paul	6	House mice	Rats, rabbits(?)	
Heard	386	None		Chapuis et al. (1994), Frenot et al. (2004)
McDonald	25	None		
Macquarie	128	Rats, house mice, rabbits	Cats	Copson (1986), Copson and Whinam (1998), Pye et al. (1999), Frenot et al. (2004), Anon (2005)
Auckland	510	House mice, cats, pigs	Goats	Clark and Dingwall (1985), Shirihai (2002)
Enderby	7	None	Rabbits, house mice, cattle	
Adams	100	None		
Disappointment	5	None		
Antipodes	60	House mice		McIntosh (2001)
Bounty (various)	1.3	None		Clark and Dingwall (1985), Shirihai (2002)
Campbell	130	None	Rats, sheep, cats, cattle	Towns and Broome (2003)

Islands where house mice are now the only mammal are in bold. Only associated islands $\geq$4 km^2 are reported

native plants over introduced species, possibly related to the lack of defensive traits such as secondary compounds, which may be lost among native island plants (Bowen and van Vuren 1997). There is, however, no evidence of plant species having gone extinct on any of these islands due to mice (Wace and Dickson 1965; Godley 1989; Copson and Whinam 1998). Excluding Marion Island, there are no studies on the possible population-level impacts that mouse predation has on the plants on any of these islands, possibly reflecting a paucity of data rather than a lack of effect. The importance of plant material compared to invertebrates in mouse diet on Marion Island has increased over time, from occurring on average in 36% of stomachs in the late 1970s to 59% in the 1990s, particularly during mid to late-summer (Avenant 1999; Smith et al. 2002). The seasonal pattern may reflect prey-switching from invertebrates to seeds as invertebrate densities decrease (Avenant and Smith 2004), but could also be due to optimal foraging in the presence of abundant seed loads. Similar patterns of seasonal changes in the importance of dietary groups have been found on Guillou and Gough islands (Le Roux et al. 2002; Jones et al. 2003b).

Impacts on invertebrate fauna

Although mice are omnivorous they can also be highly selective and may prefer invertebrate prey. This has been documented for Southern Ocean islands such as Marion, Macquarie, Antipodes and Guillou (Gleeson 1981; Copson 1986; McIntosh 2001; Le Roux et al. 2002). Comparative studies of mouse-free and mouse-invaded island pairs (Bollons-Antipodes and Prince Edward-Marion) strongly suggest that mice have a major impact on invertebrates at three levels: species composition, relative abundances and size distributions. Predation by mice is considered responsible for local extinctions of several invertebrate species on Antipodes Island (Marris 2000) and also for the absence of the flightless moth *Pringleophaga kerguelensis* on Marion (Vári 1971). Differences in invertebrate abundances between Bollons Island and Antipodes Island are dramatic and have been attributed to mouse predation on Antipodes (Marris 2000). Mice on Marion are strongly size-selective feeders, preferring the larger individuals of moth larvae and weevils (Crafford and Scholtz 1987). This has resulted in quantitative differences in invertebrate body size and biomass between Marion and Prince Edward islands (Crafford and Scholtz 1987; Chown and Smith 1993). Further quantitative and robust analyses of population trends of moth larvae and weevil larvae on Marion Island showed that densities decreased significantly, by approximately an order of magnitude, between 1976/77 and 1996/97 (Chown et al. 2002). Flightless island species are particularly vulnerable to introduced predators (Carlquist 1965; Hobbs 1989; Quammen 1996), and the flightless Lepidoptera on Antipodes and Gough islands are heavily impacted by mouse predation (Patrick 1994; Jones et al. 2002); indigenous moths are major prey items wherever mouse diets have been studied in the Subantarctic (Gleeson and van Rensburg 1982; Copson 1986; Le Roux et al. 2002). Inter-decadal comparisons from Marion Island showed that the relative importance of the main invertebrate species in mouse diet has changed since the late 1970s (Chown and Smith 1993). By the 1990s, endemic moth larvae had been replaced by native weevil adults, in particular *Ectemorrhinus similis* and *Bothrometopus randi*, as the main prey. This prey shift suggests a marked impact on their previously preferred prey (Chown and Smith 1993).

A strong preference by mice for large, slow-growing invertebrate species has serious consequences, given the life-history traits of some species (Peters 1983; Brown et al. 1993). For example, adults of the flightless moth *Pringleophaga marioni* are short-lived (10–14 days) and have very low dispersal abilities (Rowe-Rowe et al. 1989) and larvae take 2–3 years to mature (Crafford 1990). The decreased abundance of this species in mouse diets on Marion suggests over-harvesting, and unless remedial action is taken, local extinction is possible. *P. marioni* plays a critical role in Marion Island's nutrient cycle; where invertebrate species are also keystone species, predation can have deleterious effects for the whole ecosystem (Smith 1978; Smith and Steenkamp 1992; Smith and Steenkamp 1993). House mice could have an indirect negative effect on invertebrates, by reducing the abundance of important resources, such as a particular native plant that is important for a stage of an invertebrate's life-cycle.

Impacts on terrestrial birds

Relatively few reliable studies have shown any direct impacts of mice on native terrestrial birds. On Gough Island, direct nest predation and competition are believed to explain the reduced abundance of the endemic Gough Bunting *Rowettia goughensis* in the lowlands, but there are few quantitative data to support this contention. During the 2000/01 breeding season, four of 15 monitored Gough Bunting nests (27%) were apparently depredated by mice, one during incubation, and three during the chick stage (Cuthbert and Hilton 2004). A study using artificial nests and eggs found evidence of mouse predation, although such studies are difficult to interpret (Faaborg 2004; Thompson and Burhans 2004).

Mouse predation on invertebrates may have an indirect influence on several island bird species.

Lesser Sheathbill *Chionis alba* numbers on Prince Edward Island have remained relatively constant since the 1970s but decreased on Marion Island by 20% over the same period (Burger 1978; Huyser et al. 2000). Observations on Marion over the last 20 years indicate that Lesser Sheathbills now forage mostly on the coast during winter and not inland as they did previously and still do on Prince Edward (Huyser et al. 2000). The change in foraging behaviour is thought to be due to mouse predation reducing invertebrate densities (Crafford and Scholtz 1987; Rowe-Rowe et al. 1989). The sheathbill population relies heavily on invertebrates during the winter when other, preferred food resources in penguin or seal colonies are not available (Burger 1982). Now sheathbills on Marion commence breeding at a lower body mass and lay smaller clutches (Huyser et al. 2000). Kelp Gulls *Larus dominicanus* also forage more on invertebrates during winter (Burger 1978). Mouse predation on invertebrates may thus impact this species in a similar manner as it does the Lesser Sheathbill.

A comparative study of Antipodes Island Snipe *Coenocorypha aucklandica meinertzhagena* and Auckland Island Snipe *C. aucklandica* on Adams Island (free of introduced mammals) found that the former was much less abundant than expected, and they are probably affected by mice consuming invertebrates in a similar manner to the Lesser Sheathbills on Marion Island (Miskelly et al. 2006). Mice on Antipodes Island may also be in direct competition with the Antipodes Parakeet *Cyanoramphus unicolor* as scavengers of Subantarctic Skua *Catharacta antarctica* and Northern Giant-Petrel *Macronectes halli* kills (Imber et al. 2005).

Impacts on seabirds

In this section we draw on all available data, not just from Southern Ocean islands. The direct impact of house mice on seabird populations was until recently considered negligible (Moors and Atkinson 1984; Atkinson 2001, Witmer et al. 2007). Reported impacts were restricted to predation of eggs and young chicks of very small seabirds, such as storm-petrels (of which newly hatched chicks may weigh only 10 g). Only four credible examples are known to us, excluding Gough Island. Mice were suspected of depredating eggs of the Grey-backed Storm-Petrel *Garrodia nereis* on Antipodes Island (Burger and Gochfeld 1994), eggs and chicks of the White-faced Storm-Petrel *Pelagodroma marina* on Selvagem Grande Island, Madeiran Archipelago (Campos and Granadeiro 1999), eggs and small chicks of the Ashy Storm-Petrel *Oceanodroma homochroa* on the Farallon Islands (Ainley et al. 1990) and Blue Petrel *Halobaena caerulea* chicks (ca 30 g) on Marion Island (Fugler et al. 1987), where a chick was found with deep wounds on its back and neck. We have disregarded an unsupported statement of depredation of nests of the Polynesian Storm-Petrel *Nesofregetta fuliginosa* (BirdLife International 2004) and other unsubstantiated reports in the grey literature. Bird remains in mouse stomach samples are a possible indication of mouse predation, e.g. on Macquarie and Antipodes islands, although these could derive from scavenging (Copson 1986; McIntosh 2001). Also on Antipodes Island, the abundance of species such as Black-bellied Storm-Petrels *Fregatta tropica* on Bollons and other mouse-free offshore islets, but their extremely low density on Antipodes, has been speculatively attributed to predation by mice (Imber et al. 2005).

All of the above reported incidents of predation are incidental, inferred or based on *post hoc* observations of gnawed egg shells, wounded chicks and mice eating dead chicks. Without direct observations of mice depredating nests or killing live chicks, the possibility that mice were only scavenging abandoned eggs and moribund or dead chicks cannot be excluded. Research conducted on Gough Island during 2003/4 was the first to show conclusive evidence that large and previously healthy chicks of the burrowing Atlantic Petrel *Pterodroma incerta* (weighing 70–700 g) and surface-nesting Tristan Albatross *Diomedea dabbenena* chicks (weighing 0.3–8 kg) were being preyed upon and killed by mice (Wanless et al. 2007; see also Wanless 2007). Wanless et al. (2007) suggest that this behaviour may not be restricted to Gough Island and may have been overlooked on other islands, for example due to the practical difficulties in studying activity in burrowing petrel nests, and the more obvious impacts of rats and cats where present with mice. Recent events on Marion Island support this hypothesis. House mice on Marion became the sole introduced mammal following the eradication of cats *Felis catus* in the 1990s (Bester et al. 2000). Since 2004, several Wandering Albatross *Diomedea exulans* chicks have succumbed to wounds consistent with mouse attacks (P. G. Ryan, personal communication; RMW personal observation). These are the first records of wounded chicks in over 20 years of intensive study (P. G. Ryan, personal communication). A key observation is that to date, the only records of (probable or confirmed) mouse predation on seabird eggs and chicks are from islands on which mice are the only introduced mammal. On islands where the mice are part of a complex of invasive mammals, the effects of dominance, competition and predation by larger species may render them less of a threat to native vertebrates (Courchamp et al. 1999; Wanless et al. 2007, Harris and Macdonald 2007; Quillfeldt et al. 2008).

The dynamics of seabird-nutrient cycle interactions have been well studied in the Subantarctic (Smith 1978, 1979; Smith and Steenkamp 1990, 1992, 1993) and elsewhere (Croll et al. 2005; Fukami et al. 2006). The transport of nutrients from marine to terrestrial systems is a critical determinant of terrestrial productivity on Subantarctic and other seabird-dominated islands (Smith 1978; Smith 1979; Smith and Steenkamp 1993; Erskine et al. 1998; Croll et al. 2005; Fukami et al. 2006; Maron et al. 2006; Mulder et al. 2008). Significant reductions in seabird densities due to predation will ultimately reduce nitrogenous fertilisation, leading to lower primary productivity (e.g. Croll et al. 2005; Fukami et al. 2006). This could cause mice to rely more heavily on predation of seabird nests, setting up a positive feedback and precipitating rapid decreases in seabird numbers.

Effects of climate change on mouse impacts

Climatic change is expected to be marked in the Southern Ocean, and empirical evidence of change already has been reported from Macquarie, Kerguelen, Marion, Heard and South Georgia (Allison and Keague 1986; Bergstrom and Chown 1999; van Aarde and Jackson 2006). There is now abundant evidence that temperatures and hours of sunshine/day are increasing and rainfall regimes are changing at several islands (Allison and Keague 1986; Smith and Steenkamp 1990; Smith 2002). The actual causes for these changes are unknown, but they may reflect changing atmospheric circulation patterns, associated with changes in the oceanic circulation patterns (Smith and Steenkamp 1990).

The impacts of climate change may affect mouse populations directly in two ways. First, if mice are temperature-stressed and experience thermally induced die-offs during winter (e.g. at Marion Island, Crafford and Scholtz 1987; Crafford 1990), then ameliorating conditions could facilitate higher survivorship in winter, leading to higher densities at the start of the breeding season and potentially higher average or peak densities (Rowe et al. 1964; King 1982; Singleton et al. 2001, 2005; Ruscoe et al. 2005; Ferreira et al. 2006). Second, climate change has the potential to increase mouse densities by enhancing terrestrial productivity, through lengthened growing seasons for plants or longer breeding seasons for mice and invertebrates. A relaxation of the constraints of temperature and resource limitation could facilitate greater variability in annual density cycles, possibly leading to irruptions, such as has been observed in Australia and New Zealand (King 1982; Singleton et al. 2001, 2005). This would only add complexity and difficulty to mouse population management. However, these effects may be self-regulating or offset because of deleterious effects of higher mouse densities on ecosystem functioning. On Marion Island, an increasing mouse population is likely to place enhanced predation pressure on soil invertebrates. This will decrease rates of nutrient cycling (nutrient availability and mineralization) with a negative effect on primary productivity (Crafford 1990; Chown and Smith 1993; Smith et al. 2002). Similarly, on Gough Island it is possible that increased mouse densities in response to climate-linked variables could be offset by reduced terrestrial productivity due to lower seabird densities and concomitant reduction in nitrogenous fertilisation.

Global relevance

The impacts of introduced mice on island ecosystems and species are poorly described across most of their range (see reviews by Harris (2008) and Traveset et al. (2008) on impacts of introduced rodents on islands). However, the islands of the Southern Ocean represent an exception to this pattern. Mice are the only introduced mammal on at least five of these islands (Antipodes, Australie, Gough, Marion and St. Paul), and it is on three of these islands that their impacts appear to be the most significant of all mouse-invaded islands, although to some extent this may reflect relative research effort and/or time since eradication of other invasive species. Where mice co-occur on islands with other introduced mammals, their densities are suppressed (e.g. Miller and Miller 1995; Choquenot and Ruscoe 2000; Russell and Clout 2004; Witmer et al. 2007; Caut et al. 2008; Simberloff 2008); for example, the eradication of *Rattus rattus* from Buck Island (Caribbean) was followed by an irruption of house mice (Witmer et al. 2007). It is probable that their (visible?) impacts are diminished as a consequence. However, eradications of other introduced mammals from islands are leaving increasing numbers of islands with mice as the only introduced mammal, including the Southern Ocean islands of Marion, St. Paul and Australie (Kerguelen group) (Bester et al. 2000; Micol and Jouventin 2002; T. Micol, in litt.). Far more islands around the world have had rats *Rattus* spp. eradicated than mice (Howald et al. 2007), and the total island area cleared of rats globally dwarfs that cleared of mice (Fig. 2). Ironically, the largest island cleared of house mice to date is Enderby (710 ha, Auckland Island group), but the operation was targeted at rabbits and the successful eradication of mice was incidental (Torr 2002). To date, the simultaneous eradication of mice and rats has been achieved on nine islands, three of which involved *R. rattus* and six involved *R. norvegicus*. At least five rat eradications have failed to eradicate mice simultaneously (including the Southern Ocean islands of St. Paul and Australie) (Micol and Jouventin 2002; Howald et al. 2007; MacKay et al. 2008; T. Micol, in litt.).

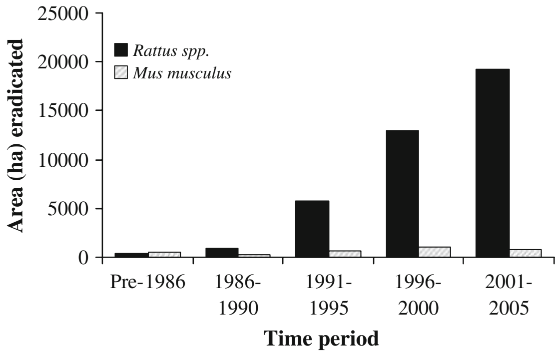

Fig. 2 Island area cleared of rats (*Rattus* spp.) and house mice (*Mus musculus*). All known efforts prior to 1986 are summed. Modified from Wanless et al. (2007)

The incidence and impacts of rat predation on island biota vary widely and depend on factors such as the physical environment of the island, seasonal availability of food, the size, behaviour and population density of the rats and the presence of other rat species and/or other predators or competitors (Woodward 1972; Atkinson 1978; Taylor 1979; Moors and Atkinson 1984). Although the effects of these factors have been studied principally for rats, there is evidence that the impacts of mice vary according to similar factors (Chown and Smith 1993; Smith et al. 2002; Wanless et al. 2007). The evidence of significant impacts by mice on birds of the Southern Ocean islands is limited. What little evidence we found was mostly indirect, due to competition for food. Wanless et al. (2007) have, however, shown significant effects of mouse predation on the chicks of seabirds as large as albatrosses. Outside the Southern Ocean, especially on islands where small passerines or ground-nesting birds breed that do not have strong nest-defence or predator-avoidance instincts, the impacts of mouse predation could be/become significant. Small rodents have been shown to be significantly more motivated to attack chicks and depredate eggs when denied food, in contrast to when provided with alternatives ad libitum (Bradley and Marzluff 2003). This finding is in agreement with the general pattern of mouse predation of seabirds on Gough Island, which is mostly restricted to the lean winter months (Wanless et al. 2007). We predict that where house mice are or become the only introduced mammal, including on temperate or tropical islands, nest predation is likely to occur during times of severe food-stress, such as winter seasons or dry monsoons.

Mouse impacts have probably been overlooked to some extent, but this review shows that rat-like behaviour and impacts can be expected, especially on islands where mice are the only introduced mammal. Predation by introduced mice on seeds, invertebrates and the eggs and chicks of birds is causing significant changes to species distributions, densities and persistence on islands in the Southern Ocean. Some of these impacts are likely to result in extinction of impacted taxa and irreversible effects on ecosystem functioning and similar effects are likely to occur on islands outside the Southern Ocean. There is thus a strong case for eradicating introduced mice from islands. It may be important to eradicate mice and other species simultaneously, or to give careful consideration to the best order of a staged, multi-species eradication programme, for three reasons. First, if toxic baits are applied to eradicate mice, primary or secondary poisoning of ‘non-target’ species could achieve eradication or substantial knockdown of numbers (e.g. of cats), making subsequent operations for those species cheaper and more efficient. Second, higher densities of mice following release from competition or predation could conceivably accelerate extinction of prey sources (e.g. endemic invertebrates) (Courchamp et al. 1999; Harris and Macdonald 2007; Caut et al. 2007, 2008); thus eradication of one invasive species could lead indirectly to the extinction of a native or endemic species (Zavaleta 2002). Third, a rebounding mouse population or rejuvenating island ecology (e.g. higher seed loads after release from herbivory) might compromise the susceptibility of mice to eradication for an unknown period of time, while exacerbating their negative biodiversity impacts.

Island ecosystems are beguilingly simple, but should nevertheless be treated as a whole (Poiani et al. 2000; Zavaleta et al. 2001; Caut et al. 2008). Where several invasive mammals coexist, eradicating one could have profound and perhaps unpredictable effects on the interactions between native species and other invasive species. We recommend that the management of mice be included in island restoration plans while taking due cognisance of the difficulties of eradicating multiple species from an island, such as is being planned for Subantarctic Macquarie Island (Anon. 2007). Reliable methods that result in the simultaneous eradication of mice and rats should be a high priority for island conservation research. In addition, changes in the diet and behaviour of mice on Marion, St. Paul and Australie should be studied, as these provide excellent and immediate ‘natural’ experiments on the effects of competitive release or meso-predator release and could give insights into causal mechanisms for the evolution, or the lack of evolution, of predatory behaviour in house mice.

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