A Review of Invasive Rodent (*Rattus* spp. and *Mus musculus*) Diets on Pacific Islands

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ABSTRACT: Three rat species, the Norway rat, black rat or ship rat, Pacific or Polynesian rat, and the house mouse are among the most widespread and destructive invasive mammals affecting islands. Through mostly unintentional introductions by humans, these rodents occupy >80% of the major islands worldwide. As a consequence of their omnivorous diet and large incisor teeth, introduced rats are probably the invasive animals responsible for the greatest number of plant and animal extinctions on islands. The effects of house mice on island ecosystems are less well known when compared with rats. We have reviewed past diet studies of these 4 omnivorous rodent species. Our review suggests that due to the high variability in diet, as well as direct and indirect effects of predation, all 4 species pose potential threats to many plants and animals on Pacific islands. Although rodent diets greatly differ among sites, diets appear to roughly follow this pattern: Norway rats and house mice generally consume proportionally more animal than plant (Norway rats consume many vertebrates and house mice mostly consumes arthropods), whereas black and Pacific rats generally consume proportionally more plant than animal. Studies specifically linking rodent diets with the population status of surrounding biota are needed in order to clarify the effective impacts of these rodent species. Much could be learned from rodent removal experiments, which could further expand our knowledge of invasive rodent species effects, and native species conservation, on islands.

KEY WORDS: black rat, eradication, food web, house mouse, invasive species, island biology, *Mus musculus*, native biodiversity, Norway rat, predation, *Rattus exulans*, *Rattus norvegicus*, *Rattus rattus*, rodent control

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INTRODUCTION

Three invasive rats in the genus *Rattus* (*R. norvegicus*, *R. rattus*, *R. exulans*), and the house mouse (*Mus musculus)*, have long been recognized for their destruction to anthropogenic products and predation of native species. Perhaps the most important characteristic for the success of these 4 rodent species is that they are highly commensal. Their ability to live closely and successfully with humans has facilitated their transport to, and establishment on, most islands in the Pacific, as well as into most of the world's biomes. The following factors also help these 4 species prosper in a wide range of environments: possession of large incisor teeth enabling access to a wide range of food items; an omnivorous diet that reflects pronounced integration into local food webs; nocturnal activity that spans below- to above-ground habitats; few effective predators, high fecundity, a relatively short period to sexual maturity; and tolerance to a wide range of temperatures and conditions (Aplin et al. 2003, Shiels 2010, Shiels et al. 2014).

The first rodent species arriving to many oceanic islands in the Pacific was *R. exulans* (Pacific/Polynesian rat); this rat accompanied Polynesian voyagers as they colonized from west to east (Matisoo-Smith et al. 1998, Wilmshurst et al. 2008). Because many Pacific islands lacked native land mammals, the island flora and fauna were not well adapted to the feeding behaviors of invasive rodents and therefore much of the native biodiversity suffered following the arrival of these first rats. For example, in both Hawaii and Rapa Nui (Easter Island) paleoecological evidence suggests that *R. exulans* played an important role in the vast reduction of the native palm forests that dominated the lowland vegetation on those islands (Athens et al. 2002, Hunt 2007). By the time Europeans, *R. norvegicus* (brown/Norway rat), *R. rattus* (black/ship rat), and *M. musculus* arrived on many Pacific islands (late 18th Century for most of the insular Pacific), *R. exulans* had already been present for at least 500 years (Wilmshurst et al. 2011). Thus, contemporary Pacific island settings have up to 4 rodent species coexisting with a highly vulnerable native flora and fauna.

There are many forms of measuring rodent impacts; however, diet assessment provides direct evidence of the types of prey items consumed. Here we have focused on the diets of 3 invasive rats and the house mouse as a means of reviewing the species and life forms that are vulnerable to invasive rodent predation on Pacific islands. We also identify some research opportunities for future study.

METHODS

We have collated peer-reviewed publications covering *R. norvegicus*, *R. rattus*, *R. exulans*, and *M. musculus* diets on islands in the Pacific. We have largely limited our review to natural areas (i.e., non-urban and non-anthropogenic habitats) on Pacific islands, and we have incorporated the reviews of these rodent species' diets from relevant chapters in King (2005) and the *R. rattus* recent review by Shiels et al. (2014). We have not attempted to separate *R. tanezumi* (Asian house rat) or any other species within the "*R. rattus* complex" from *R. rattus* (see discussion in Shiels et al. 2014); therefore, for the purposes of this review we are considering all of those species within the *R. rattus* complex as the black/ship rat.

RESULTS

Norway Rats

On a Japanese island (Mayake-Jima), Yabe (1979) found that approximately 75% of the *R. norvegicus* diet (n = 16) was animal (ca. 25% insect, 30% slug, 20% earthworm), whereas the remaining 25% was split between plant and unidentified material. The few rats (n = 14) sampled by Witmer et al. (2006) for stomach contents on Kiska Island, Alaska, revealed that the majority of the diet was plant material and bird (feathers and meat, probably from auklet, Family Alcidae); however, kelp, fish meat, and sand were the dominant stomach content components at one location. In the Queen Charlotte Islands, Drever and Harestad (1998) found that gastropods (including bivalves), fish, and crustaceans (including amphipods and decapods) comprised the majority of the *R. norvegicus* diet. In stomach contents and remains found in burrows, *R. norvegicus* preyed upon 40 different intertidal species, including keyhole limpets (gastropods) and multiple species of crab (Navarrete and Castilla 1993). In 36 stomachs analyzed by Moors (1985) in New Zealand, the majority of the diet was fruit, seed, insects, mollusks, and annelid worms.

Black Rats

By reviewing Pacific island *R. rattus* diet studies, Shiels et al. (2014) found that 17 of 20 diet studies of *R. rattus* had plants as the dominant component in stomachs; fruit and seed comprised the greatest portion of their diet. Animals, mainly arthropods, are also a common component of *R. rattus* diet; for example, Sugihara (1997) determined that invertebrates (primarily Lepidoptera) comprised 40% of *R. rattus* diet. Earthworms (Norman 1970, Sugihara 1997), terrestrial molluscs (St Clair 2011), and crabs (Fall et al. 1971) can also be components of *R. rattus* diet on Pacific islands. A more extensive review of *R. rattus* diet can be found in Shiels et al. (2014).

Pacific Rats

The major food items consumed by *R. exulans* in 2-year New Zealand study in forest-grassland were grass seeds, vegetation material (mainly grass leaves), and invertebrates (Bunn and Craig 1989). Arachnids, orthopterans, and larvae of Lepidoptera (i.e., caterpillars) and craneflies were the major arthropods consumed; earthworms (annelids) were also regularly consumed (Bunn and Craig 1989). Shiels et al. (2013) also found that Lepidopteran caterpillars were a common food item in *R. exulans* (28% by volume), and that seed comprised 16% of their stomach contents. Sugihara (1997) determined that invertebrates (primarily Lepidoptera) comprised 83% of *R. exulans* in high elevation rain forests in Hawaii. In coastal Kure Atoll, *R. exulans* diet was 62% plant material, 30% insect, and 8% vertebrate flesh (including seabird) (Wirtz 1972). The semi-aquatic *Uca* sp. crabs were consumed by *R. exulans* on Midway Atoll (Carlton and Hodder 2003). In the Tokelau Islands, *R. exulans* diet was comprised almost entirely of plant material, the majority of which (88%) was coconut. The other components of their diet were small and were represented by insects and crustaceans (Mosby and Wodzicki 1973). Similarly, in wet forest on Hawaii Island, the diet of *R. exulans* was nearly completely composed of plant material (Beard and Pitt 2006); in Pohnpei the diet of 46 *R. exulans* was 89-99% plant material (Stecker and Jackson 1962).

House Mice

Few diet studies of *M. musculus* have been conducted in the Pacific. Mice captured in high-elevation wet forest in Hawaii had diets composed of mainly arthropod (33%) and seed (44% approximately half of which was monocot; Cole et al. 2000). In mesic Hawaiian forest, Shiels et al. (2013) determined that *M. musculus* diet mainly comprised caterpillars (54%) and seeds (19% of the 39% total plant material). *Mus musculus* diets were approximately equal in plant (including seeds, stems, and inflorescenses of grasses and dicots) and insect (mainly caterpillars) in high elevation (2,200-2,800 m) woodland Hawaii (Amarasekare 1994). Insects and grass seeds were the primary diets of *M. musculus* in cane fields in Hawaii (Kami 1966).

DISCUSSION

Reviewing invasive rat and mouse diets reinforces previous evidence showing that all 4 of these rodent species are omnivores; however, species-specific feeding preferences are evident (Figure 1). For example, *R. norvegicus* and *M. musculus* generally consume proportionally more animal than plant (*R. norvegicus* consume many vertebrates, and *M. musculus* mostly consumes arthropods), whereas *R. rattus* and *R. exulans* generally consume proportionally more plant than animal (Figure 1). Even without clear identification of the species consumed, an understanding of the life-forms most vulnerable to, or consumed by, each rodent species should assist in management of native resources in areas that are invaded by these rodent species.

Past reviews have identified many plant and animal species consumed by invasive rodents. Towns et al. (2006) collated the studies that had claimed negative effects on native prey by invasive *R. norvegicus*, *R. rattus*, and *R. exulans*. A review by Jones et al. (2008) built upon Towns et al. (2006) to better focus on the negative effects of the 3 invasive rat species on seabirds. *M. musculus* are thought to have little, if any, direct negative effects on seabirds or forest birds (e.g., Figure 1) simply on account of their size and feeding behavior; however, on Gough Island where *M. musculus* are 2-4 times the size of those in the Pacific, they have been documented feeding (as a colony) on petrel chicks (70-700 g) and albatross chicks (0.3-8 kg) (Wanless et al. 2007). Indirect effects such as competition for invertebrates may be a more likely negative effect of *M. musculus* on native terrestrial birds than is (direct) bird predation (Angel et al. 2009). The effect of the 4 invasive rodent species on island invertebrates was recently reviewed by St Clair (2011). Finally, the effects of invasive rats on plants have also been reviewed for French Polynesia (Meyer and Butaud 2009) and for Pacific *R. rattus* (Shiels et al. 2014). Some native, threatened, and endangered Hawaiian plant species have also been assessed for rat predation (Pérez et al. 2008, Shiels and Drake 2011, Pender et al. 2013).

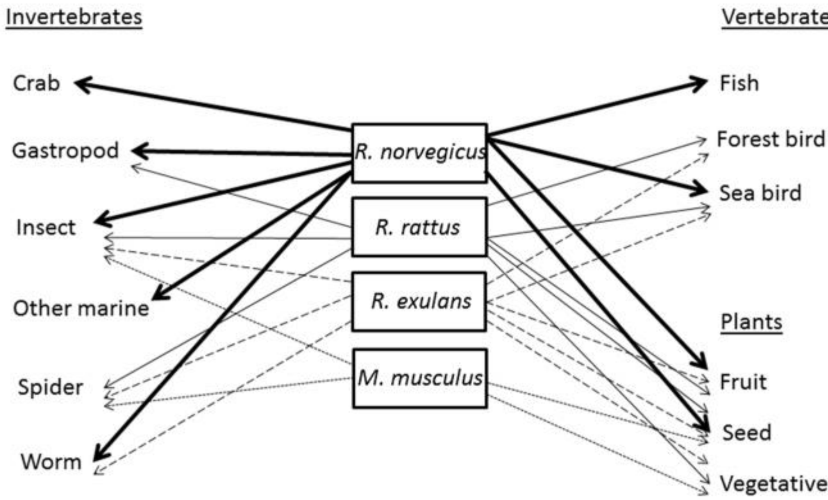

Figure 1. Organisms that *Rattus norvegicus*, *R. rattus, R. exulans*, and *Mus musculus* are known to regularly consume on Pacific islands. The 4 thicknesses and patterns of arrows reflect the 4 rodent species (i.e., thick solid arrow for *R. norvegicus*, thin solid arrow for *R. rattus*, long dashes for *R. exulans*, short dashes/dots for *M. musculus*). Connections between rodent predators and prey are based on the average diet recorded on Pacific islands, measured by the relative proportion of food items in stomach contents and in some cases other indicators of diet (see text). Items that were infrequent or <10% (by volume) in stomach contents were not connected with arrows. The vegetative category includes stems and leaves. All categories and relationships are based on reviewed literature (see text).

Bias is involved in our dietary conclusions involving *R. norvegicus*, because in tropical islands these rats are largely found in urban and agricultural areas (therefore excluded from the tropical portion of our review), and many of the studies for which *R. norvegicus* diets have been assessed are near coastlines in temperate Pacific islands. Nevertheless, *R. norvegicus* commonly consumes animals as a regular part of their diet. Crabs, gastropods, marine invertebrates, earthworms, fish, seabirds, and insects are all life forms vulnerable to *R. norvegicus* consumption (Figure 1). Fruit and seed can also be a regular component of *R. norvegicus* diet, as Moors (1985) documented in New Zealand.

A key dietary difference between *R. norvegicus* and the two smaller rats (*R. rattus* and *R. exulans*) is the vast difference in plant consumption: *R. norvegicus* consume far less plant material than the other two rat species. Plant material often comprises 75-80% of *R. rattus* diets in the Pacific (Kami 1966, Norman 1970, Clark 1981, Cole et al. 2000, Beard and Pitt 2006, Sweetapple and Nugent 2007, Shiels et al. 2013, Shiels et al. 2014). Fruit was a dominant component in *R. rattus* diets in wet and dry habitats in Hawaii (55% in Shiels et al. 2013; 44% in Cole et al. 2000; 23-53% in Sugihara 1997). Nearly all of the plant material in the diet of *R. exulans* and *R. rattus* was fruit in Hawaii wet forest (Beard and Pitt 2006). Although plant material can be 65-90% of *R. exulans* diet (Wirtz 1972, Mosby and Wodzicki 1973, Bunn and Craig 1989), their fruit consumption by can be more variable than that of *R. rattus* (41% in Shiels et al. 2013 versus 3-16% in Sugihara 1997). However, grass seed was the major food consumed by *R. exulans* during the breeding season in New Zealand (Bunn and Craig 1989) and seed was 16-25% of the diet of *R. exulans* and *R. rattus* in Hawaii mesic forest (Shiels et al. 2013). Arthropods are also an important component of *Rattus* spp. diet, yet they often comprise <30% of their stomach contents (Wirtz 1972, Yabe 1979, Cole et al. 2000, Beard and Pitt 2006, Shiels et al. 2013).

M. musculus consume relatively small portions (<10%) of fruit (especially fleshy fruit) compared to seed, vegetative material, and arthropods (Kami 1966, Cole et al. 2000, Angel et al. 2009, Shiels et al. 2013). Fruit was absent from all 25 mouse stomachs analyzed from gulches adjacent to sugar cane fields on Hawaii Island (Kami 1966). Instead of fruit, seed and vegetative material (stems and leaves) are a common component of *M. musculus* diet (Figure 1); nevertheless, arthropods (primarily insects) are typically the most common food component in their diet (Angel et al. 2009, Shiels et al. 2013). In fact, in a review of the Southern Ocean, Angel et al. (2009) found that arthropods were the food of choice for *M. musculus* on islands. In Hawaii woodlands, arthropods comprised 33-57% of *M. musculus* diets (Amarasekare 1994, Cole et al. 2000, Shiels et al. 2013). Although caterpillars appear to be a highly attractive food item to all 4 rodents species, the proportion of stomach contents composed of caterpillars appeared greatest in *M. musculus* (e.g., 22-54% in Cole et al. 2000, Shiels et al. 2013); among the most common groups eaten by *R. exulans* (Bunn and Craig 1989); and least common in the diets of *R. rattus* (e.g., 3-4% in Cole et al. 2000, Shiels et al. 2013).

Although the 4 rodent species are omnivores and thus appear to occupy the same general trophic level, they occupy different dietary niches (reviewed by Shiels et al. 2013) and clearly consume proportionally distinct life-forms on Pacific islands (Figure 1). Future studies that specifically link rodent diets with the population status of surrounding biota, particularly prey species, are needed in order to clarify the effective impacts of these rodent species. Additionally, sampling across seasons should occur whenever possible to avoid biased interpretations of local rodent diets. Finally, due to the complexities of rodent species behaviors where sympatric and where occurring alone in various habitats (e.g., Shiels 2010, Shiels et al. 2013), single- and multi-rodent species experimental removals are recommended to expand our knowledge of invasive rodent species effects, and native species conservation, on islands.

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