Biology and Impacts of Pacific Island Invasive Species. 11. *Rattus rattus*, the Black Rat (Rodentia: Muridae)[1]

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Abstract: The black rat, roof rat, or ship rat (*Rattus rattus* L.) is among the most widespread invasive vertebrates on islands and continents, and it is nearly ubiquitous on Pacific islands from the equatorial tropics to approximately 55 degrees latitude north and south. It survives well in human-dominated environments, natural areas, and islands where humans are not present. *Rattus rattus* is typically the most common invasive rodent in insular forests. Few vertebrates are more problematic to island biota and human livelihoods than *R. rattus;* it is well known to damage crops and stored foods, kill native species, and serve as a vector for human diseases. *Rattus rattus* is an omnivore, yet fruit and seed generally dominate its diet, and prey items from the ground to the canopy are commonly at risk and exploited as a result of the prominent arboreal activity of *R. rattus.* Here we review the biology of this invasive species and its impacts on humans and the insular plants and animals in the Pacific. We also describe some of the past management practices used to control *R. rattus* populations on islands they have invaded.

Few undomesticated animals are as widespread and well known as the black rat, *Rattus rattus* L. (Figure 1). This rat's behavior results in countless negative interactions with humans in most parts of the world, including consuming and spoiling foods, causing fires and electrical interruptions by gnawing wiring in buildings, nesting in and around human dwellings, and carrying diseases such as the bubonic plague that has killed millions of people (Wilson 1968, Twigg 1978, Alderton 1996). Human impacts and associated costs in attempts to control or eradicate this species have continued for centuries. The success of *R. rattus* in such a range of different environments across the planet is intriguing, especially when considering that rodents compose over 40% of the world's mammal species (Alderton 1996); thus there must be some characteristics facilitating the success of *R. rattus* that further separate this species from the other 2,000 or more rodent species on the planet. Perhaps the most important characteristic for success is that *R. rattus* is highly commensal. The ability of black rats 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 (Alderton 1996).

In addition to affecting human health and economies, *R. rattus* is well known for its negative effects on a large suite of native biota and ecosystems. *Rattus rattus* has been identified as the most damaging invasive rodent to island ecosystems (Ruffino et al. 2009, Traveset et al. 2009, Banks and Hughes 2012); and globally, *R. rattus* is associated with the greatest number of declines or extinctions of native island biota (Towns et al. 2006). Because most of the islands in the Pacific lacked native land mammals, native flora and fauna are particularly at risk to the negative effects of introduced rodents such as *R. rattus*. Unlike most other introduced mammals on Pacific

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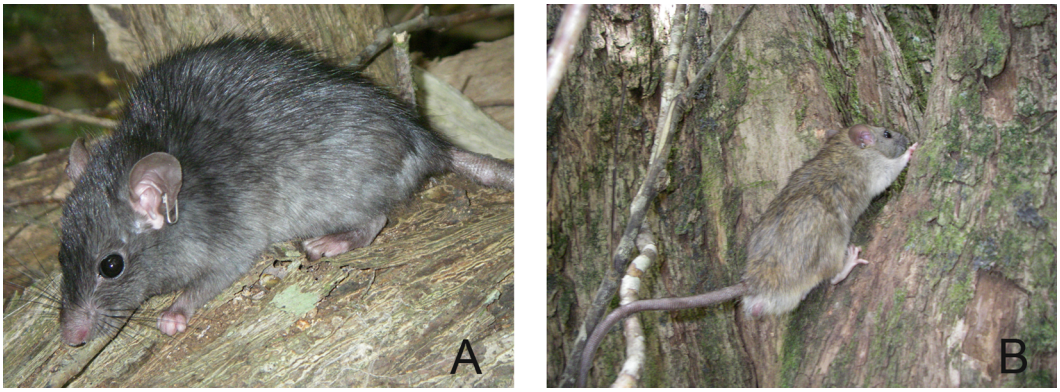

FIGURE 1. Adult black rats (*Rattus rattus*) with (*A*) a black pelt and (*B*) a brown pelt, shown climbing a tree in native forest, O'ahu, Hawai'i. Note the shiny metal ear tags in both photos. (Photographs by A. B. Shiels.)

islands (e.g., ungulates, dogs, cats, mongooses, or stoats), *R. rattus* was unintentionally introduced to islands.

NAME

Rattus rattus Linnaeus, 1758 (Rodentia: Muridae), is commonly called the black rat, roof rat, or ship rat. Past synonyms have included *Mus rattus* Linnaeus, 1758; *Mus alexandrines* Geoffroy, 1803; *Musculus frugivorus* Rafinesque, 1814; *Mus novaezelandiae* Buller, 1870; plus numerous others (Innes 2005*a*). In evolutionary terms, the genus *Rattus* originated about 2–3 million years ago (Aplin et al. 2003).

Rattus rattus has been separated into two subgroups based on chromosome numbers (Yoshida et al. 1974). The Oceania group of *R. rattus* generally has $2n = 38$ chromosomes (Musser and Carleton 2005), and it was this species that was thought to have originated in the Indian Peninsula and reached Britain by the 3rd century A.D. (Innes 2005*a*). The second group of *R. rattus* is an Asian form that has $2n = 42$ chromosomes and is indigenous to Southeast Asia; today it is also found in Japan, Taiwan, the Philippines, New Guinea, Fiji, and other islands (Robins et al. 2007). This Asian group is potentially multiple species and called *R. tanezumi* (syn. *R. diardii*) by Musser and Carleton (2005). Phylogenetic restructuring of the "*R. rattus* complex" (Oceanic and Asian groups) continues to progress, and based on molecular evidence there are almost certainly multiple species within what has historically been identified as *Rattus rattus* (e.g., five to seven species in the *R. rattus* complex described by Robins et al. [2007] and Pagès et al. [2010], respectively). In the Mariana Islands, Wiewel et al. (2009) reported that all species in their sampling that had been previously believed to be *R. rattus* or *R. tanezumi* were most closely related to the *R. diardii* group described by Robins et al. (2007). Without molecular analysis of individuals within the *R. rattus* complex, it is very difficult to separate the species, and *R. rattus* and *R. tanezumi* are almost impossible to distinguish morphologically (Aplin et al. 2003). In addition, three interbreeding color morphs of *R. rattus* have been described in the Pacific (Tomich 1986, Innes 2005*a*): *R. r. rattus* (black individuals), *R. r. frugivorous* (white-bellied), and *R. r. alexandrinus* (gray-bellied). For simplicity, we have not distinguished among species or color morphs within the *R. rattus* complex and therefore consider all of those species within the complex as the black rat, *R. rattus*.

DESCRIPTION AND ACCOUNT OF VARIATION

Species Description

The black rat, *R. rattus*, is an arboreal, ground-active, and fossorial rodent that is not always black in pelage (Figure 1). A recent review of

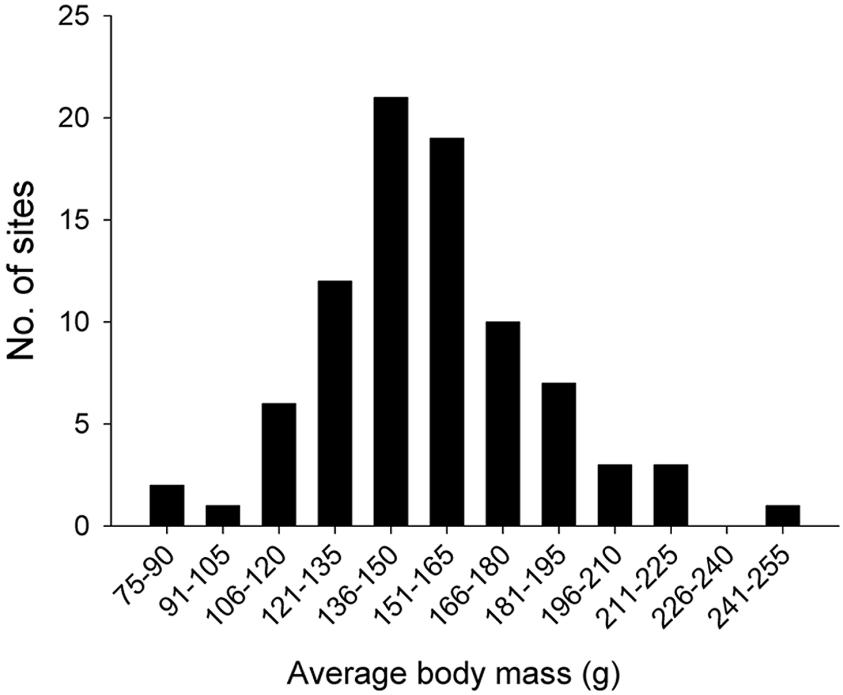

FIGURE 2. Frequency of average adult body mass of *Rattus rattus* on Pacific island sites ($n = 85$ sites, representing 59 islands; latitudinal range of islands was 0–55 degrees).

R. rattus body sizes from islands extending across the Pacific basin reveals that mean (±SE) adult body mass is 153 ± 3 g (range, 76–243 g; $n = 85$ sites, 59 islands) (Figure 2) (A.B.S., J. Russell, and W.C.P., unpubl. data), whereas the mean adult head-body length (measured from snout to base of tail) is 175 ± 2 mm (range, 134–207 mm; $n = 71$ sites, 53 islands) (A.B.S., J. Russell, and W.C.P., unpubl. data). These Pacific-wide *R. rattus* body size measurements were similar to those summarized across New Zealand (Innes 2005*a*). Unlike other invasive *Rattus* species (Yom-Tov et al. 1999, Atkinson and Towns 2005), there does not appear to be a Pacific-wide pattern of greater body size with increasing latitude for *R. rattus* (Yom-Tov et al. 1999; A.B.S., J. Russell, and W.C.P., unpubl. data). Adult male *R. rattus* are larger in both mass and body length than adult females (Innes 2005*a*, Shiels 2010), whereas average tail length has been recorded as similar between sexes (Innes 2005*a*) or slightly greater in males than in females (Shiels 2010).

Black rats, like most nocturnal rodents, have well-developed senses of touch, smell, and hearing. Both their whiskers and guard hairs (on their pelt) are very sensitive to touch, and they are used in orientation and movement in the dark. Their keen sense of smell allows them to find food and water, detect sexually active individuals, and distinguish foreign and familiar individuals and locations (Mallick 1992, Innes 2005*a*,*b*). They have round, dark eyes that are specialized for nocturnal vision; their eyes are very sensitive to light, but their vision is not acute (Innes 2005*a*).

The fur of black rats is smooth, and the guard hairs on their back are longer than any other hair on their body. As a result of their frequent grooming, they incidentally swallow some of their hair and it may compose an average of 5% by volume of their stomach

contents (Shiels et al. 2013). All four feet are dorsally hairy and ventrally bare, and each foot has clawed toes that are essential for climbing: the forefeet have four clawed toes and the hind feet have five. Unlike *R. exulans* (Pacific or Polynesian rat), the dorsal hair on the hind feet is uniformly colored in *R. rattus*, and the hind feet measure 3–7 mm longer on *R. rattus* (28–30 mm) than on *R. exulans* (Atkinson and Towns 2005). Female *R. rattus* generally have 10 nipples (range, 10–12), consisting of two pectoral pairs and three inguinal pairs (Atkinson and Towns 2005).

Like *R. exulans* and *R. norvegicus* (Norway rat), *R. rattus* has 16 teeth, which are comprised of four incisors (two on the top and two on the bottom) and six molars on each side of the mouth (Innes 2005*a*). All teeth grow continuously throughout life, and the large incisors, which are specialized for gnawing and grinding, must be kept to a usable length by grinding and self-sharpening (Innes 2005*a*). The skull is also specialized for gnawing, and the average length of *R. rattus* skulls in the Pacific region is 40–43 mm (Yom-Tov et al. 1999). Because of the size variability across ages, the size of *R. rattus* droppings (6.8–13.8 mm) cannot always be used to distinguish the species from other species of common invasive rats (Atkinson and Towns 2005).

Distinguishing Features

Body mass is a characteristic that can occasionally be used to distinguish *R. rattus* from other invasive rodents, but it is often unreliable given that rat body size varies depending on location of capture and level of maturity (Miller and Miller 1995, Shiels 2010) (Figure 2). For example, when adult body masses were reviewed in New Zealand, *R. rattus* individuals were 52–295 g (Innes 2005*a*), which overlaps with the smaller *R. exulans* (30–187 g) (Atkinson and Towns 2005) and the larger *R. norvegicus* (103–422 g) (Innes 2005*b*). Instead of body size, features that distinguish *R. rattus* from other coexisting rodents (e.g., *R. exulans*, *R. norvegicus*, and *Mus musculus* [house mouse]) include tail length and ear length. The tail of *R. rattus* is approximately 27 ± 2 mm (or $16\% \pm 1\%$) longer than the rest of its body (Innes 2005*a*, Shiels 2010), whereas *R. exulans*, *R. norvegicus*, and *M. musculus* all have tails approximately equal to or shorter than their body length exclusive of the tail (Atkinson and Towns 2005). The longer tail and sleek body shape of *R. rattus* may be adaptations related to their arboreal activity (Figure 1), which is more frequent than that of other introduced *Rattus* spp. and mice (Shiels 2010, Foster et al. 2011, King et al. 2011*a*). Ear length of *R. rattus* (19.0–26.0 mm) is generally the largest among the four main invasive rodents introduced to Pacific islands, including *R. exulans* (15.5–20.5 mm), *R. norvegicus* (14.0–22.0 mm), and *M. musculus* (12.0–15.0 mm). The ears of *R. exulans*, like those of *R. rattus*, cover the eyes when pulled forward, and the fine ear hairs do not extend beyond the edges of the ears, which is unlike those of *R. norvegicus* and *M. musculus* (Atkinson and Towns 2005). The fur on the back of all four invasive rodents can be brown (agouti); however, the only species of the four invasive rodents in the Pacific that includes some individuals with black fur on their backs is *R. rattus* (Tomich 1986, Atkinson and Towns 2005).

DIET

The diet of *R. rattus* in the Pacific has been well studied using a variety of methods, including examination of stomach contents (Kami 1966, Yabe 1979, Clark 1981, Sugihara 1997, Cole et al. 2000, Sweetapple and Nugent 2007, Caut et al. 2008*a*), field observations of chewed food items (Norman 1970, Meyer and Shiels 2009, Pender et al. 2013), field trials measuring food item removal (Norman 1970, Abe 2007, Shiels and Drake 2011), captive-feeding trials (Amarasakare 1994, Williams et al. 2000, Pérez et al. 2008, Gregory and Macdonald 2009, Meyer and Shiels 2009, Shiels 2011), and stable isotope analysis (Harper 2006, Caut et al. 2008*a*,*b*, Shiels et al. 2013). As a whole, these dietary assessments confirm that *R. rattus* is highly omnivorous, eating a wide variety of plants, invertebrates, vertebrates, and fungi (Figure 3).

Based on literature reviewed from Pacific islands, Figure 3 summarizes the relative im-

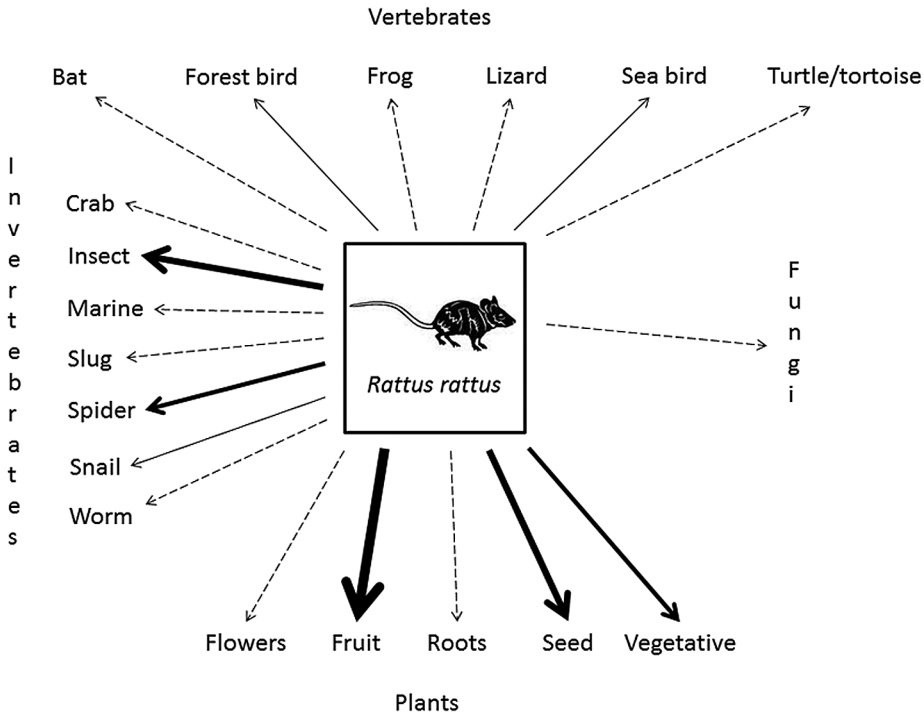

FIGURE 3. Organisms that *Rattus rattus* are known to consume on Pacific islands. The arrows' thickness indicates the average diet of *R. rattus* on Pacific islands, measured by the relative proportion of the food item in stomach contents and in some cases other indicators of diet (see text); dashed lines indicate items that have been recorded but are least common in diets. In general, thickened solid arrows = common consumption of food item; thinnest solid arrows = generally infrequent by volume but commonly consumed on some islands (i.e., snail, forest bird, seabird); dashed arrows = uncommon consumption of food item (i.e., infrequent in most studies and islands). The vegetative category includes stems and leaves. All categories and relationships are based on reviewed literature (see text and Figure 4).

portance of various food items in the diet of *R. rattus*. The most frequent food items consumed by *R. rattus* are plants (fruit, seed, vegetative), insects, and spiders; yet most of the terrestrial food web may be vulnerable to *R. rattus* consumption. By collating available stomach content analyses of *R. rattus* across the insular Pacific ($n = 20$ sites) and determining the ratio of plant to animal contents in their diets (based on mass or volume), we found that plant material dominated the diet of *R. rattus* at 17 of 20 sites (Figure 4), and plants were generally nine times more frequent in its diet than animals (i.e., average ratio in Figure 4 is 9 : 1). The three sites where animals were proportionally more frequent than plants in the diet of *R. rattus* (i.e., ratio was <1.0) included two sites at the highest latitudes sampled (47° S) and one at 38° S (Figure 4).

Plant material often composes 75%–80% of the diet of *R. rattus* in the insular Pacific (Kami 1966, Norman 1970, Yabe 1979, Clark 1981, Cole et al. 2000, Beard and Pitt 2006, Sweetapple and Nugent 2007, Shiels et al. 2013), and fruit and seed are the most common plant items in their diet (see review by Grant-Hoffman and Barboza [2010] and Figure 3). After a literature review, Grant-Hoffman and Barboza (2010) found that 36 plant families have been documented containing species consumed by *R. rattus*, and the majority of these families had the fruit as the plant part that rats consumed. Clark (1982) found that one population of *R. rattus* in the Galápagos Islands consumed at least 22

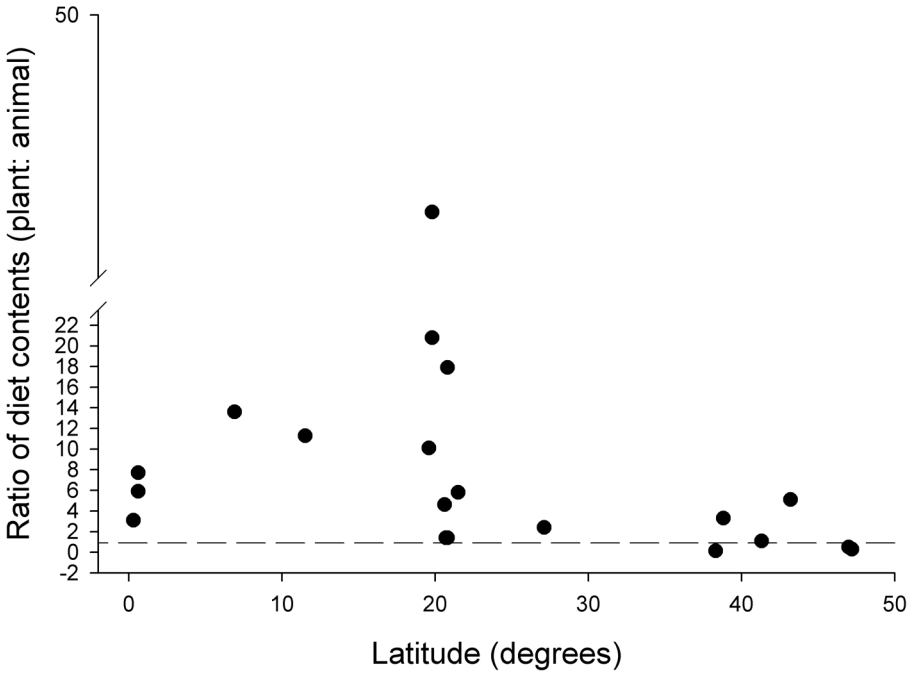

FIGURE 4. Ratio of plant to animal contents in the diet of *R. rattus* trapped on Pacific islands. The dashed horizontal line represents the 1 : 1 line where the plant component of the rat diet is equal to the animal component (i.e., a diet of 50% plant, 50% animal). Diets are based on mass or volumetric quantities from stomach content analyses. Twenty entries from 14 islands in the Pacific are shown. The three points below the 1 : 1 line (latitudes 38.8° S, 47.0° S, and 47.2° S, each from New Zealand) indicate the only studies where *R. rattus* diets contained proportionally greater amounts of animal than plant contents. Data are from Strecker and Jackson (1962), Kami (1966), Norman (1970), Fall et al. (1971), Daniel (1973), Clout (1980), Clark (1981), Gales (1982), Tobin et al. (1994), Sugihara (1997), Robinet et al. (1998), Cole et al. (2000), Beard and Pitt (2006), Harper (2007), Sweetapple and Nugent (2007), Yabe et al. (2009), Shiels et al. (2013).

species of vascular plants. In Hawai'i, the relative abundance of fruit in *R. rattus* stomachs was 55% in mesic forest (Shiels et al. 2013), 23%–53% in wet forest (Sugihara 1997), and 44% in arid shrubland (Cole et al. 2000). Fruit fragments of *Clidemia hirta*, *Rubus rosifolius*, and *Psidium cattleianum*, which are all invasive species on many Pacific islands, were found in *R. rattus* trapped on O'ahu (Shiels et al. 2013), and *Clidemia hirta* and *Rubus rosifolius* were found in *R. rattus* trapped on Hawai'i Island (Beard and Pitt 2006). Fruit composed 26% of the stomach contents of *R. rattus* trapped in a New Zealand forest, which included 12 native species, and *Eleaocarpus hookerianus* was the most abundant species, composing 13% of the stomach contents (Sweetapple and Nugent 2007). Ripe fruit is most commonly eaten by rats; however, green (immature) fruit of a variety of coastal species including coconut (*Cocos nucifera*) and some high-elevation legume fruits and seeds (*Sophora chrysophylla*) are often consumed by *R. rattus* in the Pacific (Marshall 1955, Fall et al. 1971, Amarasekare 1994).

Seed consumption by *R. rattus* is generally an antagonistic relationship (seed predation), yet some intact seeds are found in stomach contents (see Shiels et al. 2013) and can survive gut passage and therefore represent a mutualistic relationship (seed dispersal) with plants (Williams et al. 2000, Shiels 2011, Shiels and Drake 2011) (see subsection on Impact on Plant Communities). Seeds of multiple species of the native Hawaiian palm *Pritchardia* are commonly depredated by *R.*

rattus (Pérez et al. 2008), and several other native trees in Hawai'i also suffer *R. rattus* seed predation (Shiels and Drake 2011). In a New Zealand forest, seed fragments were the dominant food item in adult *R. rattus* stomach contents, composing 48% of their total diet (Sweetapple and Nugent 2007), whereas in a Hawaiian forest approximately 25% of the stomach contents were seed fragments (Shiels et al. 2013). Many seeds of economically important species (e.g., macadamia nuts [*Macadamia integrifolia* and *M. tetraphylla*] and coconuts) are consumed by *R. rattus* in the Pacific and can form the dominant parts of their diets (Fall et al. 1971, Twibell 1973, Tobin et al. 1994, Sugihara 2002, Elmouttie and Wilson 2005). Flowers are not commonly consumed by *R. rattus* (Sweetapple and Nugent 2007), yet in arid habitats in the Galápagos Islands flowers were occasionally found in *R. rattus* stomachs (Clark 1981); in southern Tasmania *R. rattus* foraged on *Acrotriche serrulata* flowers (Johnson et al. 2011), and rats (probably *R. rattus*) in Hawai'i consumed *Freycinetia arborea* inflorescenses (Drake et al. 2011) and destroyed some *Clermontia fauriei* flowers while presumably accessing nectar (D. Drake, unpubl. data).

In general, vegetative material (e.g., seedlings, leaves, and shoots) is less abundant than fruit and seed in *R. rattus* diet. However, in some environments and seasons, vegetative material can account for a substantial portion (20%–30%) of a fruit-dominated diet (Kami 1966, Norman 1970, Clark 1981, Cole et al. 2000). The pith tissue in twigs of 23 plant species is consumed by *R. rattus* when fruit production is low in the Ogasawara Islands, Japan (Yabe et al. 2010, Abe and Umeno 2011). Rats (probably *R. rattus*) also wound legume trees (*Acacia koa*) in Hawai'i in young (<6 yr old) but not old (7- to 11-yr-old) plantations by stripping the bark (Scowcroft and Sakai 1984); they also eat *Clermontia fauriei* bark in wet forest on Kaua'i (D. Drake, unpubl. data). In addition, Campbell (1978) found that *R. rattus* ate the bark on two species of Araliaceae (*Pseudopanax arboreus* and *Schefflera digitata*), and they ate leaves, stems, and roots of a third species in this family (*Stilbocarpa lyallii*). Sugihara (1997) found that leaves, stems, roots, and rhizomes could compose 2%–28% of *R. rattus* diet on Maui, and the greatest abundance of these vegetative components occurred in rat stomachs during the summer. Clark (1982) found that fern rhizomes (*Blechnum* sp.) were a frequent component in most *R. rattus* stomachs from montane forest in the Galápagos Islands; and leaves from 24 species were found in stomachs analyzed across eight *R. rattus* populations (Clark 1981). Moss was also present in *R. rattus* diets in Hawaiian macadamia nut orchards and in New Zealand forests, although it accounted for a very small (1%–4%) portion of their diet (Tobin et al. 1994, Sweetapple and Nugent 2007). In general, vegetative parts are most commonly consumed by *R. rattus* when other food types are limited.

Fungus is an additional component of *R. rattus* diet, and it has generally been identified in stomachs from cool and moist temperate islands, such as North Island, New Zealand, and Stewart Island, New Zealand, where it composed <2% of *R. rattus* diet (Daniel 1973, Gales 1982, Sweetapple and Nugent 2007), and on offshore islands of Tasmania where partly eaten *Agaricus campestris* and *Lepiota rhacodes* were documented (Norman 1970). Winter sampling of *R. rattus* stomachs revealed relatively high (12%) fungi content in pine (*Pinus radiata*) plantation forest in New Zealand (Clout 1980). In montane forest in the tropical Galápagos Islands, fungi composed up to 12% of the *R. rattus* seasonal diet (Clark 1981). In addition, fungi dispersal may be enhanced by gut passage of fungal spores (Vernes and Dunn 2009, Vernes and McGrath 2009).

Arthropods, particularly insects, are an important dietary component of most *R. rattus* individuals, but they typically compose a smaller component of the *R. rattus* diet relative to plant material (Kami 1966, Norman 1970, Yabe 1979, Clark 1981, Cole et al. 2000, Sweetapple and Nugent 2007, Shiels et al. 2013) (Figures 3, 4). For example, arthropods composed 14%–16% of *R. rattus* stomach contents in Tasmania, Maui, and O'ahu (Norman 1970, Cole et al. 2000, Shiels et al. 2013) and just 2% in stomachs in lowland wet forest in Hawai'i (Beard and Pitt 2006).

However, insects dominated *R. rattus* diets on some high-latitude islands, such as Stewart Island and Taukihepa Island (Big South Cape Island), New Zealand (47° S latitude) (Gales 1982, Harper 2007). In addition, seasonality and rat age and sex can influence the abundance of arthropods eaten (Clark 1982, Miller and Miller 1995, Sugihara 1997, Caut et al. 2008*a*). Clout (1980) attributed the dominance of arthropods (particularly Lepidoptera and weta [Rhaphidophoridae]) in *R. rattus* diet to winter scarcity of fruit and seed. The tree weta, *Hemideina thoracica*, was a year-round prey item for *R. rattus* in New Zealand broadleaf forest and composed 26% of their annual diet (Daniel 1973). Clark (1982) in the Galápagos and Gales (1982) on Stewart Island found that young rats ate more arthropods than did adult rats, which may indicate a greater protein demand for growing animals. Similarly, Gales (1982) found that mature females consumed more birds and arthropods than did males, which may reflect a protein demand for reproduction. Beetles (Coleoptera) and crickets (Orthoptera) were common components of *R. rattus* diets in New Zealand (Innes 2005*a*, Ruscoe and Murphy 2005, St. Clair 2011) and Hawai'i, and 11%–42% of the *R. rattus* stomachs sampled in Hawai'i also contained spiders (Araneae) (Cole et al. 2000, Shiels et al. 2013). Caterpillars appear to be an attractive food item for *R. rattus*, but their proportion of total stomach contents can differ widely among sites (e.g., 25% in montane Maui [Cole et al. 2000]; 3% in montane O'ahu [Shiels et al. 2013]).

Earthworms (Norman 1970, Clark 1980, Copson 1986, Sugihara 1997), terrestrial mollusks (St. Clair 2011), and crabs (Fall et al. 1971, Wegmann 2009) (Figure 5) are components of the *R. rattus* diet on some Pacific islands (Figure 3). Because some food items (e.g., egg yolk, blood, nectar, soft tissues) are not easily identifiable via standard stomach content analyses, captive feeding trials provide another useful technique for determining rat diets. Under captive feeding conditions, *R. rattus* fed on ghost crabs (*Ocypode* sp.), which occupy sandy shorelines on many tropical Pacific islands (Jackson and Carpenter 1966 cited in Fall et al. 1971). In Hawai'i, two nonnative invasive snails, *Achatina fulica* and *Euglandina rosea*, were readily consumed by *R. rattus* during captive feeding trials (Meyer and Shiels 2009). Introduced slugs were also consumed by *R. rattus* in New Zealand (Miller and Miller 1995) and in captive feeding trials in Hawai'i, yet not to the extent observed in consumption of introduced snails (A.B.S. and S. Joe, unpubl. data). Several studies indicate that various bird eggs (seabirds and forest birds) are consumed by *R. rattus*, and the sizes of the eggs appear to influence the likelihood of consumption (Norman 1970, Amarasekare 1994, Igual et al. 2006, Zarzoso-Lacoste et al. 2011). Because rats generally consume little if any of the shell when eggs or snails are eaten (Amarasekare 1993, Caut et al. 2008*a*, Meyer and Shiels 2009) or exoskeletons when crabs are eaten (Fall et al. 1971), captive feeding trials are often needed to complement other means of assessing the importance of such prey in diets of *R. rattus*.

In addition to bird eggs, feathers in *R. rattus* stomachs are evidence that either juvenile or adult birds have been consumed directly or scavenged (Clark 1981, Harper 2007, Sweetapple and Nugent 2007). Caut et al. (2008*a*) found that approximately half of the *R. rattus* stomachs analyzed ($n = 9$ of 16 stomachs) had seabird feathers on an isolated New Caledonian island during the seabird nesting season; yet there was no evidence of seabirds in rat stomachs during the nonnesting season. On Higashijima, Ogasawara Islands, 28% of the stomach contents of *R. rattus* were seabirds, particularly the Bulwer's Petrel (*Bulweria bulwerii*, 78–130 g [Yabe et al. 2009]). Forest birds typically compose <9% of *R. rattus* stomach contents (Gales 1982, Harper 2007, Sweetapple and Nugent 2007), and birds may be absent from *R. rattus* stomach contents even in forests where both native and nonnative birds are present (Sugihara 1997, Shiels et al. 2013). It should be noted that some animals, such as large seabirds (Norman 1970; e.g., *Sula* spp. in Caut et al. 2008*a*), goats (*Capra hircus*), burros (*Equus asinus*), and other rodents, appear in *R. rattus* stomachs from scavenging rather than direct predation (Clark 1981).

Rattus rattus has been observed killing hatchlings of the giant Galápagos tortoise

FIGURE 5. *Rattus rattus* interacting with a strawberry hermit crab (*Coenobita perlatus*) on Palmyra Atoll. (Photograph courtesy of A. S. Wegmann.)

(*Geochelone elephantopus* [Clark 1981]) and green sea turtle (*Chelonia mydas* [Caut et al. 2008*a*]), even though there was no evidence of these vertebrates in the rat stomachs analyzed at those sites. Gnawed eggshells of Royal Penguin (*Eudyptes schlegeli*) were found in coastal tussock grasslands of Macquarie Island where *R. rattus* occur (Pye et al. 1999). Skinks were found in <10% of *R. rattus* stomachs in New Caledonia (Caut et al. 2008*a*) and Tasmania (Norman 1970), and remnants of a lizard were uncovered in a *R. rattus* stomach in Borneo (Harrison 1954 cited in Fall et al. 1971). Both lizards (*Tropidurus duncanensis*) and geckos (*Phyllodactylus galapagensis*) were found in *R. rattus* stomachs in arid habitats in the Galápagos, but they never accounted for more than 3% of the average stomach contents (Clark 1981). Bats, frogs, and snakes are potential food items of *R. rattus*, but studies documenting consumption of these food types in the Pacific are largely lacking. The Pacific boa (*Candoia bibroni*) coexists with *R. rattus* in Southwest Pacific forests, yet *R. rattus* stomach contents did not reveal any evidence of snakes (Robinet et al. 1998). However, the milk snake (*Lampropeltis triangulum*) "reappeared" 2 yr after *R. rattus* removal from San Pedro Mártir Island off Baja Peninsula, Mexico (Samaniego-Herrera et al. 2011), and there is reference to *R. rattus* in the Caribbean nearly causing the extinction of an endemic racer snake (Towns 2009). Beard and Pitt (2006) did not find any evidence of *Eleutherodactylus coqui* frogs in *R. rattus* stomachs in Hawaiian rain forest, yet *R. rattus* has been observed consuming *E. coqui* in Puerto Rican rain forest (Stewart and Woolbright 1996).

Two species of bats (greater short-tailed, *Mystacina robusta*, and lesser short-tailed, *M. tuberculata*) went extinct on Taukihepa Island, New Zealand, after *R. rattus* was introduced (Daniel 1990), yet documentation of bats in *R. rattus* dietary studies across the Pacific is absent. *Rattus rattus* has been documented foraging in the intertidal zone in several locations in the Pacific, including Chile and Midway Atoll, but the types of marine organisms and the extent to which they prey upon them is unknown (Carlton and Hodder 2003). Although some prey species are infrequent or minimally represented in *R. rattus* diets, it is possible that such prey may still suffer population-level changes from *R. rattus* that result from relatively rare consumption (e.g., VanderWerf 2001).

ECONOMIC IMPORTANCE AND ENVIRONMENTAL IMPACTS

Much of the economic impact resulting from *R. rattus* populations relates to agricultural and horticultural damage; they can destroy up to 30% of crops annually (Hood et al. 1971, Elmouttie and Wilson 2005) and spoil foods that result in millions of dollars of losses each year for islands or island chains (Sugihara 2002, Pimentel et al. 2005). Disease transfer to humans and alteration of native habitats are additional negative aspects of *R. rattus* invasions. It can be difficult to determine impacts of *R. rattus* unambiguously without experimental studies because additional rodent species and/or other animals with overlapping diets are often sympatric with *R. rattus*. Therefore, studies that have implicated *R. rattus* in damaging species and habitats by use of correlative factors should be interpreted with caution. Knowing the breadth of organisms that *R. rattus* consumes (e.g., from dietary studies) is an important first step toward determining their environmental impacts or the ecosystem changes that result from *R. rattus* behaviors. However, all interested parties (e.g., agriculturalists, academics, conservationists, natural historians, or land managers) will benefit greatly if causal factors can be identified and linked to *R. rattus*' environmental impacts. For example, it would be valuable to know why some birds and plants are highly at risk to predation by *R. rattus* when other species appear to be unaffected.

Direct and Indirect Impacts

Rattus rattus can have both direct and indirect effects on native biota. Many of the direct impacts have been reported in the preceding diet section. A growing body of evidence of indirect effects of rats on island ecosystems is reported from a group of 18 offshore islands in northern New Zealand, where half of the islands were rat-free at the time of the study (Fukami et al. 2006, Wardle et al. 2007, 2009, Mulder et al. 2009, Towns et al. 2009, Peay et al. 2013). The main conclusions from these studies were that islands with rats (*R. rattus*, *R. exulans*, and *R. norvegicus*) had few seabirds present (presumably because the rats ate the seabirds), which caused reduced inputs of seabird-transferred marine nutrients and subsequent changes in soil fauna, fungi, decomposition, and plant nutrient concentrations (Fukami et al. 2006, Wardle et al. 2007, 2009, Mulder et al. 2009, Towns et al. 2009, Peay et al. 2013). The extent to which *R. rattus* (versus other rodent species) was involved in these ecosystem-level changes to New Zealand islands is unclear, yet *R. rattus* is certainly capable of such changes given direct evidence of predation on burrowing seabirds on islands (Jones et al. 2008). Additional indirect effects of rats include competition for various food items. For example, birds that rely on either arthropods or fruit may suffer from resource competition by *R. rattus* in areas where these animals have overlapping diets.

Impact on Plant Communities

The impacts of *R. rattus* on plant communities can be difficult to determine because of the substantial time lag between effects on seeds and seedlings and the responses of adult plant populations. Such lag times are particularly relevant for longer-lived plants like trees. Some responses to *R. rattus* impacts may mask others, particularly over extended periods, which makes the species composition of the community potentially important for assess-

ing rat impacts. For these reasons, assessments of plant community change as a result of *R. rattus* are generally restricted to their effects on seeds and seedlings (Shaw et al. 2005, Abe 2007, Wegmann 2009, Auld et al. 2010, Shiels and Drake 2011).

Seed removal in field trials is an important step in determining seed fate, and several characteristics of the seeds (e.g., size, nutritional value, and defense chemicals) can affect seed removal by rodents (Forget et al. 2005). *Rattus rattus* individuals remove and eat fruit, including seed, on the ground and in the canopy (Auld et al. 2010, Shiels and Drake 2011, Pender et al. 2013). As indicated by a recent literature review of plant reproductive parts (i.e., fruit, cone, seed) consumed by *R. rattus*, the small parts (<15 mm, but especially 5–10 mm) were the most frequently consumed (Grant-Hoffman and Barboza 2010). Shiels and Drake (2011) found that the three largest seeds (17.9–30.3 mm longest axial length) monitored in the field were among the most unattractive to *R. rattus*, whereas intermediate-sized seeds (5.2–17.7 mm) suffered the highest level of predation (>50%), and the smallest seeds (0.5–1.2 mm) were ingested but not destroyed. On Lord Howe Island, Auld et al. (2010) found that *R. rattus* removed 94% of *Lepidorrhachis mooreana* palm fruit from trees, but a sympatric palm (*Hedyscepe canterburyana*) that has fruits 18 times larger in dry mass suffered much less (54%) removal by *R. rattus*. Pender et al. (2013) showed that trapping *R. rattus* in a Hawaiian forest resulted in the reduction of fruit consumption and seed predation from 46% to just 4% for the endangered tree *Cyanea superba*. In Hong Kong, Hau (1997) concluded that forest restoration by direct seeding would not be feasible due to rat (*R. rattus* and *Niviventer fulvescens*) predation of 12 plant species. Yamashita et al. (2003) suggested that *R. rattus* may be facilitating the invasion of the non-native tree *Bischofia javanica* in the Ogasawara Islands because *R. rattus* depredates the seeds of the dominant native tree *Elaeocarpus photiniae-folius* both before dispersal (27%–33% of the seed crop) and after dispersal (41%–100%). Several other studies of fruit and seed removal have occurred on Pacific islands that include *R. rattus* as part of the rodent community, but the particular rodent species responsible for such removals were not identified (e.g., Moles and Drake 1999, Uowolo and Denslow 2008, Meyer and Butaud 2009, Erwin and Young 2010, Grant-Hoffman et al. 2010, Chimera and Drake 2011).

Evidence of rat-gnawed seeds is commonly found in habitats where *R. rattus* has invaded; the spatial distribution of such rat-gnawed seeds is often clumped due to their presence in "husking stations," which are sheltered areas where rats process food items after collection (McConkey et al. 2003, Elmouttie and Wilson 2005, Wegmann 2009) (Figure 6). Rats may use husking stations to hide from predators or competitors while they consume food items (Campbell et al. 1984). *Rattus rattus* generally does not cache or store foods; however, excess cereal bait was cached by *R. rattus* held in 5 × 5 × 2 m pens (Morriss et al. 2012), and at the edge of their latitudinal distribution (55° S [Macquarie Island]) Shaw et al. (2005) found that on average 30 g of fruit (equivalent to 20,000–30,000 fruit and seed) of the megaherb *Pleurophyllum hookeri* were frequently stored by *R. rattus* in small (20 × 20 cm) piles on the surface just before winter. The number of seedlings and adult plants that originate from intact seeds deposited in husking stations is rarely known. However, due to the characteristic substrates of husking stations (e.g., rock piles, root and tree bases), they are often unsuitable sites for germination and plant establishment from intact seeds that are left by rats.

Kukui nut (*Aleurites moluccana*) is a common tree in tropical Pacific island forests, and the hard seed coats are often found in husking stations and valley bottoms with distinct markings of rat gnawing (McConkey et al. 2003, Shiels and Drake 2011). It is interesting that both field and laboratory trials in which *A. moluccana* fruit and seed were offered to *R. rattus* revealed that it was not an attractive food item (Shiels 2011, Shiels and Drake 2011). One explanation for this enigma is that consumption of *A. moluccana* in the field may be overestimated because the stony seed coats of the chewed seeds persist indefinitely on the

FIGURE 6. *Rattus rattus* processing the fruit and seed of *Terminalia catappa* in a husking station at the base of a tree on Palmyra Atoll. Note the many discarded husks (seed coverings) on the ground surrounding the rat. Food items are typically discarded at individual husking stations over a period of many days. (Photograph courtesy of A. S. Wegmann.)

forest floor (Shiels 2011). An additional explanation for the presence of chewed *A. moluccana* seeds may be that rats target the very hard and readily available *A. moluccana* seeds to grind or sharpen their teeth. Extending prior captive feeding trials with *R. rattus* and *A. moluccana* (Shiels 2011, Shiels and Drake 2011) showed that several *R. rattus* gnawed the seed coats without penetrating them (A.B.S., unpubl. data). Thus, seeds of *A. moluccana* do not appear to be a favored food for rats (particularly *R. rattus* [Shiels 2011, Shiels and Drake 2011]); it may be a "famine food" or simply a hard item that enables rats to grind their incisor teeth to sharpen and maintain them.

Rattus rattus disperses some seeds of both native and nonnative species, as demonstrated in the Galápagos (Clark 1980), Hawai'i (Shiels 2011, Shiels and Drake 2011), New Zealand (Williams et al. 2000), and the Ogasawara Islands (Abe 2007). The majority of the seeds that are dispersed by *R. rattus* are small (<1.5–2.2 mm) and survive ingestion and gut passage (Williams et al. 2000, Shiels 2011). In addition, larger-seeded species (>2.5 mm long) may also be dispersed by *R. rattus* by transporting collected seeds and then failing to eat them (Abe 2007, Shiels and Drake 2011). Such dispersal of native species could be particularly important for plant community change if there are no longer native frugivores to disperse large-seeded, fleshy fruited species, such as the Hawaiian forest species *Planchonella sandwicensis* (syn. *Pouteria sandwicensis*), which has seeds that are 18 mm in length and are sometimes dispersed by *R. rattus* (Shiels and Drake 2011).

Future studies that will extend our understanding of *R. rattus* effects at the seed stage to the seedling stage will also help clarify the ultimate impacts of *R. rattus* on plant communities. For example, on subantarctic Macquarie Island, Shaw et al. (2005) found that *R. rattus* reduced initial seedling establishment and seedling survival of the megaherb *Pleurophyllum hookeri*, yet high seedling mortality in areas protected from *R. rattus* for 1 yr resulted in an absence of sustained impacts on seedling densities. It is more common for *R. rattus* to consume seeds than seedlings (Grant-Hoffman and Barboza 2010). However, on Palmyra Atoll where both *R. rattus* and land-crab densities were particularly high (>50 individuals/ha), *R. rattus* killed 63% of monitored seedlings of five native species (Wegmann 2009).

Impact on Vertebrate Communities

Vertebrate species, such as turtles, tortoises, lizards, and bats, are prey items of *R. rattus*, as evidenced by diet assessments or observations (Clark 1981, Daniel 1990, Caut et al. 2008*a* [see section on Diet]); however, the community-level impacts of this consumption have yet to be investigated. The threat of predation by rats on birds seemingly attracts more attention than threats posed to any other type of rat prey. With the strong climbing capabilities of *R. rattus*, few predators pose a greater threat to insular forest birds. Some seabirds are also at risk from *R. rattus*, particularly at the egg and chick life stages, yet many other vertebrate predators also threaten seabirds of all life stages and these other species can be more successful seabird predators than rats (see Mulder et al. 2011).

Forest and wetland birds have suffered substantial predation and extinction from *R. rattus* (Towns et al. 2006). Five species of birds (saddleback, *Philesturnus carunculatus;* robin, *Petroica australis;* fernbird, *Bowdleria punctate;* banded rail, *Rallus philippensis;* snipe, *Coenocorypha iredalei;* and bush wren, *Xenicus longipes*) went extinct following *R. rattus* invasion of Taukihepa Island, New Zealand (Bell 1978, Atkinson 1989, Towns et al. 2006). Also in the southern Pacific, five endemic forest birds on Lord Howe Island went extinct during the years after a shipwreck occurred and *R. rattus* colonized the island (Towns 2009). *Rattus rattus* is thought to be the primary factor in the extinction of the translocated populations of Laysan Rail (*Porzana palmeri*) and Laysan Finch (*Telespiza cantans*) on Midway Atoll (Fisher and Baldwin 1946, Seto and Conant 1996). Similarly, translocating an endangered parakeet (*Eunymphicus cornutus uvaeensis*) was deemed unfeasible in New Caledonian islands because of *R. rattus* nest predation of eggs (Robinet et al. 1998). *Rattus rattus* predation of robin (*Petroica australis*) eggs and chicks was observed directly by automated cameras on North Island, New Zealand (Brown 1997); in Australia, cameras linked 96% of predation events at artificial nests and eggs to *R. rattus* (Major and Gowing 1994), and *R. rattus* was also documented removing chicks from nests (Major 1991). Similarly, photographic evidence revealed that *R. rattus* was the only nest predator of an endangered flycatcher (the ʻelepaio, *Chasiempis sandwichensis*) on Oʻahu Island, Hawaiʻi, where it reduced nest success by 45%–55% (VanderWerf 2001). In high elevations (2,100–2,500 m) in Hawaiʻi, nest predation by *R. rattus* was just 4% ($n = 500$ artificial nests), which may be due to low rat densities (<1 individual/ha) or high abundance of alternative foods (plants and arthropods [Amarasekare 1993]). Amarasekare (1994) offered captive *R. rattus* different-sized bird eggs as proxies for native Hawaiian bird eggs. All but the largest eggs (Japanese quail, *Coturnix coturnix;* 25 × 40 mm) were eaten by the rats, implying that some native bird eggs (e.g., endangered palila, *Loxioides bailleui;* 16.8 × 25 mm) would be consumed by *R. rattus*. Using rat-control methods to reduce *R. rattus* abundance, ʻelepaio reproduction increased 112%, and the population growth rate (lambda) increased from 0.76 to 1.00 (VanderWerf and Smith 2002). Furthermore, long-term (15 yr) nest monitoring of ʻelepaio in Hawaiian forests revealed the importance of nest height in forest invaded by *R. rattus;* nests ≤3 m in height produced offspring less often than nests positioned higher in the canopy (VanderWerf 2012). Nesting height may therefore be one

useful factor for determining forest bird vulnerability to *R. rattus*.

The effects of *R. rattus* on seabirds are more variable than those on native forest birds; some seabirds are highly vulnerable, whereas others appear largely unaffected by presence of *R. rattus* (Jones et al. 2008, Ruffino et al. 2009). In a Mediterranean-wide analysis of historical data sets that included four seabird species (three shearwaters that were each >350 g, and one petrel weighing 25–29 g), only the smallest species (the Storm Petrel, *Hydrobates pelagicus*) appeared to have its abundance limited by *R. rattus* (Ruffino et al. 2009). Jones et al. (2008) conducted a global meta-analysis on the effects of introduced rats on seabirds and found that *R. rattus* was the invasive rat that had the largest negative effect on seabirds, thus surpassing *R. norvegicus* and *R. exulans* in frequency of seabird predation. Furthermore, *R. rattus* had the largest effect on burrowing seabirds (22 species preyed upon), followed by ground-nesting (12 species), those nesting in holes and crevices (six species), and branch-nesting (one species) (Jones et al. 2008). One caution with global generalizations about seabird vulnerability to *R. rattus* is that most knowledge about the impacts of introduced rats on seabirds is from temperate ecosystems (e.g., only five of 115 studies in Jones et al. [2008] were from tropical regions).

Examples of seabird mortality on Pacific islands are also largely limited to temperate regions. On Anacapa Island, California, *R. rattus* removal resulted in pronounced artificial nest success of Xantus' Murrelet (*Synthliboramphus hypoleucus scrippsi*); 96% of artificial eggs that mimicked eggs of this small seabird (148–167 g) were depredated before eradication, and just 3% of eggs were depredated (probably by gulls and ravens) after eradication (Jones et al. 2006). Harper (2007) monitored nests of a burrowing seabird, the Sooty Tern (*Puffinus griseus;* 800 g), on Taukihepa, New Zealand, in areas where *R. rattus* and weka (an introduced large rail, *Gallirallus australis*) were trapped and in sites where they were not trapped to determine the effects of each of these predators on nest successes of sooty terns. Weka were the primary predators of sooty terns chicks (90–150 g), and about 40% of their stomach contents was sooty terns, whereas predation by *R. rattus* was much lower, and <9% of their stomach contents was sooty tern and forest bird combined (Harper 2007). Norman (1970) experimentally determined that *R. rattus* does not kill Short-Tailed Shearwater (*Puffinus tenuirostris*) adults (ca. 425 g) or 3-week-old juveniles in Tasmania but does remove and consume unattended eggs (46–47 mm length) and eats dead chicks. Chicks of Cory's Shearwater (*Calonectris diomedea*) that were 2–7 days old were commonly eaten by *R. rattus*, but chicks ≥3 weeks old (equivalent to 2/3 of the adult body mass) were never depredated (Igual et al. 2006). In addition, Igual et al. (2006) suggested that egg consumption by *R. rattus* occurs only when eggs are abandoned and likely broken by the adult; the large size of the Cory's Shearwater likely enables them to fend off *R. rattus* and protect their eggs. Zarzoso-Lacoste et al. (2011) offered different-sized bird eggs to captive wild *R. rattus* and found that only the small eggs (14 × 18 mm) and not the 27 × 35 mm or the 43 × 56 mm eggs were consumed; however, when eggs were damaged by puncturing before being offered to *R. rattus* all egg sizes were consumed. Most nocturnal burrow-nesting species periodically leave their offspring unattended once the chick is only a few days old (Igual et al. 2006), which enables *R. rattus* the opportunity to access unattended eggs and chicks. On Midway Atoll (28° N), 79% of Bonin Petrel (*Pterodroma hypoleuca*, 180–200 g adults) nests failed due to *R. rattus* predation of both abandoned eggs (size 38 × 50 mm) and those being incubated (Seto and Conant 1996). There were no adult Bonin Petrels consumed by *R. rattus*, and chicks were unlikely to suffer *R. rattus* predation (Seto and Conant 1996). In the tropics, the number of Galápagos Petrel (*Pterodroma phaeopygia*) chicks that fledged during two seasons increased 50%–100% following *R. rattus* control (Cruz and Cruz 1996).

Seabird characteristics that are associated with vulnerability to *R. rattus* appear to include burrowing and ground-nesting habits, small adult or chick body sizes (i.e., <170 g, which is within the average *R. rattus* body size

range [Figure 2]), leaving eggs or young offspring unattended while foraging, and possibly small egg sizes (e.g., ≤50 mm longest length [Norman 1970, Amarasekare 1994, Seto and Conant 1996, Zarzoso-Lacoste et al. 2011]). Procellariiformes (e.g., petrels and shearwaters) may be particularly vulnerable to population-level impacts of *R. rattus* because they lay just one egg per year, have delayed maturity and long reproductive cycles, and often leave their offspring unattended to forage when the chick is only a few days old (Warham 1990, Seto and Conant 1996).

Native and nonnative rodent communities have also been altered by *R. rattus* invasion of Pacific islands. Harris (2009) conducted a review of the negative impacts of invasive rodents on native mammals and found that *R. rattus* has been implicated in at least six extinctions in the Pacific, including four from the Galápagos Islands (*Nesoryzomys* spp. rats), one from New Zealand (*Mystacina robusta* bat), and one from the Marías Islands in Mexico (*Oryzomys nelsoni* rat). Stokes et al. (2009) in Australia, and Harris and Macdonald (2007) in the Galápagos demonstrated that native rats (*Rattus fuscipes* and *Nesoryzomys swarthi*, respectively) suffered from interference competition with nonnative *R. rattus*. Furthermore, removal of *R. rattus* can result in population increases in coexisting nonnative rodents on Pacific islands, which has been observed with *M. musculus* in New Zealand (Ruscoe et al. 2011) and in the Galápagos (Harper and Cabrera 2010).

Impact on Invertebrate Communities

Population- and community-level impacts of *R. rattus* on invertebrates have rarely been studied, despite the importance of terrestrial invertebrates as detritivores, primary consumers, predators, prey, and pollinators. In a global review of the impacts of invasive rodents on island invertebrates, St. Clair (2011) highlighted cases in which invertebrate populations may have been driven to extinction by invasive *R. rattus* (e.g., flightless beetles *Hadramphus stillborcarpae* [Kuschel and Worthy 1996] and *Dorcus helmsi* [Ramsay 1978]) in southern New Zealand), but the majority of the recorded impacts have been population suppressions, which commonly involve beetles (Coleoptera), crickets/katydids (Orthoptera), and mollusks (especially large terrestrial snails). Additional arthropods that are commonly at risk from *R. rattus* include spiders (Araneae) and caterpillars (Lepidoptera) (Cole et al. 2000, Towns 2009, St. Clair 2011, Shiels et al. 2013). Towns (2009) suggested that the nocturnally active invertebrates are also particularly vulnerable to *R. rattus* predation. One generalization that was apparent from the St. Clair (2011) review was that larger-bodied invertebrates, relative to smaller-bodied ones, tend to be more vulnerable to local extinction and suppression by invasive *R. rattus*. Large beetles, weta (large flightless Orthoptera), giant land snails (Gastropoda), and large millipedes and centipedes (Arthropoda) are common prey items for introduced rodents in New Zealand islands, and giant stick insects (Phasmatodea) are preyed upon by *R. rattus* on Lord Howe Island (St. Clair 2011).

Terrestrial snails are at risk of predation by *R. rattus* in the Pacific (Clark 1980, St. Clair 2011). Snails that reside in trees, such as many of those native to Pacific islands, are often depredated by arboreal *R. rattus*; damaged shell remains from snail predation by *R. rattus* have closely correlated with declines in native tree snails in both the Hawaiian Islands (Hadfield et al. 1993, Hadfield and Saufler 2009) and the Ogasawara Islands (Chiba 2010*a*). Most sizes of snails are at risk of predation by *R. rattus*, including egg masses (Clark 1981) and 11–59 mm nonnative snails (*Achatina fulica* and *Euglandina rosea* [Meyer and Shiels 2009]). However, in the Ogasawara Islands, larger native snails (>10 mm) are at greater risk of *R. rattus* predation than smaller snails (<10 mm) (Chiba 2010*a*). In addition, native snails that occupy the ground are at risk of predation by *R. rattus*, particularly if they do not reside deeply within the leaf litter (Chiba 2010*a*,*b*).

The general traits most useful for predicting invertebrate vulnerability to *R. rattus* appear to be large body size, nocturnal activity, flightless nature, and residence or activity at shallow leaf litter depths or exposed surfaces (Towns 2009, Chiba 2010*a*,*b*, St. Clair 2011).

Future research on *R. rattus*–invertebrate interactions is clearly needed on islands outside temperate New Zealand and tropical Hawai'i, where the majority of our generalizations have originated (St. Clair 2011).

Agricultural Impacts

Rodents cause substantial losses to food production in all regions of the world (Witmer and Singleton 2010). In fact, Meerburg et al. (2008) estimated that 280 million malnourished people worldwide could benefit from pre- and postharvest rodent control. Pimentel et al. (2005) estimated that annual economic losses due to nonnative rats (including *R. rattus*) in the United States are approximately $19 billion, and the majority of such losses result from consumption of grain and spoiling foods. Further estimates described in Pimentel et al. (2005) include a cost of $15/yr of grain or other material for each rat in the United States, and they estimated that roughly 250 million rats are in the United States. Of the 60 or more species in the genus *Rattus*, at least 14 are substantial agricultural pests, and *R. rattus* is likely to be the most damaging to agricultural crops globally (Aplin et al. 2003).

Most types of fruits and vegetables can be damaged by *R. rattus* in the field and in storage. Coconuts are well known as desired food items for rats in tropical countries, and in Tonga *R. rattus* was the sole cause of the 20% loss of the coconut crop during one study (Twibell 1973). *Rattus rattus* has pronounced negative effects on rice (*Oryza sativa*), particularly in the Philippines and Southeast Asia (Fall and Sumangil 1980, Aplin et al. 2003, Miller et al. 2008). The macadamia nut industry in both Australia and Hawai'i suffers 5%–30% crop losses from nut consumption by *R. rattus* (Tobin et al. 1990, 1994, 1996, Elmouttie and Wilson 2005). *Rattus rattus* consumes most macadamia nuts by foraging in the canopy (Tobin et al. 1996), yet in the rows that are adjacent to crop edges *R. rattus* removes numbers of nuts that drop to the ground equivalent to those that are consumed in the canopy (Elmouttie and Wilson 2005). Seeds, fruits, and vegetables that are stored in bags and boxes are also damaged by *R. rattus*, including cauliflower (*Brassica oleracea*), sweet orange (*Citrus sinenis*), mango (*Mangifera indica*), grape (*Vitis vinifera*), and apple (*Malus pumilla*) (Ahmad et al. 1993).

Introduced rats have been a major threat to agriculture in Hawai'i for at least the past 170 yr (Tobin et al. 1990). In 1990, it was estimated that annual revenues from sugarcane (*Saccharum* spp.) alone in Hawai'i exceeded $350 million, with annual losses from rat destruction of sugarcane averaging about 11% (Tobin et al. 1990); however, it was not uncommon to lose about 30% of a sugarcane crop to invasive rodents (Hood et al. 1971). The timing of crop damage was critical for planning control strategies for rat impacts, and damage to sugarcane became appreciable at 14 months and peaked at 19–21 months. The edges of the sugarcane fields suffered the most damage, despite trapping showing uniform rat abundance across the fields (Hood et al. 1971). *Rattus rattus* damages tropical fruit (e.g., rambutans [*Nephelium lappaceum*], bananas [*Musa* spp.]) and seed crops (e.g., corn [*Zea mays*], soybeans [*Glycine max*] [Pitt et al. 2011*a*]), and such damage may be more common in modern Hawai'i than in the past because of the increased tropical fruit and seed crop acreage following the demise of the sugarcane industry (R.T.S., unpubl. data). Much increased labor and costs due to necessary *R. rattus* control strategies are required to protect crops on Pacific islands, including control efforts in crop fields, adjoining noncrop areas, and in storage and transportation units (Hood et al. 1971, Ahmad et al. 1993, Elmouttie and Wilson 2005).

Human Health Impacts

Meerburg et al. (2009) reviewed the large number of pathogens that rodents can directly or indirectly transmit to humans. *Rattus rattus* is a carrier of a number of diseases that are serious threats to humans. Such diseases are typically transferred to humans via urine and droppings or through hosts that interact with both *R. rattus* and humans. We describe some of the most problematic human-threatening diseases that are carried by *R. rattus*, including those resulting from bacteria (e.g., bubonic

plague, leptospirosis) and nematodes (rat lung worm disease); we then describe some infections that are much less threatening to humans but can be relatively common within *R. rattus* in the Pacific.

More than 200 species of mammals may host fleas that harbor the bubonic plague (*Yersinia pestis*). Although most mammalian species can suffer from the impacts of *Y. pestis*, both *R. rattus* and *R. norvegicus* show moderate levels of resistance (Aplin et al. 2003), and *R. rattus* was the main host of this disease that historically affected humans (Alderton 1996). By the 1800s, the bubonic plague, or Black Death, had wiped out more than 25 million people in Europe and an additional estimated 50 million in Asia and Africa; by the early 1900s the plague had reached many Pacific islands and popular ports (Twigg 1978, Alderton 1996). In an effort to arrest the plague outbreak in Hawai'i, the Chinatown district of Honolulu was burned and strict quarantine measures were practiced (Tomich 1986). The plague in Hawai'i caused at least 370 human fatalities, and the last reported case of human infection in Hawai'i occurred in 1949 (Sugihara 2002). *Rattus rattus* was also the likely source of the plague outbreak in Australia in the early 1900s, where about 180 people died, mainly in the densely populated cities of Sydney, Brisbane, and Melbourne (Curson and McKracken 1989). Improved sanitation, mechanized agriculture, and natural and/or human-mediated control of the reservoir (rat) and vector (flea) populations have likely reduced outbreaks of the plague (Tomich et al. 1984). However, even today bubonic plague is a potential killer; antibiotics can help overcome the bacterium and a vaccine is available, yet the infection can spread around the world at frightening rates due to our modern means of transportation (Alderton 1996).

In addition to the fleas that harbor *Yersinia pestis*, ticks and mites carried by *R. rattus* can harbor bacteria that can infect humans. In eastern Australia and Tasmania some of the bacterial infections that have resulted from *R. rattus* include *Rickettsia* spp., which causes tick typhus or spotted fever (Singleton et al. 2003); *Orientia tsutsugamushi*, or scrub typhus; and *Coxiella burnetii*, which may cause Q fever (Banks and Hughes 2012). Symptoms of these bacterial infections in humans can include headaches and muscle aches, nausea, vomiting, mental confusion, rash, pneumonia, encephalitis, and heart failure (Banks and Hughes 2012). *Streptobacillus moniliformis*, or rat-bite fever or Haverhill fever, can be transmitted to humans through rat bites or scratches, as well as via contact with infected rat urine or feces. Symptoms from human contraction of the bacteria generally include fever and arthritis (Singleton et al. 2003). *Salmonella* spp. are also carried by *R. rattus*, and although they do not appear to have any ill effects on *R. rattus*, they can be transferred to humans and livestock (Lapuz et al. 2008).

Leptospirosis is a worldwide zoonotic infection that occurs from *Leptospira* bacteria transferred to humans through exposure to water or soil contaminated with urine or feces from infected mammalian hosts, such as *R. rattus* (Wong et al. 2012). The *Leptospira* bacteria become concentrated in the rats' kidneys and are passed out of the rat via their urine. These bacteria survive well in water and can enter humans through any damaged skin, mucous membranes, or the conjunctiva of the eye. Infection by *Leptospira icterohaemorrhagiae*, which results in the human illness called Weil's disease, is the most serious form of human infection. Dogs are also at risk from a strain called *L. canicola*, and they may spread this to their owners, but a vaccine for dogs has led to dramatic declines in the incidence of this disease (Alderton 1996). In Hawai'i, approximately 13% of *R. rattus* are carriers of *Leptospira* spp. (Wong et al. 2012).

Rattus rattus (as well as *R. exulans* and *R. norvegicus*) are definitive hosts of the nematode *Angiostrongylus cantonensis*, or rat lung worm (Wang et al. 2008). Human infections of rat lung worm can result in the main clinical manifestation of eosinophilic meningitis, and human infection generally arises from consumption of the intermediate host (typically slugs and snails). Thus, to complete its life cycle, the nematode needs both the rat host and a gastropod intermediate host. Humans, birds, and other mammal hosts can suffer from meningitis symptoms and death from *A. cantonensis* infection (Prociv et al. 2000). Since

1945, more than 2,800 human cases have been reported in over 30 countries; symptoms of the infection range from headaches and neck stiffness to numbness, coma, and death (Wang et al. 2008). Screening of *R. rattus* for *A. cantonensis* infection during the last 70 yr in the Pacific has revealed infection rates ranging from 3% (Taiwan) to 20%–30% (Australia, Fiji, Japan) to 100% (Thailand) (Wang et al. 2008).

Calodium hepatica is another nematode that is found in *R. rattus*, and it can infect humans through ingestion of the *C. hepatica* eggs. Human infection is rare (37 cases reported globally) despite *R. rattus* infection rates reaching 79% in some Pacific regions (Waddell 1969, Banks and Hughes 2012). *Rattus rattus* may also act as reservoirs for the protozoan *Toxoplasma gondii*, which requires cats to complete its life cycle. Humans can obtain *Toxoplasma* oocytes through contact with cat feces. Some species of *Cryptosporidium* are a threat to human health, particularly in urban areas, and *R. rattus* is known to be a carrier of the protozoa (Banks and Hughes 2012).

There are several types of parasites that infect *R. rattus* that are much less likely to be transferred to, or infect, humans. *Rattus rattus* can be carriers of a number of blood parasites, such as *Trypanosoma lewisi* and *Grahamella* sp., which occurred in 10%–25% of *R. rattus* examined in Hawai'i (Kartman 1954). Also in Hawai'i, ear mites (*Notoedres muris*) that cause ear lesions can infect 26% of the *R. rattus* population in some forests but other populations suffer very little (<2%) infection (Shiels 2010). Intestinal worms (helminths), likely the nematode *Mastophorus muris*, are common in wild *R. rattus* on many Pacific islands (Fall et al. 1971, Sugihara 1997, Shiels 2010), and the majority of the *R. rattus* captured were parasitized by this worm on Palmyra Atoll (Lafferty et al. 2010) and on Rangitoto Island, New Zealand (Miller and Miller 1995). Because the nematodes *M. muris* and *Physoloptera getula* have obligate life cycles involving arthropods as intermediate hosts, *R. rattus* is likely infected directly by eating its arthropod prey (Miller and Miller 1995). In addition, parasitic mites cause mange in *R. rattus* in both the tropical North Pacific (Shiels 2010) and South Pacific (Caut et al. 2008*a*).

Regulatory Aspects

On all islands in the Pacific *R. rattus* is generally consider a pest, and therefore importation of *R. rattus* (accidentally or intentionally) is unwanted. However, *R. rattus* inhabits most island groups in the Pacific, so movement of rats probably has little impact on established populations in most situations beyond the potential for rats to spread diseases. One notable exception is islands and areas that have never had rats or have eradicated rats and maintained biosecurity measures to prevent reestablishment. Formal regulations against *R. rattus* transport and establishment are lacking for most Pacific islands (Moors et al. 1992). However, the International Health Regulations of 1969 states that all ships containing overseas goods must have a certificate stating that their vessel is maintained as rodent-free or is "periodically deratted"; certificates are issued by the health authority at approved ports and they are valid for 6 months (World Health Organization 1995). It is unlikely that such certification prevents rodent movements among landmasses, although some reductions may result. Aircraft and ships are vectors for repeated introductions of stowaway species like *R. rattus* because of routine routes traveled and regularity of transport schedules. Ship personnel control rodents aboard aircraft and ships, and some countries require routine inspection of ships in their ports and also require biosecurity measures for ships docking to reduce the risk of importing rodents. Such ship-to-shore measures may include rat guards on mooring lines, separation of gangways and cargo nets from piers at night and when not in active use, and maintaining rodent control with rodenticide baiting and trapping on ships and 200 m distant from the wharf (Moors et al. 1992). On islands where rats have been eradicated, additional biosecurity measures are typically required (Moors et al. 1992, Russell et al 2008).

Beneficial Aspects

Despite its remarkable adaptability, *R. rattus* is highly destructive and is generally unpopular with people. There are few beneficial im-

pacts of *R. rattus*, and its destructive impacts on island ecosystems seem to far outweigh any positive ones. One potentially positive impact of *R. rattus* is its possible functional replacement of extinct island fauna, such as taking a role in seed dispersal (Abe 2007, Shiels and Drake 2011) or possibly pollination (Cox 1983, Innes 2001). Additional benefits related to *R. rattus* may include personal financial gain through rat catching and control, as well as a source of food and entertainment (at least historically).

Many species of rodents are popular cuisine in many parts of the world, and rats are often hunted in Africa and Asia as a readily available source of protein. Early Polynesian voyagers in the Pacific may have purposefully kept *R. exulans* on their ships as an emergency food source, and *R. exulans* was trapped and eaten as an esteemed food source during Māori ceremonial feasts in New Zealand (Atkinson and Towns 2005). The degree to which *R. rattus* was consumed on islands or historical voyages in the Pacific is unknown, yet news reports from the 1940s indicated that men survived in part by eating rats on Wake Atoll (Fisher and Baldwin 1946), and at least one entry from Captain Cook's journal noted that a midshipman on the *Resolution* cleaned, roasted, and consumed part of a rat that the ship cat had caught (Beaglehole 1969).

Rat capture and removal have been a major income source in many countries. During the Victorian Era in Britain (1837–1901) when rats were particularly widespread pests, money was to be gained by using live rats for entertainment purposes. In public houses, rat pits were often established where pet dogs were encouraged by their owners and spectators to kill as many rats as possible within a set period. One dog, a terrier, killed a record 500 rats in just 5.5 min (Alderton 1996). Because of the great supply of rats needed for this type of entertainment, many rat-catchers (as many as 20 per public house) were employed for this purpose. Rats from sewers were avoided because they would most likely cause the dogs to become ill (Alderton 1996); therefore some of the rats used in rat pits would probably have been *R. rattus*. Today, control and extermination of *R. rattus* can result in relatively large financial gains in some urban and natural settings (e.g., Scofield et al. 2011).

In the early and mid-1900s rats became popular pets, especially with young women, who often kept them in squirrel cages. Breeders would develop strains with new colors and patterns. Although most modern pet rats are descendants of *R. norvegicus*, there were several color variants of *R. rattus* bred during the early 1920s; the most unusual of these was a bizarre greenish-colored strain (Alderton 1996).

GEOGRAPHIC DISTRIBUTION IN THE PACIFIC REGION

Rattus rattus is distributed globally outside the polar regions, with perhaps the highest latitude of occurrence at 63° N in Sweden (J. E. Brooks and F. P. Rowe, 1987, unpubl. report on commensal rodent control, WHO/VBC/87.949 [cited in Innes 2005*a*]). In the Pacific, *R. rattus* extends from the Queen Charlotte Islands, British Columbia (53° N) (Golumbia 2000) to subantarctic Macquarie Island (55° S) (Copson 1986). Of the 30 archipelagos in the Pacific that were identified by Carvajal and Adler (2005), which included those between 25° N and 25° S and from 120° W westward through the Bismarck and Palau archipelagos, *R. rattus* occurs on at least 27 of the archipelagos (A.B.S., J. Russell, and W.C.P., unpubl. data); those that *R. rattus* are potentially absent from include Rotuma, Pitcairns, and Tokelau, which may harbor *R. exulans* or other invasive rodents (A.B.S., J. Russell, and W.C.P., unpubl. data).

Island colonization by *R. rattus* in the Pacific varied greatly during the past 300 yr (see Atkinson [1985] for a review). From Britain it was spread throughout the world along shipping routes and probably reached the Pacific by the 1850s (Atkinson 1985). Of course many islands in the Pacific were first discovered by Europeans before 1850 (e.g., the Galápagos in the late seventeenth century and most other Pacific islands in the late eighteenth century). However, Atkinson (1985) pointed out that the European ships that first landed on most of the Pacific islands would have been

carrying *R. norvegicus* stowaways rather than *R. rattus;* the reasoning behind this is that *R. rattus* was the only nonnative rat in Britain until *R. norvegicus* was introduced about 1716, and it competitively displaced *R. rattus* from the wharfs and thereby the ships traveling to the Pacific. Records indicate that *R. rattus* suddenly reappeared on European ships during the 1850s, which is a change that still remains unexplained (Atkinson 1985). Nevertheless, the first *R. rattus* that arrived on most Pacific islands are believed to have arrived from this British stock (Atkinson 1985).

Once *R. rattus* was established in the Pacific, islands that are relatively close to one another (i.e., 300–750 m) could be colonized by swimming rats (Innes 2005*a*). Russell and Clout (2004) determined some of the predictive factors that influence whether or not New Zealand islands are colonized by *R. rattus*. The factors that positively influence the presence of *R. rattus* on New Zealand islands included island area, presence of a landing structure (wharf), and whether or not the island was inhabited by humans. Factors shown to negatively influence the presence of *R. rattus* included elevation, distance to nearest island, and the number of rock types. Finally, the factors that had no significant effect on *R. rattus* presence included number of seabirds, number of nonnative land birds, number of introduced rodents, number of introduced mammals, and the number of abandoned settlements (Russell and Clout 2004).

HABITAT

Climate Requirements, Limitations, and Ecosystems Invaded

Rattus rattus is widely distributed throughout tropical, alpine, and subpolar climates, and the species has invaded ecosystems from shorelines to mountain peaks. The only places where *R. rattus* is not found in the Pacific seem to be within the highest latitudes (those >55°) (A.B.S., J. Russell, and W.C.P., unpubl. data) and the highest elevations (in most cases >3,000 m) (Amarasekare 1994). On Hawai'i Island, Amarasekare (1994) did not find *R. rattus* above 2,837 m, which is approximately the vegetation boundary in the alpine desert ecosystem; *R. rattus* generally occurs in low abundances near those upper elevations (less than one individual/ha at 2,100–2,500 m [Amarasekare 1993]; 0.2 individuals/trap-night at 1,785–2,600 m [Banko et al. 2002]). *Poa foliosa* tussock grassland is the principal habitat for *R. rattus* on Macquarie Island (55° S), probably because it provides year-round food, shelter, and a slightly warmer microhabitat than outside the tussock canopy (Pye et al. 1999). Black rats have not been found in the windswept uplands of Macquarie Island, where lichens and cushion-forming plants dominate, including *Azorella* and bryophytes (Pye et al. 1999). The upper latitudes and elevations may reflect the boundaries of cool temperatures that *R. rattus* can withstand, yet food scarcity and lower ambient oxygen levels may also be factors contributing to distributional limitations in such cool environments. *Rattus rattus* does not seem to be limited by an upper temperature level, or at least this has not been investigated. Thus, *R. rattus* is abundant and spans most terrestrial communities, from arid lowland and montane ecosystems (Tamarin and Malecha 1971, Clark 1981, Amarasekare 1994, Harris and Macdonald 2007, Chimera and Drake 2011) to lowland and montane rain forests (Daniel 1973, Sugihara 1997, Lindsey et al. 1999, Wegmann 2009). Even in highly disturbed environments, such as Eniwetok Atoll, which suffered numerous nuclear explosions, *R. rattus* survived in densities of approximately 20 individuals/ha 10 yr after the last nuclear test (Fall et al. 1971).

Rattus rattus survives on islands that do not contain bodies of fresh water (e.g., many atolls, dry forests). Unlike *M. musculus*, *R. rattus* appears incapable of concentrating its urine, and *R. rattus* was unaccepting of seawater when offered it (Norman and Baudinette 1969). Therefore, much or all of black rat water requirements for survival probably comes from foods consumed (e.g., fleshy fruits, vegetative material), yet dew and rainfall are other sources of water to fill survival requirements for *R. rattus* (Alderton 1996).

Habitat Resource Requirements and Limitations

Rattus rattus commonly utilizes belowground, ground, and aboveground habitats. Relative to other invasive *Rattus* spp. and *Mus musculus*, *R. rattus* uses a much greater proportion of the arboreal habitat (Lindsey et al. 1999, Shiels 2010), and *R. rattus* prefers forests over open, heath, and scrub macrohabitats in Australia (Cox et al. 2000). Preference of *R. rattus* for arboreal habitats is further supported by its numeric dominance over other coexisting rodents in most insular forests in the Pacific (Tamarin and Malecha 1971, Daniel 1973, Clark 1981, Sugihara 1997, Yabe et al. 2010). However, *R. rattus* does not require forest or substantial vertical structure, as evidenced by its high abundance in savannahs (Clark 1981) and on atolls with low scrub vegetation (Fall et al. 1971).

Unlike its high abundance in most insular forests, *R. rattus* is not always the dominant rodent species in agricultural settings. Tobin and Sugihara (1992) examined the relative abundances of three species of sympatric rats in sugarcane fields in Hawai'i. They found that either *R. norvegicus* or *R. exulans* was the most numerous within any given field and that *R. rattus* was captured mainly near field edges where trees were present. During 11,200 trap-nights, Tobin and Sugihara (1992) captured 526 *R. norvegicus*, 335 *R. exulans*, and 139 *R. rattus* in four sugarcane plantations that regularly experienced pronounced rat damage. The importance of arboreal habitat availability for *R. rattus* is evident historically in the United Kingdom, where *R. rattus* was not able to coexist with *R. norvegicus* because of interference competition (*R. norvegicus* is larger than *R. rattus*) coupled with the presence of an arboreal rodent (the native red squirrel *Sciurus vulgaris*) that already occupied the arboreal niche (King et al. 2011*a*).

Den sites are important habitat features for black rats because roughly half of their lives are spent in them. Common den sites for *R. rattus* include cavities in trees or rocks, beneath woodpiles or dense vegetation cover, fern and stick-lined arboreal nests, and in burrows belowground (Lindsey et al. 1999, Rutherford et al. 2009, Shiels 2010). In Hawaiian montane rain forests, Lindsey et al. (1999) used radio tracking to determine that *R. rattus* ($n = 9$) nested in trees or treeferns, whereas Shiels (2010) found that *R. rattus* ($n = 24$) used a mixture of aboreal and belowground den sites and nearly half of the monitored individuals switched their den site uses between tree cavities and burrows. Larger trees (in height and girth) were the most common trees in which *R. rattus* denned in Hawaiian forests, and these included nonnative *Aleurites moluccana* and *Grevillea robusta*, and native *Acacia koa* and *Metrosideros polymorpha* (Lindsey et al. 1999, Shiels 2010). In New Zealand forest, Hooker and Innes (1995) found that all of the *R. rattus* radio-collared in their study had dens in trees and that the den sites were too high (>2 m) to pinpoint from the ground. Unlike other studies where *R. rattus* was typically found denning only in trees, all of the 14 *R. rattus* followed on a 797 ha offshore island in southern New Zealand (Taukihepa) had dens belowground despite the presence of a short-statured forest; many of the dens were in seabird burrows, beneath logs and branches, and in fern cover (Rutherford et al. 2009). On Macquarie Island, where trees are absent, Pye et al. (1999) documented extensive tunneling that connected entrances to *R. rattus* den sites in coastal tussock habitat.

Habitat partitioning, which can reduce competition, has been previously observed for *R. rattus* when it is sympatric with other introduced rodents (Shiels 2010). Experimental evidence of habitat partitioning between *R. rattus* and *R. exulans* was demonstrated by Strecker and Jackson (1962), where several rats of each species were confined in 3 × 3 m enclosures for 14 days and then examined for signs of conflict and weight loss. The authors concluded that if food and available microsites were present, these rats could coexist in a confined space. However, when smaller cages limited space and microhabitats to a greater extent or arrival times of different rat species into the cage were altered, then there was strong evidence of interference competition that resulted in fighting and high death rates (Barnett 1964, Norman 1970). In Australia,

Stokes et al. (2012) experimentally determined that the resident species (*R. rattus* or native *R. fuscipes*) were dominant in their behavior relative to intruders 88% of the time, irrespective of the rodent species that was the intruder.

PHYSIOLOGY AND BEHAVIOR

The physiological and behavioral adaptations of *R. rattus* have likely aided in its successful establishment in Pacific island ecosystems. *Rattus rattus* has a relatively high metabolic rate and keen sense of smell. Black rats are agile, move beneath vegetation cover rather than in exposed areas, use aboveground habitat (trees) more than other introduced rodent species, and typically move food items upon collection but generally do not store (cache or hoard) them (see section on *Impact on Plant Communities* under Economic Importance and Environmental Impacts). An important point for rat control and eradication programs is that rats typically suffer from "neophobia," which is fear of new objects; it occurs when there is a change in an otherwise familiar situation (Barnett 1963, Clapperton 2006).

Rodents have large surface areas relative to their volume, which results in greater heat losses from their bodies when compared with larger mammals. Thus, to maintain their body temperatures, rodents have high metabolic rates. Some rodents must find and eat up to 70% of their body weight each day to support their metabolic requirements (Alderton 1996). Captive *R. rattus* consumed 14–18 g of pellet bait and a slice of apple each day (Clapperton 2006). *Rattus rattus* does not hibernate, and in winter and early spring months on Macquarie Island (55° S) black rats retrieved seeds from established surface caches to sustain themselves until natural seedling recruitment commenced in the spring (Shaw et al. 2005).

Rattus rattus has a keen sense of smell that is readily used during foraging and communication with other individuals (Mallick 1992, Innes 2005*a*,*b*). Mallick (1992) found that both sexes of *R. rattus* mark substrates with urine at equal rates, and that urine marking probably contains olfactory cues that are used in intraspecific communication. Scent markings from other animals do not always affect *R. rattus* behavior. Stokes et al. (2012) experimentally determined that *R. rattus* does not appear to respond to traps scented with a competing rat species (*Rattus fuscipes*) in Australia. However, scents of predators, such as mongooses, were avoided by *R. rattus* (Tobin et al. 1995). *Rattus rattus* also follows scents to revisit locations and to find prey; rats are constantly, or nearly so, sniffing the air and are well attuned to foreign sounds (Innes 2005*a*). In New Zealand, *R. rattus* located some bird nests before eggs were laid, then returned regularly to the nests during the egg-laying period, and finally depredated several eggs (Innes 2001). Exposed and concealed nests were equally vulnerable to predation, suggesting that rats do not readily rely on visual cues to locate nests (Innes 2001). Selvaraj and Archunan (2006) determined that male *R. rattus* scent provided by both cheek cells and urine increased the acceptance of poison bait by female *R. rattus*.

Black rats are agile, good climbers, excellent jumpers, and adept swimmers (Meehan 1984, Innes 2005*a*, Foster et al. 2011, King et al. 2011*a*). They have been documented jumping higher than 150 cm (Meehan 1984), and all 20 adults of various body sizes (range, 87–173 g) that were tested in Hawai'i were able to jump at least 40 cm high (Pitt et al. 2011*d*). When *R. rattus* was compared with *R. norvegicus* in New Zealand pen trials, Foster et al. (2011) determined that *R. rattus* was faster moving and more agile, more easily overcame obstacles, was less dependent on footholds, was less likely to fall, and could more easily reach unsupported ends of small branches. *Rattus rattus* can also fit through small holes, and all 16 adults tested of various body sizes (range, 85–162 g) were able to pass through 35 mm diameter holes to access food (Pitt et al. 2011*d*). Black rats have been known to swim 300–750 m to colonize adjacent islands (Innes 2005*a*).

Rodents are often in areas of relatively high vegetation cover presumably to limit their exposure to predators (Alderton 1996, Cox et al. 2000, Atkinson and Towns 2005). Using spool-and-line tracking in the Wai'anae

Mountains on O'ahu, *R. rattus* was observed under vegetation ground cover an average of 88% of the monitoring time when rats were out of their dens and active on the ground and aboveground (Shiels 2010). In eastern Australia, Cox et al. (2000) found that *R. rattus* preferred densely vegetated understories and showed a significant attraction to habitats with increased leaf litter when their population density was relatively high. The directions of rat movements are often unpredictable because their exploratory behavior is influenced by both scents and other features that are encountered in the environment (Barnett 1963). Often a *R. rattus* individual doubles back over its same pathway by circling or moving a few decimeters in one direction, then returns to a point that it had already traveled before it quickly changes paths and explores a new direction (Key and Woods 1996, Shiels 2010). The average height *R. rattus* was observed active aboveground was 2.8 m (Shiels 2010), yet black rats can spend an average of 30%–90% of their night activity on the ground (Dowding and Murphy 1994, Hooker and Innes 1995, Lindsey et al. 1999, Shiels 2010).

Rattus rattus typically leaves its den just after sunset and returns just before sunrise (Hooker and Innes 1995, Shiels 2010); however, some rats return to their den partway through the night and then resume foraging (Dowding and Murphy 1994). One female rat in the study by Shiels (2010) left her den site at sundown (three nights) or 17 min before sundown (one night). In macadamia nut orchards, black rats left their dens 1–2 hr after sunset and returned 1–2 hr before sunrise (Tobin et al. 1996). *Rattus rattus* is rarely active during the day unless densities are high (>50 individuals/ha) and predators are absent, such as previously documented on Palmyra Atoll (Wegmann 2009). As evidence of their pronounced social behavior, multiple *R. rattus* individuals den together, and they do not typically occupy just one den site during the period that they are monitored (Dowding and Murphy 1994, Lindsey et al. 1999, Rutherford et al. 2009). Over a range of monitoring periods (1–20 weeks), *R. rattus* changed den sites to different trees one to three times at Hakalau Forest on Hawai'i Island (Lindsey et al. 1999), three to five times in the Rotoehu Forest, North Island, New Zealand (Hooker and Innes 1995), two to nine times in Puketi Forest, North Island, New Zealand (Dowding and Murphy 1994), and one to 11 times in Kahanahāiki Forest on O'ahu (Shiels 2010).

Determining *R. rattus* home ranges helps elucidate rat distribution and habitat preference and assists with rat control strategies such as trap and bait-station spacing (Howald et al. 2007). Home ranges of *R. rattus* in two montane mesic forests on O'ahu (1.5–9.1 ha [Shiels 2010]) were nearly as variable as those in a South Island, New Zealand, beech forest (0.3–11.4 ha [Pryde et al. 2005]). Other New Zealand studies in North Island forests found that *R. rattus* home ranges were much smaller (e.g., 0.3–1.8 ha in a study by Dowding and Murphy [1994], and 0.3–2.2 ha in Hooker and Innes [1995]). When 55 *R. rattus* were monitored in Hawaiian macadamia nut orchards, average home-range sizes were 0.2 ha (Tobin et al. 1996). Lindsey et al. (1999) determined that *R. rattus* home range averaged 4.2 ha for three males and was 1.8 ha for one female in montane wet forest on Hawai'i Island. Male *R. rattus* often have larger home ranges than females (two times larger in Whisson et al. [2007]; three times larger in Hooker and Innes [1995]; more than nine times larger in Pryde et al. [2005]), yet average home range sizes do not always differ between sexes (Dowding and Murphy 1994, Shiels 2010). Movements between captures can range from 18 to 174 m (Clapperton 2006), and in Hawaiian mesic forest the maximum distances that *R. rattus* ($n = 12$) was recorded from den sites during nighttime foraging averaged 45 m (Shiels 2010).

REPRODUCTION AND POPULATION DYNAMICS

Owing to the prolific nature of rodents, rapid, exponential increases in populations are common (Krebs et al. 1973), especially on islands (Martin et al. 2000). The female *R. rattus* reproductive biology includes an estrous cycle of 4–6 days, a 20- to 22-day gestation period, and 21–29 days to complete weaning (Innes

2005*a*). According to laboratory studies, *R. rattus* reaches sexual maturity at 2–4 months (Watts and Aslin 1981). *Rattus rattus* is capable of having litters every 32 days (range, 27–38 [Innes 2005*a*]), and four to six litters per year is common (Tobin et al. 1994, Efford et al. 2006). Each litter typically averages 3–6.5 individuals (Tobin et al. 1994), yet in laboratory trials the litter size ranges from three to 10 and averages five to eight (Innes 2005*a*). On a small New Zealand island, Moller and Craig (1987) found that female *R. rattus* produced 19–21 young per year (in three litters). *Rattus rattus* is not monogamous, and multiple paternity in a single litter has been demonstrated for wild *R. rattus* (Miller et al. 2010).

Rattus rattus density can vary greatly among sites and islands in the Pacific. For example, density estimates for *R. rattus* in Hawai'i include 0.7 individuals/ha in high-elevation shrubland (Amarasekare 1994), 3.6 individuals/ha in lowland wet forest (Beard and Pitt 2006), 7.1 rats/ha in montane mesic forest (Shiels 2010), and 8–15 individuals/ha in lowland dry forest (Tamarin and Malecha 1971). In New Zealand, *R. rattus* density estimates in forests ranged from 0.5 to 6.8 rats/ha (Dowding and Murphy 1994, Hooker and Innes 1995, Brown et al. 1996, Innes et al. 2010). *Rattus rattus* populations on Pacific islands have densities comparable with those within its native range in India, which includes 14.5 individuals/ha in tropical forest (elevation 340–2,400 m) (Chandrasekar-Rao and Sunquist 1996) and 2–36 individuals/ha in tropical forest and savannah (elevation 1,800–2,500 m) (Shanker and Sukumar 1999); however, density comparisons should be interpreted cautiously because of the wide range of factors that are dissimilar among rat-trapping studies (e.g., habitat, trapping regime, rodent species composition, abundance and density calculation).

Estimates of *R. rattus* abundances based on the number of individuals per 100 trap-nights were 8–17 in montane wet forest on Maui (Sugihara 1997), 8–14 in montane mesic forest on O'ahu (Shiels 2010), and 11–25 in montane wet forest on Hawai'i Island (Lindsey et al. 1999). In a study on South Island, New Zealand, Alterio et al. (1999) found that abundances of *R. rattus* ranged from 1.8 to 5.6 individuals/100 trap-nights. In a 5-yr study of *R. rattus* in North Island, New Zealand, Innes et al. (2001) found that abundances were 1–20 individuals/100 trap-nights (mean ca. 8–10). Other studies of *R. rattus* from North Island, New Zealand, found that abundances ranged from 5 to 35 individuals/100 trap-nights (Dowding and Murphy 1994, Wilson et al. 2007).

Determining the causes of pronounced population fluctuations and density differences among sites has been one of the greatest challenges in animal ecology (Krebs et al. 1973). Availability of resources, rainfall, predator abundance, and disease are all factors that can potentially influence population dynamics of *R. rattus*. For example, dramatic seasonal increases in rat and mouse populations in New Zealand were explained by several correlated factors including litter arthropods, beech (*Northofagus truncata*) flowers (Fitzgerald et al. 1996), fruit and seed availability (Alley et al. 2001), and predator populations (Efford et al. 2006). Studies in New Zealand have suggested that stoats and cats are key predators that may partly regulate *R. rattus* populations (Innes et al. 2001, Blackwell et al. 2003, Efford et al. 2006), and cats and mongooses are rodent predators in Hawai'i that may influence *R. rattus* populations (Tamarin and Malecha 1971, Shiels 2010). Food availability may be an important factor influencing rodent reproduction and abundance (Blackwell et al. 2003). Juvenile *R. rattus* abundance in mesic montane forests on O'ahu was highest in June–December, which coincides with the seasonal timing of the heaviest fruiting and seed fall of *Psidium cattleianum* (June–October) and may influence the reproductive timing and juvenile abundance of *R. rattus* (Shiels 2010). *Psidium cattleianum* is a common tree in most wet and mesic forests in Hawai'i that produces high seed rain, and it is a highly desired food item for *R. rattus* (Shiels and Drake 2011, Shiels et al. 2013). Late summer and autumn are also seasons when juvenile *R. rattus* abundance is highest in lowland dry forest on O'ahu (Tamarin and Malecha 1971) and in New Zealand (Innes et al. 2001).

There are typically more male rats in a given population than females (Sugihara 1997, Innes 2005*a*,*b*), and peak *R. rattus* densities (all age classes and both sexes) occurred from October through January (autumn and winter) in montane and coastal forest on O'ahu (Tamarin and Malecha 1971, Shiels 2010). Similarly, in a 27 yr snap-trap study in Orongorongo Valley, New Zealand, autumn and winter were also the peak seasons for *R. rattus* density (Efford et al. 2006).

Maximum survival of *R. rattus* is about 2 yr in the wild, but mean survival is usually 1 yr or less (Weinbren et al. 1970, Shiels 2010). In the laboratory, however, mean longevity for *R. rattus* is much longer, and Bentley and Taylor (1965) recorded average life spans of 3.9 yr for males and 3.4 yr for females. Annual disappearance rates for *R. rattus* during a 2 yr live-trapping study exceeded 90% for both sexes in the Orongorongo Valley, New Zealand. Few rats survived more than a year in the field, and the maximum longevity recorded was 11 months for males and 17 months for females (Daniel 1972). In Hawaiian montane forest, *R. rattus* individuals that were recaptured at the end of a 2 yr study had lived 10.9 ± 1.4 months (mean ± SE), and four of 18 individuals were alive at 19 months of age (Shiels 2010).

NATURAL ENEMIES

Cats (*Felis catus*) and owls (particularly the Barn Owl *Tyto alba*) are the most ubiquitous predators of *R. rattus* on most Pacific islands, and these predators are generally nocturnally active like *R. rattus*. Other raptors, primarily hawks and eagles, also consume *R. rattus* on Pacific islands. Mongooses (*Herpestes auropunctatus*) consume *R. rattus* on several Pacific islands (Hays and Conant 2007). In New Zealand, *Mustela* spp. (stoats, weasels, and ferrets) are predators of *R. rattus*. Several species of civets (Viverridae), which are nocturnal mammals, are predators of *R. rattus* in the Philippines (Rickart et al. 1993). Monitor lizards (*Varanus indicus*) and the brown tree snake (*Boiga irregularis*) are predators of *R. rattus* in the Mariana Islands (Wiewel et al. 2009), and *R. rattus* has been found in the gut of several brown tree snakes in Guam (R.T.S., unpubl. data). In Tasmania, Tasmanian devils (*Sarcophilus harrisii*) and quolls (*Dasyurus* spp.), which are carnivorous marsupials, introduced foxes (*Vulpes vulpes*), feral cats, and raptors are predators of *R. rattus* (H. Stephens, pers. comm.). Skua (*Stercorarius* spp. [a predatory seabird]) are capable of consuming *R. rattus*, but there have not been any such reports for Pacific islands.

RESPONSE TO MANAGEMENT

Much interest in Pacific island rodent management occurred during the late 1800s and early 1900s as a result of expanding plantation agriculture and associated rodent damage. An additional period of increased interest in rodent research and management in the Pacific occurred during the 1940s–1950s, and it was associated with increased military operations in the Pacific and heightened incidences of rodent-borne diseases (Wilson 1968). Such interests initiated several multiyear research projects that focused on rat ecology and control in the Pacific; perhaps the most substantial ones were in Ponape (Pohnpei) from 1955 to 1958 (Storer 1962), Enewetak (Eniwetok) Atoll from 1964 to the late 1970s (Devaney et al. 1987), the Philippines from 1967 to 1983 (Fall and Sumangil 1980, Singleton and Petch 1984), Malaysia during the late 1970s (Dubock 1984, Richards and Ku 1987), and Hawai'i from 1960 to the 1970s for bubonic plague monitoring research (Tomich et al. 1984) and 1966 to the present for ecology, crop damage evaluation, toxicant screening and registration, and conservation (Sugihara 2002, Pitt et al. 2011*a*).

The longest-standing and most common control measures that have been implemented are chemical control using rodenticides, physical control, and exclusion. Biological control has been unsuccessfully attempted several times with often unexpected and negative secondary effects. Often there are multiple control measures used simultaneously, woven into an integrated pest management strategy to control rodents (Witmer 2007). The management of rodents can be broadly separated into two distinct operational approaches:

control and eradication. Rodent control (population and damage reduction) has historically been used to protect agricultural crops, human health, and natural resources. Control projects attempt to minimize the effects of rodents but require ongoing operations. Efforts to eradicate rodents from islands or fenced areas attempt to remove all rodents from an area over a short period and then maintain the area as rodent free using quarantine methods. Although eradicating rodents from small areas has been accomplished using ground-based trapping and persistent control methods, techniques developed over the last 20 yr to effectively aerially broadcast rodenticides have enabled much larger areas to be targeted (Howald et al. 2007). Since eradication programs began on small islands in the early 1960s, rats have been removed from over 300 islands around the world (Howald et al. 2007, Towns 2009, Witmer et al. 2011).

Gaining local community support for rat control or eradication, particularly when it involves the use of toxicants (rodenticides), is an important yet often difficult procedure. Ogden and Gilbert (2009) identified three reasons why gaining local support for rat eradications is typically challenging: (1) a lack of appreciation of the ecological damage resulting from rats, and therefore a low priority placed on their elimination, (2) suspicion by community members that conservationists want access to private lands and island-wide biosecurity, and 3) numerous regulatory barriers that delay decisions and actions and ultimately result in disinterest in such projects. Witmer et al. (2011) discussed many other challenges to invasive rodent eradication on islands.

Chemical Control

Rodenticides, such as those containing the anticoagulants diphacinone or brodifacoum, have been used on many Pacific islands to control *R. rattus*; one benefit over trapping is that rodenticide bait can simultaneously affect many rats over longer periods than a single baited trap. Rodenticide baiting is also generally less labor-intensive than trapping. Witmer et al. (2007) reviewed the use of rodenticides for conservation efforts. Hawaiian sugarcane growers began using a myriad of mostly acute rodenticides (e.g., strychnine alkaloid, 1080) in the late 1800s, but due to environmental health and human safety concerns these acute rodenticides were replaced in agricultural settings by first- and second-generation anticoagulant products like those containing warfarin or diphacinone (Sugihara 2002). Anticoagulants became the toxicants of choice for controlling rats beginning in the 1950s and were applied by placing the poison in plastic baggies and tossing them into agricultural fields and surrounding habitat (Lindsey et al. 1971). Threats to nontarget animals, including humans eating feral pigs (*Sus scrofa*) that were contaminated with rodenticides such as diphacinone, prompted the use of tamperproof bait stations (Tobin et al. 1990, Pitt et al. 2011*c*). Bait stations are used in agricultural, urban, and natural areas in contemporary Pacific islands to help control rodents. Bait degradation by fungi (especially in wet habitats) and consumption by ants, slugs, and other invertebrates reduces bait availability and palatability (Tobin et al. 1990, Mosher et al. 2010). In addition, prolonged use of a single type of rodenticide decreases its effectiveness (Doty 1945).

Pitt et al. (2011*a*) tested the efficacy and palatability of nine commercial rodenticide bait formulations; second-generation anticoagulants (e.g., brodifacoum) generally had the highest efficacy on *R. rattus*. Several types of toxicant baits require multiple feedings by each individual rat (e.g., diphacinone), whereas others are more toxic and typically require fewer feedings for a lethal dose (e.g., brodifacoum). Witmer et al. (2011) identified 40 islands or archipelagos in the United States where rodent (primarily *Rattus* spp.) eradication has been attempted, of which approximately half were Pacific islands, and almost all of them had used diphacinone; approximately 75% of these eradication attempts were successful. The larger islands where eradication has been attempted in the Pacific include Rat Island (2,900 ha) in Alaska where *R. norvegicus* was the target rodent species (Howald et al. 2007), and most recently Macquarie Island

(128,860 ha) where *R. rattus* and *M. musculus* were the target rodents (Springer 2011).

Natural and artificial scents have been tested for their effectiveness in deterring *R. rattus* from particular food items. Synthetic scents were unsuccessful at deterring *R. rattus* from macadamia nut trees in Hawai'i (Burwash et al. 1998); yet mongoose urine and feces deterred *R. rattus* from traps in Hawai'i (Tobin et al. 1995). Capsaicin from chili fruits (*Capsicum annuum*) helped reduce *Rattus* spp. predation of bird eggs in New Zealand (Baylis et al. 2012). Price and Banks (2012) recently tested the effectiveness of pre-exposing *R. rattus* to scents of native species to potentially protect them before reintroducing such native species into areas with *R. rattus*. When *R. rattus* had encountered the prey odor (quail feces and feathers) before encountering the prey (quail eggs, which were used as surrogates to native bird eggs), there was a 62% reduction in quail egg predations relative to areas where the prey and odor were introduced simultaneously (Price and Banks 2012). It is unlikely that use of odors would be an effective long-term rat deterrent because individuals become accustomed to foreign scents and objects over time (Clapperton 2006).

Campaigns to sterilize wild rats were also attempted where the chemosterilant was administered in bait. Despite the successful sterilization of male rats in the laboratory, field trials failed as evidenced by many female rats impregnated in populations containing "sterile" males (Bowerman and Brooks 1971). Fumigating rat dens with poison gas has been attempted to reduce *R. rattus* populations, but it was also unsuccessful (Doty 1945).

Nelson et al. (2002) measured the costs and effectiveness of rat control (*R. rattus* and *R. exulans*) over 3 yr (January–April each year) using toxic bait and snap-traps in a remote Hawaiian montane rain forest. A 48 ha treatment area was monitored before, during, and after control. The cost was about US$7000/km^2 ($70/ha) to reduce the rat population 58%–90% during 1 yr, yet the rat population rebounded from incursion from the perimeter each year such that rat numbers had returned to pretreatment levels by the beginning of the subsequent treatment. After the first year, the costs decreased to about $2000/km^2 ($20/ha). The authors' main conclusion from the study was that it is feasible to reduce rat abundance during a 4-month period each year during the forest bird breeding season (Nelson et al. 2002).

Howald et al. (2007) collated economic costs for 47 eradication campaigns that used toxicant bait; costs varied widely by island even when standardized by size (US$3000–$20,000/ha [adjusted to 2005 prices]) and bait delivery method (aerial broadcast, hand broadcast, bait station). Minimizing impacts of rodenticides to nontarget animals while ensuring that enough bait remains to expose all of the rats is important for successful rodent eradication programs (Witmer et al. 2007, Witmer et al. 2011).

Physical Control

Physical control methods (e.g., trapping, fencing) are frequently used to manage *R. rattus* because they do not require the use of toxicants. Both live- and kill-trapping techniques have been used to control *R. rattus* throughout the Pacific (see Sugihara et al. 1977). Continuous trapping campaigns almost certainly increases trap shyness, thereby affecting the degree to which rat populations are reduced and desired resources are protected (Tobin et al. 1990, Mosher et al. 2010). Many other factors may cause failure in rat control programs, and such factors may not always be obvious. For example, between 1914 and 1922, averages of 141,000 rats were removed annually using trapping methods from sugarcane plantations on Hawai'i Island, yet there was no apparent effect on the populations of the rats, and sugarcane continued to be damaged (Pemberton 1925).

Most trapping regimes place traps on the ground for ease of maintenance. However, in macadamia nut orchards in Hawai'i, Tobin et al. (1994) established snap-traps (41–49 traps/ha) in 8 to 11 ha blocks by attaching the traps to lower lateral branches in the trees. New Zealand and Hawai'i have both established large trapping grids in natural areas to control *R. rattus* and other rodents. In these large trapping grids, traps are checked,

rebaited, and reset approximately every 2 weeks for several years or decades (King et al. 2011*b*, Pender et al. 2013). In Hawai'i, such large-scale (26 ha, 440 traps) snap-trapping grids have reduced *R. rattus* abundance and subsequently their fruit removal and seed predation of an endangered plant (Pender et al. 2013). However, Ogden and Gilbert (2009) found that trapping alone was not enough to reduce rat (primarily *R. rattus*) numbers for successful avian reintroductions on Great Barrier Island, New Zealand. After determining that ground-based rodent control was ineffective for improving nest success of the endangered cavity-nesting Kaua'i Thrush, puaiohi (*Myadestes palmeri*), Pitt et al. (2011*b*) developed a ratproof artificial nest box, using a design that was essentially a 36 cm length of 15 cm diameter plastic pipe with an entrance cut at an angle of 49 degrees. Multiple techniques are often needed to conserve and restore native species that are vulnerable to *R. rattus*.

Predatorproof fencing has been used in New Zealand for over a decade to wall-off problematic mammals (Scofield et al. 2011). More recently (within the last 3 yr), other Pacific islands have begun to use predatorproof fencing to keep predators that are the size of *M. musculus* and larger out of natural and conservation areas. At Ka'ena Point Natural Area Reserve on O'ahu, the number of breeding pairs of some seabirds, such as the Laysan Albatross (*Phoebastria immutabilis*), has apparently increased by 15%, and Wedge-tailed Shearwater (*Puffinus pacificus*) chicks have tripled since the installation of the predatorproof fencing and the removal of introduced *R. rattus*, *M. musculus*, mongoose, cats, and dogs (Pala 2012). Often the individual impacts of *R. rattus* are unknown or cannot be easily determined because methods of control (e.g., trapping, toxicants, rodentproof fences) can apply to multiple invasive rodent species (e.g., mice, rats) and in many cases nonrodent species (e.g., mongoose, stoats). The cost-effectiveness of predatorproof fencing in New Zealand is commonly debated, and Scofield et al. (2011) described the areas enclosed by predatorproof fencing as large zoos that do not allow population expansion and do not make economic sense over other methods of predator control. However, for animals that rely upon particular areas for annual reproduction (e.g., seabird nesting sites) or endangered animals that do not migrate great distances (e.g., tree snails), predatorproof fencing may be a particularly useful conservation technique.

Biological Control

Predators of *R. rattus* have been intentionally introduced to some Pacific islands in attempts to reduce the negative effects of rats. The small Indian mongoose is currently found in eight Pacific islands, including four in the Hawaiian Islands, two in Fiji, and two in Japan (Hays and Conant 2007). Although rodents were the dominant part of the mongoose diet in some Hawaiian sugarcane fields (Baldwin et al. 1952), rodents continued to thrive after mongoose introduction. In 1958, Hawai'i's Commissioners of Agriculture and Forestry approved the introduction of the Barn Owl to help control rodents (Tomich 1962), but this measure largely failed despite Barn Owls consuming many rats. Failed biocontrol attempts are worsened when the species introduced becomes problematic for native species or human health and safety (Pitt and Witmer 2007). For example, in contemporary Hawai'i, the Barn Owl and mongoose are predators of some native birds (Funasaki et al. 1988, Hays and Conant 2007; F. Duvall, pers. comm.). In addition, it is important to consider the eradication or control of introduced *R. rattus* from a multitrophic-level perspective (e.g., Zavaleta et al. 2001, Caut et al. 2009) because these rats are highly integrated into the food web (Figure 3) and consume both native and nonnative (in some cases highly invasive) organisms. In some situations, removal of rats can have negative repercussions by benefitting coexisting nonnative species (e.g., *M. musculus*, which is often a competitor with *R. rattus*), and these may include (1) extensive population growth, (2) equivalent or larger impacts than those of introduced *R. rattus*, and (3) greater difficulty of eradication relative to *R. rattus* (e.g., Courchamp et al. 1999, Zavaleta et al. 2001, Caut et al. 2007, Meyer and Shiels 2009).

Dogs (*Canis lupus familiaris*) can be used to detect rats on islands. To prevent rodent reinvasion of islands, parts of New Zealand utilize specially trained rat dogs to find introduced *Rattus* spp. and *M. musculus* in conservation areas and on cargo transported between ports and islands (Towns 2009, Gsell et al. 2010). Additional rat control methods that have been historically attempted to reduce rat populations include destroying habitat around agricultural fields (Sugihara et al. 1977, Sugihara 2002) and introducing viral diseases (Doty 1945).

PROGNOSIS

When *R. rattus* arrived on most Pacific islands, there was probably at least one other nonnative rat species present (most likely *R. exulans*); therefore, the magnitude of ecosystem change resulting from *R. rattus* introduction may have been less than if no other rodents had been present. However, contemporary studies have indeed depicted *R. rattus* as the rodent species responsible for the most detrimental impacts on islands (Towns et al. 2006, Jones et al. 2008, Ruffino et al. 2009, Traveset et al. 2009). With a highly omnivorous diet (Figure 3), few organisms are safe from possible predation and/or indirect consequences of *R. rattus* invasion. There are many factors that may affect the future distribution of *R. rattus*, including changes in land uses, climate, and additional ecological factors such as the changes in densities, distributions, and dominance of other invasive rodents, particularly *M. musculus* and *R. norvegicus*. *Rattus rattus* will almost certainly continue to negatively affect the human food supply, spread disease, and alter native ecosystems.

Increased rat control and eradications across larger insular areas are expected in the future as tools and technology continue to improve. To ensure that such control and eradication campaigns are of value and will succeed, we first suggest that the conservation, human health, or economic goals are clear and feasible before initiation of the campaign. Local field research is necessary to identify species or ecosystem functions that suffer impacts from *R. rattus*. An understanding of the local food web will help reduce the chances of unexpected or negative consequences resulting from *R. rattus* removal (e.g., *M. musculus* population increases, which is often a more difficult species to eradicate than *R. rattus* [Harper and Cabrera 2010]), as well as help guide actions that will minimize both nontarget impacts and pollution from toxicants (Bowie and Ross 2006). Second, gaining social acceptance for the campaign is often an underestimated barrier to success; outreach and education early in the campaign as well as clear articulation of the goals and expected responses of the local species should therefore be disclosed (Moors et al. 1992, Ogden and Gilbert 2009). Finally, it is critical to secure posteradication funding and operational commitments for biosecurity and reinvasion response. To ensure success, posteradication monitoring and prevention of *R. rattus* reinvasions must occur indefinitely.

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