ECOLOGY AND IMPACTS OF INTRODUCED RODENTS (*RATTUS* SPP. AND *MUS MUSCULUS*) IN THE HAWAIIAN ISLANDS

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We certify that we have read this dissertation and that, in our opinion, it is satisfactory in scope and quality as a dissertation for the degree of Doctor of Philosophy in Botany (Ecology, Evolution, and Conservation Biology).

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For Opa

(Martin C. Pohle, 1907-2002)

and

My Parents

(Stephen and Linda Shiels)

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I am most grateful for my wife, Laura Shiels, and all of the support that she has furnished during the past 10 years. She has provided me with the necessary balance in my life. I am also grateful to my parents (Steve and Linda) and brother (Josh) for continually giving me opportunities and a wealth of support that has helped me to get to where I am today.

ABSTRACT

Introduced rats (*Rattus rattus*, *R. norvegicus,* and *R. exulans*) and/or mice (*Mus musculus*) occur on more than 80% of the world's island groups, where they pose great threats to native species. Understanding the interactions between these introduced rodents and the environments which they have invaded can assist in land management and conservation efforts on islands. In three mesic forests in the Waianae Mountains, Oahu, Hawaii, rat and mouse abundances were estimated using mark-and-recapture, microhabitat use and den sites were determined using spool-and-line tracking, and rat home-ranges were estimated using radio-tracking. The diets of three of the rodents (*R. norvegicus* was absent from the three sites) were assessed using stomach content and stable isotope analyses. Additionally, field and captive-feeding trials were used to assess fruit and seed removal and consumption, and seed predation and dispersal, by *R. rattus*. *Rattus rattus* dominates these forests in abundance (7.1 indiv./ha) relative to the two smaller rodents, *R. exulans* (0.3 indiv./ha) and *M. musculus* (3.7 indiv./ha). Home-range estimates for *R. rattus* (N = 19) averaged 3.8 ha, and the single radio-tracked *R. exulans* had a home-range of 1.8 ha. Except for one individual *M. musculus,* all den sites of *R. exulans* and *M. musculus* were belowground, whereas dens of *R. rattus* were both above- and belowground. Most (> 88%) rodent activity occurred in areas where vegetation closely (10-30 cm above individuals) covered the rodent; 70% of the monitored movements of both *M. musculus* and *R. exulans* were on the ground surface, whereas *R. rattus* was mainly arboreal (32% ground, 64% arboreal) and was typically observed at ca. 3 m height when aboveground. Consistent with the evidence for (micro-) habitat partitioning among these three rodents, the diets of the three rodents may also provide evidence of niche partitioning. *Rattus exulans* had an intermediate diet (stomachs containing 60% plant and 38% arthropod; N = 12) between the more carnivorous *M. musculus* (36% plant, 57% arthropod; N = 47) and the more vegetarian *R. rattus* (81% plant, 14% arthropod; N = 95); yet the lifetime average diet determined by stable isotope analysis (δ^{15}N and δ^{13}C) of bone marrow of *R. exulans* was indistinguishable from the lifetime diet of *M. musculus*.

The likelihood of seed predation and dispersal by *R. rattus* was tested with field and laboratory experiments. In the field, fruits of eight native and four non-native common woody plant species were arranged individually on the forest floor in four treatments that excluded vertebrates of various sizes. Eleven species had a portion (3-100%) of their fruits removed from vertebrate-accessible treatments, and automated cameras photographed only *R. rattus* removing fruit. In the laboratory, *R. rattus* were offered fruits of all 12 species used in the field trials, as well as 21 of the most problematic non-native species in Hawaii, to assess consumption and seed fate. Rats ate pericarps (fruit tissue) and seeds of most species, and the impacts on these plants ranged from potential dispersal of small-seeded (≤ 1.5 mm length) species that survived gut passage (e.g., the native *Kadua affinis*, and the non-natives *Clidemia hirta*, *Buddleia asiatica*, *Ficus microcarpa*, *Miconia calvescens*, and *Rubus rosifolius*) to predation where < 35% of the seeds survived. Many species had some partly damaged or undamaged seeds that survived rat exposure. Combining field and laboratory findings indicates that many interactions between *R. rattus* and seeds of native and non-native plants may result in seed dispersal. Therefore, rats are likely to be affecting plant communities through both seed predation and dispersal, and these findings should be applied to aid land management efforts where introduced rodents have invaded.

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CHAPTER ONE:

INTRODUCTION

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Animals play an important role in structuring plant communities and modifying and maintaining ecosystem function (Janzen 1970; Gilbert 1980; Vitousek 1990; Jones et al. 1997). Through such processes as pollination, seed dispersal, and seed predation, animals can directly affect plant reproduction (Janzen et al. 1976; Regal 1977; Gilbert 1980; Jordano 2000; Forget et al. 2005). In tropical ecosystems, most plant species depend on animals for seed dispersal (Howe and Smallwood 1982; Howe 1986; Janson 1983; Jordano 2000). Fruit and seed removal by animals can have both positive and negative effects on plant fitness, depending, in part, on whether seeds are destroyed or left intact for germination. Seed dispersal is a critical component of regeneration and the spatial heterogeneity of vegetation (Schupp and Fuentes 1995; Reed et al. 2000). Seeds dispersed further from the parent tree often have relatively high fitness (Janzen 1970; Ausgspurger 1984; Portnoy and Willson 1993), thus highlighting the importance of the dispersers. Birds, bats, and primates are often the dominant groups of organisms contributing to primary seed dispersal (i.e., dispersal from the parent plant to the ground) in tropical regions (Howe 1986), yet secondary dispersal of fruit and seed (i.e., dispersal after the seed is on the ground) is also important for plant recruitment and determining vegetation structure (Janzen 1971; Schupp 1995; Schupp and Fuentes 1995). Tropical trees often experience extensive seed predation following animal dispersal (Janzen 1971; DeSteven and Putz 1984; Howe et al. 1985; Wenny 2000), including seed predation by rodents (Crawley 1992; Forget 1993; Wenny 2000), and this results in the termination of the regeneration process.

Plant-animal interactions on island ecosystems are unique because of the general paucity of both plant and animal species present (although there are proportionally more endemics) relative to continental equivalents (MacArthur and Wilson 1967; Carlquist 1974). The Hawaiian Archipelago is a prime example of this; the extreme isolation from other land masses is a strong barrier to plant and animal colonization. As a result, many of the descendants of the species that successfully colonized Hawaii experience close interactions with other organisms that affect both the functioning (e.g., diet) and reproduction (e.g., pollination, seed dispersal) of the organism (Freed et al. 1987).

Rapid ecosystem changes occur following human colonization of islands, such as Hawaii where over 1000 native species have gone extinct (Allen 2000). Land conversion and the introduction of non-native species, both actions directly caused by humans, can drastically change island habitats and plant-animal interactions (Vitousek 1990; Vitousek et al. 1997; Wilcove et al. 1998). While some non-native species have pronounced effects on particular biota (e.g., erythrina gall wasp, *Quadrastichus erythrinae*, on coral trees, *Erythrina* spp.; Rubinoff et al. 2010) or particular habitat types (e.g., non-native fountain grass, *Pennisetum setaceum*, in dry forests; D’Antonio and Vitousek 1992), there is one non-native species that appears to be affecting multiple species at multiple levels of the food web, and in all terrestrial habitats in Hawaii: the rat (*Rattus* spp.).

Rodents, such as rats, commonly act as seed predators in tropical environments (Crawley 1992; Forget 1993; McConkey et al. 2003). For example, in a montane forest in Costa Rica, post-dispersal seed predation was high (99.7%) for a dominant tropical tree, and over 50% of seed removal was due to small rodents (Wenny 2000). Additionally, rodents may have positive effects on plant recruitment by scatterhoarding seeds or only partially consuming them (Forget 1993; Hulme 1997; Vander Wall 2005). The impacts of seed removal on plant regeneration can be species dependent, and this process may be substantially influenced by rodents (Mendoza and Dirzo 2007). In the Pacific, invasive non-native animals such as pigs (*Sus scrofa*), rats, and mice (*Mus musculus*) can have pronounced effects on the flora and fauna of insular ecosystems (Williams et al. 2000; McConkey et al. 2003; Bieber and Ruf 2005; Towns et al. 2006) like those in Hawaii (Atkinson 1977, 1989; Tomich 1986; Cabin et al. 2000, Staples and Cowie 2001). For example, the introduction of the Polynesian rat or Pacific rat (*Rattus exulans*) is often proposed as a major contributor to the decline of the native Hawaiian palm loulu (*Pritchardia* spp.) that was once a common, perhaps dominant, tree across Oahu as well as much of the lowland forests on other Hawaiian Islands (Athens 1997; Athens et al. 2002). In contemporary Hawaii, rats (probably *R. rattus*), not pigs or mice, were found to rapidly remove *Pritchardia affinis* and *P. hillebrandii* fruits (> 50% removed within 6 days; > 80% within 22 days) from the forest floor (unpublished data). Mice in high-elevation shrubland on Maui fed on native and non-native fruit, grass seeds, and arthropods (Cole et al. 2000). Chimera (2004) showed variable patterns of seed removal by non-native rodents in a Hawaiian dry forest; all of the seeds of some species were removed within hours or days, whereas other species that were tested were never removed. Therefore, certain species of Hawaiian plants may be at risk due to seed predation by non-native rodents whereas other species are unlikely to be affected. Clearly, the potential exists for non-native rats and mice to alter forest structure (composition, distribution, diversity) by destroying and/or dispersing native and non-native plant species, yet few quantitative data on this subject exist. Instead, current management activities addressing the interaction of non-native rodents and plant communities are largely based on anecdotal information. Thus, further study is needed to understand the impact of non-native rodents (particularly rats) on Hawaiian plant communities, and this will be the focus of my research. In particular, I will address the following questions:

1. How pervasive are rats and mice in Hawaiian mesic forests? What are their distributions, habitat uses, and seasonal fluctuations?
2. What are the diets of rats and mice in Hawaiian mesic forest?
3. Which of the dominant species in Hawaiian mesic forest have their diaspores (fruits + seeds) removed from the forest floor by rats and mice? What are the fates of such rodent-handled seeds?

These questions are focused to test the overall hypothesis that rats affect seed fate of some Hawaiian forest species through seed predation and seed dispersal.

Study Site

This study will occur in three mesic forest sites in the Waianae Mountains, northwest Oahu: Kahanahaiki in Makua Valley (KHI), Honouliuli Preserve in Kaluaa Valley (HON), and Makaha in Makaha Valley (MAK) (Fig. 1). Hawaiian wet and dry seasons, as defined by Blumenstock and Price (1967), include: a warm, dry 5-month summer (May-September) and a wet, cooler, 7-month winter (October-April). All three sites are in mesic forest spanning 500-660 m a.s.l. and have a similar, mixed flora that includes both native and non-native plant species. Vegetation phenology and species composition were described at the focal study site, KHI (Chapter 1; Appendix A, B, C), and at HON (Bakutis 2005) and MAK (T. Ticktin, unpublished data).

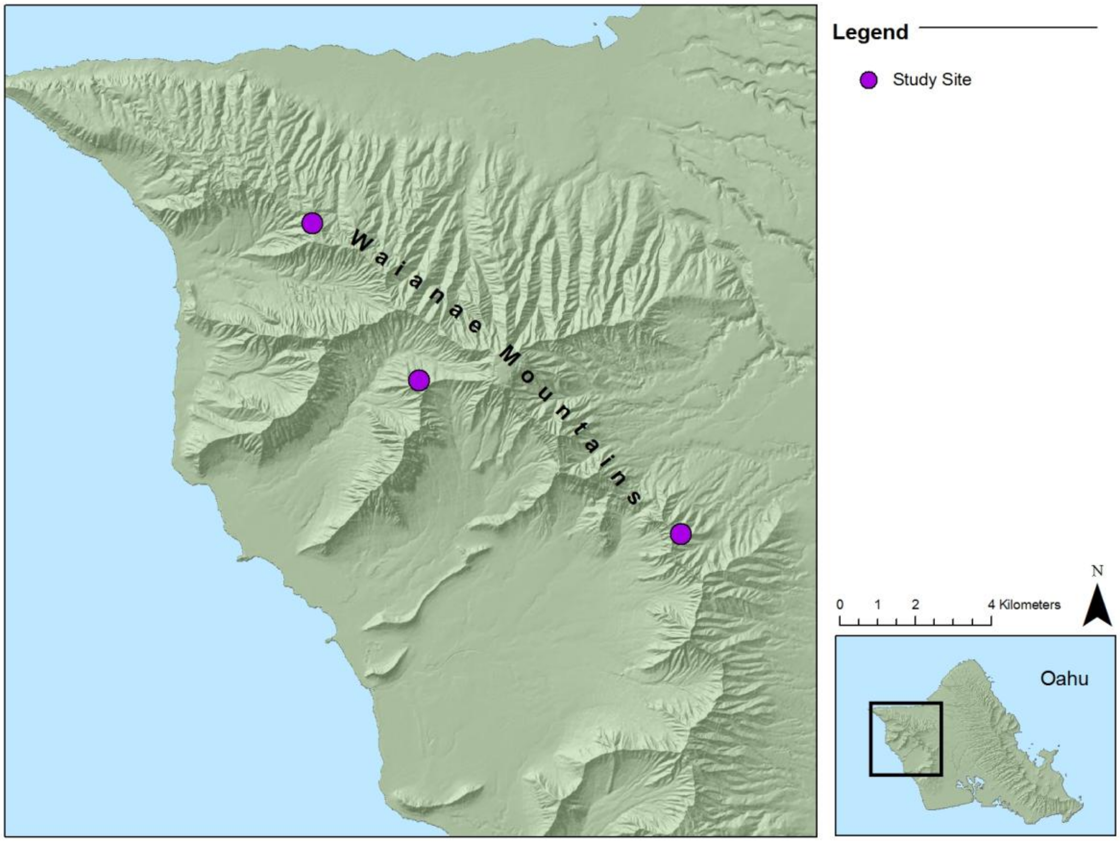

Figure 1. Map of the three study sites in the Waianae Mountains, Oahu, Hawaiian Islands. The study sites, from NW to SE, include: Kahanahaiki (KHI), Makaha (MAK), and Honouliuli (HON). KHI and MAK are the sites closest to each other (ca. 5 km, not accounting for topography).

At each of the three study sites, the dominant native trees include soapberry (*Sapindus oahuensis*), alahee (*Psydrax odorata*), lama (*Diospyros hillebrandii; D. sandwicensis*), and olopua (*Nestegis sandwicensis*). The native understory is dominated by maile (*Alyxia stellata*). Non-native vegetation, such as strawberry guava (*Psidium cattleianum*), coffee (*Coffea arabica*), Brazilian pepper tree (*Schinus terebinthifolius*), and silk oak (*Grevillea robusta*) are interspersed with the natives throughout the study sites.

Non-native animals appear to be common at, or adjacent to (e.g., Welton 1993), all three study sites. Sightings and physical evidence (e.g., chewed seeds and vegetation, soil and litter disturbance) of feral pigs, non-native rats (probably Pacific rats, *Rattus exulans*, and black rats, *R. rattus*), mice (*Mus musculus*), Erckel's francolin (*Francolinus erckelii*), mongoose (*Herpestes javanicus*), and feral cats (*Felis catus*) are common. All three sites have been fenced to exclude feral goats (*Capris hircus*) and pigs (*Sus scrofa*) and are actively managed to protect native species by Oahu Army Natural Resources. Despite the current and proposed management efforts for protecting native species, the effect of non-native animals (particularly the role of rats) on vegetation in the Waianae Mountains largely remains a mystery.

Rat History in Hawaii

The Pacific rat (*Rattus exulans*) was purposely or accidentally introduced to the Hawaiian Islands upon Polynesian arrival ca. 1000 years ago (Athens et al. 2002). This animal represents the first flightless arboreal mammal, and one of the first ground-dwelling mammals (pigs and dogs were also introduced by Polynesian voyagers) in Hawaii (Tomich 1969). Although this rat was a food source for Polynesians in New Zealand, Tomich (1969) explains that it may not have been a food source, but was a sporting animal for the Polynesian settlers who hunted it with miniature bows and arrows. Native to Southeast Asia, the Pacific rat is characteristically a lowland rodent in Hawaii but it has been recorded in montane rainforest up to 2000 m elevation (Sugihara 1997). It is especially abundant in sugarcane and pineapple fields, wooded areas, grassy gulches, and disturbed areas (Tomich 1969).

Upon Captain Cook's landing in 1778 and the discovery of Hawaii by Europeans, the house mouse (*Mus musculus*) was introduced, followed by the Norway rat or brown rat (*R. norvegicus*) and the black rat or ship rat (*R. rattus*) during the 1870s (Atkinson 1977). Each of these three rodents is native to Asia, and was unintentionally introduced to the Hawaiian Islands. The Norway rat is native to temperate Asia, and most abundant in cities and farms in Hawaii where food from domestic and agricultural sources are plentiful. Thus, it is an uncommon rodent in Hawaiian forest unless the forest is a low-to-mid-elevation wet forest (Lindsey et al. 1999) or planted forest (Tomich 1969). The black rat is endemic to the Indian subcontinent, and it spread to Britain with the Romans in ca. 20 B.C. (Reumer 1986). In contemporary Hawaii, the black rat is found in nearly every terrestrial habitat below 3000 m, and is particularly common at lower and middle elevations. The house mouse is perhaps the most ubiquitous rodent across Hawaii, and is found in most places that the black rat is found; however, the house mouse elevation range extends higher than the black rat, and on one occasion mice were documented in a cave at 3750 m in Hawaii (Tomich 1969).

Owing to the prolific nature of rodents, rapid, exponential increases in populations are common (Krebs et al. 1973), especially on islands (Granjon et al. 1992; Martin et al. 2000). For example, the Pacific rat is capable of having four to six litters (of just over four young each) per year on average (Kramer 1971), whereas black rat litters are similar and average 3-6.5 individuals (Tobin et al. 1994). On a small New Zealand island, Moller and Craig (1987) found that female black rats produced 19-21 young per year (in three litters). Because these rats are not monogamous, evidence of multiple paternity in a single litter has been recently demonstrated for wild black rats and Norway rats (Miller et al. 2010). Many of the early studies in Hawaii were inspired by the periodic and dramatic increases in rat population density. These studies focused on arresting crop damage by rats (e.g., sugarcane, macadamia nut; Fellows and Sugihara 1977; Tobin et al. 1993). Human diseases associated with introduced rodents stimulated further studies.

Rodents in Hawaii have been known carriers of the following diseases: murine typhus, leptospirosis, salmonellosis, and bubonic plague (the latter transmitted to humans by fleas that colonize rodents). Plague (infection by *Yersinia pestis*) was present in Hawaii for the period 1899-1957 and caused at least 370 fatalities. Several areas of Hawaii and Maui were bubonic plague epidemic hotspots, and the last reported case of human infection of bubonic plague occurred in 1949 (Sugihara 2002). The disease arrived from black rats and/or Norway rats from the Orient, and the carriers then contaminated rats that were already in Hawaii. There were two fleas—one that accompanied Pacific rats and one that accompanied black rats—that became carriers of the bacteria. Thankfully, the disease was unable to be maintained over time; perhaps because of improved sanitation, mechanized agriculture, and the collapse of reservoir and vector populations during droughts (Tomich et al. 1984).

Introduced rats have been a major threat to agriculture and human health in Hawaii for at least the past 170 years (Tobin et al. 1990). In 1990, it was estimated that annual revenues from sugarcane alone in Hawaii exceeded $350 million (Tobin et al. 1990). Although some estimates of annual losses from rat destruction of sugarcane averaged ca. 11% (Tobin et al. 1990), it was not uncommon to lose ca. 30% of a sugarcane crop to invasive rodents (Hood et al. 1971). To combat these severe economic losses, substantial funding was allocated to research and control of invasive rodents in Hawaiian agricultural settings (e.g., Hawaiian Sugar Planters' Association; Denver Wildlife Research Center; Tobin et al. 1990). Control measures that were quickly implemented included: large-scale trapping, poisoning, and the introduction of bio-controls such as the small Indian mongoose (*Herpestes javanicus*) in 1883 (Doty 1945). Although mongoose was a substantial predator of rodents, and diet analysis from mongoose captured in sugarcane fields revealed primarily rodent parts (Baldwin et al. 1952), rodents continued to thrive. Extensive trapping campaigns were also ineffective. For example, between 1914 and 1922, averages of 141,000 rats were removed annually from sugarcane plantations on Hawaii Island, yet there was no apparent effect on the populations of the rats or on sugarcane damage (Pemberton 1925). Additional rat control methods that were attempted and proved unsuccessful included: fumigating rat den sites with poison gas, destroying habitat around sugarcane fields, using dogs, and introducing viral diseases (Doty 1945; Sugihara et al. 1977; Tobin et al. 1990).

Rodenticides (e.g., 1080, strychnine) have been used by Hawaiian sugarcane growers since the early 1900s, and despite their early effectiveness, they became less useful because of their sublethal poison bait promoted subsequent bait shyness (Doty 1945; Tobin et al. 1990). In 1958, Hawaii's Commissioners of Agriculture and Forestry approved the introduction of the barn owl (*Tyto alba*) to help control rodents (Tomich 1962), but this measure largely failed despite barn owls consuming many rats. Anticoagulants (e.g., warfarin, diphacinone) became the toxicants of choice beginning in the 1950s and were applied by placing the poison in plastic baggies and tossing them into agricultural fields and surrounding habitat. Threats to non-target animals, including humans eating contaminated feral pigs, prompted the use of tamperproof bait stations (Tobin et al. 1990). Such bait stations are used in natural areas in contemporary Hawaii to help control rodents, despite their ineffectiveness to control rodents in agricultural fields (Lindsey et al. 1971). Additionally, bait degradation by fungi and slug consumption reduces bait-take and subsequent sublethal consumption of the poison reduces its effectiveness (Mosher et al. 2010). Continuous application of rodenticide and trapping campaigns almost certainly increases trap shyness (Hood et al. 1971; Tobin et al. 1990; Mosher et al. 2010). 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 portions of female rats impregnated in populations containing ‘sterile’ males as being equal to those in control populations where males were not sterilized (Bowerman and Brooks 1971). In modern Hawaii, variations of each of the aforementioned trapping and poisoning techniques have been applied in efforts to control invasive rodents, and new technology like aerial broadcast of toxicants has recently (February 2008) eliminated rats from one very small offshore island (4 ha Mokapu Island) in Hawaii; however, rats continue to thrive in most terrestrial habitats on all of the major Hawaiian Islands.

Following the closure of the sugarcane industry in Hawaii, research has largely shifted from reducing rodent effects on agricultural resources to documenting the negative effects of rats on Hawaiian snails (Hadfield et al. 1993) and birds (Kepler 1967; Atkinson 1977; Amarasekare 1993; VanderWerf 2001; VanderWerf and Smith 2002;

VanderWerf 2009). Understanding the ecosystem impacts resulting from these novel, non-native animals is essential for land-management and the conservation of biodiversity. Because the Hawaiian biota evolved largely without defenses against mammalian consumers, the native flora and fauna of Hawaii are particularly vulnerable to the negative effects of introduced mammals (Atkinson 1977; Athens 1997; Athens et al. 2002).

Questions, Hypotheses, and Workplans

Question I: How pervasive are rats and mice in Hawaiian mesic forests? What are their distributions, habitat uses, and seasonal fluctuations?

Factors contributing to rat and mice densities and distributions

Habitat characteristics (e.g., resources, abiotic attributes), predation, and competition are well-know factors that influence the density and distribution of animals (Krebs et al. 1973). In tropical environments, where seasonal changes are less pronounced than in temperate environments, the annual fluctuations in rodent populations have been attributed to changes in fruit production (Fleming 1971; Gliwicz 1984). However, in tropical India, where black rats are native, canopy connectivity and canopy cover can influence rat densities (Chandrasekar-Rao and Sunquist 1996). On islands, the degree of fragmentation and island size can affect rat densities but not always in consistent patterns. For example, one study showed that native rat densities on larger islands were higher than on smaller islands (Adler 1994), whereas other studies found that non-native rat densities on islands decreased with increasing area (Granjon et al. 1992; Martin et al. 2000). In Hawaii, estimated densities of rats range from < 1 to 50 indiv/ha depending on the type of habitat, elevation, and sampling methodolgy (Table 1).

Table 1. Density estimates for rats (*Rattus* spp.), with primary emphasis on studies in the Hawaiian Islands. Each study used mark-and-recapture to estimate densities except for Beard and Pitt (2006), which used kill-traps, and Granjon et al. 1992 did not report their trapping method.

Species	**Location**	**Habitat**	**Elevation (m)**	**Density (indiv/ha)**	**Reference**
R. rattus	Toro Island, Mediterranean	Scrub	5-350	50	Granjon et al. 1992
R. rattus	India	Tropical evergreen forest	340-2400	14.5	Chandrasekar-Rao and Sunquist 1996
R. rattus	India	Tropical forest/grassland	1800-2500	2-36	Shanker and Sukumar 1999
R. rattus	Big Island, HI	Dry, grassy, woodland/shrub	1600-3000	0.7	Amarasekare 1994
R. rattus	Lava Tree State Park, HI	Wet forest	180	3.6	Beard and Pitt 2006
R. rattus	Oahu, HI	Dry forest	15	8-18	Tamarin and Malecha 1971
R. rattus + *R. exulans*	Hakalau Nat'l Refuge, HI	Mesic/wet forest	1500-1650	50	Mosher et al. 1996
R. exulans	Lava Tree State Park, HI	Wet forest	180	5	Beard and Pitt 2006
R. exulans	Oahu, HI	Dry	15	1.5-8	Tamarin and Malecha 1971

Interestingly in Hawaii, the presence of particular species of rodents may be related to elevation and rainfall (Table 1). Pacific rats were not present at 1600-3000 m elevation on the western slope of Mauna Kea where both black rats and mice were present (Amarasekare 1994). At 1500-1650 m elevation on the eastern (wetter) slope of Mauna Kea, both black rats and Pacific rats co-occur, yet black rats outnumber Pacific rats nearly 2:1 (Mosher et al. 1996; Lindsey et al. 1999). Similarly, at 1600-2000 m elevation on the northeastern slope of Haleakala (rainforest), black rats outnumber both Pacific rats and house mice (8.85 indiv/100 continuous trap nights (CTN) for black rats, 5.65 indiv/100 CTN for Pacific rats, and 5.1 indiv/100 CTN for mice; Sugihara 1997). Studies of mice in Hawaii are less common than those of rats, yet mouse abundance from high elevation (1500-2500 m) on Maui and Hawaii islands ranged from 3-8 mice/100 CTN (Sugihara 1997) to 9-16 mice/100 CTN (Banko et al. 2002). Additionally, mice were trapped at 33-188 m a.s.l. and 2500-2935 m a.s.l. on Hawaii Island and at 2 m a.s.l. on Oahu (unpublished data). Taken together, these studies suggest that black rats and mice can occur from sea level to 3000 m elevation in Hawaii, yet Pacific rats are generally in lower elevations and may reach higher elevations (up to 2000 m) only in wet habitats. Additionally, interspecific competition between black rats and Pacific rats is another possibility that may explain why these two species do not always co-occur.

Predation on rats and mice may also affect their densities. Although studies separating the direct impacts of mice and rat predators (such as cat and mongoose) on population densities are lacking, diet analysis and anecdotal evidence reveals that both rats and mice make up some part of the diets of feral cats and mongoose in Hawaii (Tamarin and Malecha 1971; Amarasekare 1994; Appendix D). Tamarin and Malecha

(1971) observed mongoose either wounding or killing rats that were caught in live-traps on Oahu. Sugihara (1997) examined stomach contents of rats and found that black rats, but never Pacific rats, had rodent fur and flesh in their stomachs. However, it is probable that such cannibalism was on mice and rats that were caught in snap traps and it is unclear if rats and mice commonly cannibalize. In a detailed study of the diets of rodent predators on Mauna Kea, Hawaii, Amarasekare (1994) determined (from scat) that black rats make up 21%, and mice make up 47%, of feral cat diets, and both rat and mouse bones were found in mongoose scat. Therefore, predators of mice and rats in Hawaii include feral cats and mongoose, and these predators may affect population densities and rodent behavior.

Sampling early in this study revealed an absence of Norway rats (*R. norvegicus*) at my sites; therefore, Norway rats are no included in any of the hypotheses outlined in this dissertation.

Hypothesis 1: The abundance of coexisting rodent species is highest for the dominant rodent, *R. rattus*, second highest for *M. musculus*, and lowest for *R. exulans*.

<u>Background</u>—Animal populations fluctuate based on rates of birth, death, immigration and emigration (Krebs et al. 1973). One of the most important factors controlling demographic changes in populations is the availability of resources (Krebs et al. 1973; Staddon 1983; Forget et al. 2001). Because seasonality results in predicable changes to food availability, animal population densities respond in non-random patterns (Danell and Bergström 2002). Seasonal fluctuations in population densities of the spiny rat

(*Proechimys semispinosus*) were studied at four different sites across Panama, where it was determined that population densities are highest in the late rainy season, and lowest at the end of the dry season and beginning of the rainy season (Fleming 1970, 1971; Adler 1994). In tropical India, a similar pattern was shown with the native black rats: the highest densities were during the wet season, which is oddly when fruit production for this region is relatively low (Shankar and Sukumar 1999). However, in a separate study in India, the wet monsoon season revealed the lowest densities of rodents (including the black rat; Chandrasekar-Rao and Sunquist 1996).

In Hawaii, densities of black rats, Pacific rats, and Norway rats did not show clear seasonal patterns in wet forest (Hakalau Forest National Wildlife Refuge; Lindsey et al. 1999). Wet season rat densities were higher than dry season densities (for both Pacific and black rats) in dry forest on Oahu (Bellows Air Force Station; Tamarin and Malecha 1971). In contrast, a species-specific pattern was revealed in wet forest on Maui where Pacific rats showed seasonal patterns (peak densities in the wet season) but black rats did not (Sugihara 1997). Although it cannot be generalized that rat densities change seasonally in Hawaii, some species-specific and site specific evidence for non-random patterns exist (Tamarin and Malecha 1971; Sugihara 1997). Associating rat densities with food availability (e.g., fruit/seed) may help explain patterns of population fluctuation.

Workplan—Live trapping (mark-and-recapture technique; Seber 1982; Johnson 1994, Lindsey et al. 1999) of rats and mice will be conducted each 2-3 months at each of the three sites for at least one year to determine the distribution and abundance of each rodent species. Although several different techniques have been used to estimate rodent densities, the mark-and-recapture method is the most robust (Nichols and Pollock 1983; Bookhout 1994). Because many of the other methods used for animal rodent measures are simpler and do not require handling rodents (e.g., track plates, chew sticks, visual estimation), simultaneous sampling with tracking tunnels will complement mark-and-recapture and will be used to compare and assess techniques for future use. Haguruma live traps will be spaced at 25 m intervals along parallel transects spaced 30-50 m apart. The spacing between traps in trapping grids in other Hawaiian studies have ranged from 7.6 m (Tamarin and Malecha 1971) to 15-20 m (Siguhara 1997; Cole et al. 2000), to 50 m (Lindsey et al. 1999). Each trap will be opened just before dusk and checked at dawn daily for a 4-day sampling interval (Watts and Halliwell 1996). Trapped rodents will be identified to species, sexed, weighed, marked with an ear tag, and released (Lindsey et al. 1999). Abundance will be determined based upon the number of trap nights (one trap is equal to one trap opened for one night) in a sampling interval. Density can then be calculated for each site based on the number of individuals captured and the area sampled (Johnson 1994; Watts and Halliwell 1996).

Hypothesis 2: *The location of each rodent species' nest/den site, and activity, differs among rodent species: Black rats den and are more active in trees than on the ground, whereas Pacific rats and mice den in, and are more active on, the ground than in trees.*

Background: Environmental heterogeneity may allow species to coexist through uses of different microhabitats. For example, particular rodents prefer or avoid arboreal microhabitats more than non-arboreal microhabitats (McCartney 1970; Chandrasekar-Rao and Sunquist 1996; Lindsey et al. 1999). Although it is generally recognized that some mammals occupy three-dimensional space, home-range estimates of animals are most often confined to the two-dimensional, planar surface of the ground. Sampling methods that fail to account for use of arboreal habitats affect interpretations of the behavior, densities, and home ranges of animals that are both ground-dwelling and arboreal (e.g., see Wodzicki 1969, McCartney 1970). In Hakalau Forest National Wildlife Refuge, Lindsey et al. (1999) determined that all the nests/dens of black rats were in cavities in the canopies of trees, whereas dens of Pacific rats were always underground. A similar habitat preference was found in the study by Stecker (1962), where only black rats were caught in trees in an island environment where both black and Pacific rats coexist. This apparent dichotomy in den site location and animal activity in Hawaiian forests is most likely the result of competition between the rat species, and this was suggested by McCartney (1970), who found that Pacific rats prefer nesting in trees in a laboratory setting where black rats were absent. Interspecific competition is highly probable when black rats are present because they are extremely opportunistic and aggressive compared to other rodents (Philips 1981), and they have been suggested to competitively exclude other small mammals (Chandrasekar-Rao and Sunquist 1996) including native rats in both Australia (Stokes et al. 2009) and the Galápagos Islands (Harris and MacDonald 2007). Additionally, animals often respond to physical characteristics in their environment by choosing particular microhabitats that favor predator avoidance, such as high shrub cover (Amarasekare 1994; Chandrasekar-Rao and Sunquist 1996), or particular palm fronds in a given tree (McCartney 1970).

Workplan—Live trapping, radio telemetry, and a spool-and-line tracking will be used to determine species-specific habitat use at multiple scales for rats at each study site. Live trapping will take place in the trees and on the ground to determine the extent to which each rodent species uses these two different habitats.

Rat home-ranges will be determined using radio-tracking technology (Millspaugh and Marzluff 2001). It is necessary to determine home-ranges in order to understand some aspects of rat behavior, and this technique will provide an understanding of meso- to macro-scale habitat use to complement the microhabitat sampling (e.g., spool-and-line tracking). Specifically, the information from home-range evaluation will provide a quantification of the area that rats utilize (e.g., for foraging, mating, nesting), and to help understand the spatial arrangement of some individuals within the forest.

Up to twelve adult rats will be collared with radio transmitters at the KHI and MAK sites. Rats will be caught using Haguruma live traps, anesthetized, and measured (see methods above) immediately prior to attaching a radio collar and releasing. Nocturnal (i.e., during peak rat activity) locations of the radio-collared individuals will be determined using triangulation (Millspaugh and Marzluff 2001), and the accuracy of the locations using triangulation will be determined following blind tests where triangulation coordinates will be checked against locations of known radio transmitters. Diurnal measurements will be made in order to determine locations of den sites, and to assess activity and mortality. Locations of each fix for all radio-collared rats will be entered into program Hawth’s tools in ArcMap to generate fixed kernel home-ranges.

Higher resolution assessment of habitat use by rat and mice will be determined by using spool-and-line tracking (Jones and Barmuta 2000; Cox et al. 2000; Hoare et al. 2007). This method entails attaching (gluing) a small spool of thread to the dorsal fur of individual rodents after anaesthetizing them. One end of the thread is secured to a fixed object in the environment, and the rodent is released. Because the spool of thread (bobbin) unravels from the inside, the animal's movement through the vegetation is not impeded by drag on the thread. This method has proven successful in New Zealand (Hoare et al. 2007) and Australia (Cox et al. 2000) to follow rats ca. 200 m, allowing microhabitat assessment at intervals along the thread-line (Hoare et al. 2007). This technique will help assess species-specific microhabitat use including choice of den sites.

Question II: What are the diets of rats and mice in Hawaiian mesic forest?

Resource partitioning and diets among coexisting rodent species

Animals with similar life-history traits and close phylogenetic associations, such as different species of rodents in the same habitat, must partition resources across time and space in order to coexist (Gause 1934; Grant 1972). Although microhabitat partitioning among introduced rodents has been described previously (Lindsey et al. 1999), food is another type of resource that may be partitioned by coexisting rodent species. For example, Harper (2006) found that there was no obvious food partitioning, at least at the trophic level scale, between black rats and Pacific rats, but that black rats and Norway rats partitioned food resources in a near-shore New Zealand environment.

Identifying prey consumed by introduced predators provides insight into native species' vulnerability and can help improve strategies of native and non-native species management (Stapp 2002; Caut et al. 2008a). Introduced rodents may consume a wide variety of prey, including plants (e.g., fruits, seeds, vegetative material) and animals (e.g., arthropods, mollusks, birds; Sugihara 1997; Campbell and Atkinson 2002; Stapp 2002), and their diets can shift depending upon a number of factors, including the availability of food items, the chemical and nutritional quality of the food items, and the rodents' competitive ability relative to other animals that coexist in the environment (Clark 1982).

Hypothesis 3: *The diets of introduced rodents differ by species in the following pattern: diets of black rats are dominated by plant material, those of mice by animals, and those of Pacific rats by nearly equal proportions of plant and animal material.*

Background—Much of the literature describing stomach contents (short-term diet) of black rats suggests the main food item in their diet is plant material (Willig and Gannon 1996; Cole et al. 2000; Beard and Pitt 2006); however, arthropods can also make up a substantial portion of rodent diets, and wetas (large, flightless Orthoptera) were the dominant food found in black rat stomachs in several New Zealand studies (Innes 1979; Gales 1982; Miller and Miller 1995). On Haleakala, Maui, Pacific rats ate les plant material than they did invertebrates (Sugihara 1997). In a recent review, Angel et al. (2009) suggested that arthropods are the prey of choice for mice in the Southern Ocean.

Stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) have been widely used to determine the trophic levels at which animals have fed during tissue development (Peterson and Fry 1987;

Lajtha and Michener 1994), and bone collagen is useful for determining the long-term average feeding of a mammal because bone collagen is deposited and reworked during the lifetime of an animal (Lajtha and Michener 1994; Caut et al. 2008b). The use of stable isotopes to determine long-term diets of introduced rodents in Hawaii has not previously occurred. However, using isotopes to study diets and differentiate trophic feeding among predators may not always give a clear depiction of predator-prey interactions without supplemental dietary analysis such as stomach contents (Strapp 2002; Caut et al. 2008a; Quillfeldt et al. 2008; Flaherty and Ben-Davis 2010).

Workplan—Rodents will be kill-trapped at KHI approximately once a month. In order to avoid the impacts of kill-tapping on live-trap sampling at KHI, kill-traps will be no closer than 350 m distant from the nearest live-trap. Rodent stomach contents will be extracted and sieved (through 0.4 mm mesh; Sugihara 1997), and recovered contents will be analyzed for 1) frequency of occurrence of each food type, and 2) relative abundance of each food type for each individual using a transparent grid (5 x 5 mm for rats; 3 x 3 mm for mice) positioned beneath the sample and viewed under a dissecting microscope (Sugihara 1997; Cole et al. 2000). The plant food types that will be classified will include fruit, seed, and other plant material (including leaves, flowers, stems, wood); whereas the arthropod food types will be classified by family and perhaps by lower taxonomic levels if possible.

To determine the long-term (lifetime) diets of rodents, a subset of the trapped rodents will have their bone collagen extracted and analyzed for $\delta^{15}N$ and $\delta^{13}C$ values using methods described in Lajtha and Michener (1994). In order to provide reference for the trophic feeding of each rodent species, their probable prey items (plants and animals) will also be analyzed isotopically. The types of prey items will be based on the stomach content analysis and will be collected fresh from the study site.

<u>Question III:</u> Which of the dominant species in Hawaiian mesic forest have their diaspores (fruits + seeds) removed from the forest floor by rats and mice? What are the fates of such rodent-handled seeds?

Factors influencing seed fate

Few studies exist that explicitly determine the seed fate, or the pathway a seed follows between production and germination (Vander Wall et al. 2005; Fig. 2). However, such an understanding will elucidate the most critical steps that determine whether a seed survives or dies; and may partially influence whether or not a seedling establishes and survives. The few studies that have successfully described seed fate are outlined in Vander Wall et al. (2005) as: Holthuijzen et al. 1987; Kjellsson 1991; Hughes and Westoby 1992; Vander Wall 1994; Feer et al. 2001; and Lambert 2002. As shown in Figure 2, many different seed fates can occur. The forces exerted by an animal (e.g., rat) on the plant, which can be both positive (dispersal) and negative (predation), interact with those conditions of the natural environment (favorability of microsites) to determine whether or not seedling establishment and survival will occur (Fig. 2).

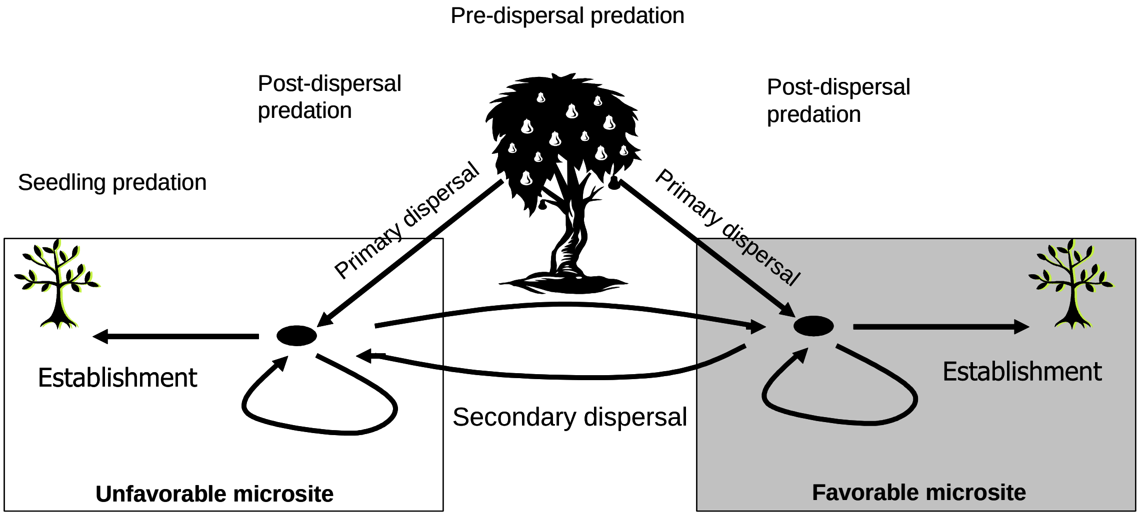

Figure 2. The processes that affect plant recruitment. Animal (e.g., rat) forces on the seed (black oval) that will determine the seed fate include: pre-dispersal seed predation, post-dispersal seed predation, and the placement of the seed (dispersal) into a particular microsite. A seed may arrive into a favorable (clear) or unfavorable (shaded) microsite for seedling establishment via primary- or secondary-dispersal. A complete understanding of the plant recruitment process cannot occur without knowledge of each of these stages.

Plant-animal interactions affect island flora

Oceanic islands are often assumed to have disharmonic floras in part because of chance dispersal to such isolated landmasses (Carlquist 1974). Birds are the most common vector for long-distance dispersal to isolated islands (Ridley 1930; Carlquist 1974). As a result, many fruits in Hawaii are fleshy, and they are consumed and dispersed by animals (Wagner et al. 1999).

Because fruit-eating animals tend to consume a wide range of fruit types and species, it is uncommon for characteristics of specific fruigivores to influence the evolution of fruit traits (Hedge et al. 1991; Mazer and Wheelright 1993; Lord et al. 2002; Lord 2004). However, it is widely accepted that frugivores are attracted to fruit based on fruit physical traits, such as color, presentation, accessibility, insect damage, and fruit size (Moermond and Denslow 1983; Jordano 1987; Hedge et al. 1991; Puckley et al. 1996; Sanders et al. 1997), and it is also likely that such attractive fruits are more susceptible to seed predation than are other types of species with abiotic or unspecialized dispersal mechanisms (Hulme 2002). Therefore, the interaction between animals and plant diaspores is important because the animal's action can affect seed fate (Fig. 2), or whether a seed is destroyed, damaged, dispersed, or avoided (Vander Wall 1994; Forget et al. 2005). Such outcomes will be influenced by both the type of animal and the type of diaspore present in the interaction (Janson 1983; Howe 1986). Additionally, because of the size of the seed reward and the ability of the rodent to move and swallow the seed, seed size may be one of the most important characteristics that determine seed removal and seed fate (Thompson 1987; Crawley 1992; Hulme 1998).

Hypothesis 3*: Vulnerability to diaspore harvest and seed predation by rats is more strongly associated with diaspore size (mass and greatest diameter) than other characteristics.*

Background—Rodents can be seed predators or seed dispersers (Price and Jenkins 1986; Crawley 1992; Foget 1993; McConkey et al. 2003), and the likelihood and frequency of seed dispersal depends on whether the individual hoards or caches seeds (Price and Jenkins 1986; Forget 1993; Forget et al. 2001, 2005), or otherwise fails to locate them after moving them (Campbell et al. 1984; Vander Wall 1994; McConkey et al. 2003; Vander Wall et al. 2005). Seed size also influences whether a seed is found by a rodent, removed or consumed in place, and destroyed or remains intact (Cowan 1992; Izhaki et al. 1995; Williams et al. 2000). Therefore, seed size can directly influence seed fate. Large seeds are more likely to be removed by rodents than small seeds (Thompson 1987; Crawley 1992; Hulme 1998), in part because the large seeds are usually the easiest for rodents to find and are the slowest to be incorporated in the soil (Thompson et al. 1994; Bekker et al. 1998). Small seeds are more likely than large seeds to be swallowed and passed through rodent's digestive system (Williams et al. 2000). Size restrictions in gape, mouth, and/or digestive tract of the animal are well known factors that can limit the size of seed that an animal can ingest (Jordano 1995; Williams et al. 2000).

Determining whether diaspores (fruit + seed) of particular species are vulnerable to rodents can be tested using field trials (Estrada and Coates-Estrada 1991; Moles and Drake 1999; Grant-Hoffman et al. 2010; Chimera and Drake, in revision), analyzing food items in husking stations (Campbell et al. 1984; McConkey et al. 2003), captive feeding trials (Estrada and Coates-Estrada 1991; Amarasekare 1994; Williams et al. 2000; Pérez et al. 2008), and also by analyzing stomach contents from captured rodents (Sugihara 1997; Cole et al. 2000; Beard and Pitt 2006). High quantities of large diaspores (> 10 mm diameter) are commonly removed from the forest floor by rodents in wet, tropical environments, such as Mexico (> 50% for 7 out of 8 species; Estrada and Coates-Estrada 1991), Panama (> 85% for *Gustavia superba*; Forget 1992), and Hawaii (> 80% for *Pritchardia* spp.; unpublished data). However, 11 large-seeded species in a New Zealand secondary forest had low seed removal (3.8-23.8%), despite evidence of introduced rodents (rats and/or mice) removing some of the seeds (Moles and Drake 1999). The important limitation to diaspore removal trials is that they do not regularly assess further aspects of seed fate (i.e., whether a removed diaspore's seed was dispersed intact or destroyed). Determining seed fate of diaspores harvested by rodents has been successful when the study animal commonly hoards (stores) seeds (e.g., agoutis in the Neotropics: Forget 1992, 1993; Forget et al. 2005; chipmunks in North America: Vander Wall 1993, 1994; squirrels in temperate and boreal forests: Steele et al. 2005). However, there is no apparent evidence that rats in the Pacific hoard seeds (Vander Wall 1990; McConkey et al. 2003), and only one study postulates seed hoarding may be occurring with black rats introduced to an Atlantic island (Delgado-Garcia 2000). Middens (partially aggregated food remains) in rat habitats give evidence that rats move food items to distinct areas for processing. Such areas (husking stations) are common throughout the Pacific (Campbell et al. 1984; McConkey et al. 2003), including Hawaii. Rats may use husking stations to reduce exposure to predators or competitors (Begg and Dunlop 1980). Additionally, the husking station probably acts as a rain shelter (Campbell et al. 1984), as common husking stations are: in rock piles, amongst tree roots, under large bases of shed palm fronds, under logs (Campbell et al. 1984; McConkey et al. 2003). Husking stations differ from seed caches because seeds are not hoarded or intentionally stored in husking stations like they are in caches. If rats move seeds but do not hoard them, the seeds are either consumed (partially or fully) or discarded. While discarded seeds can be tracked and recovered relatively easily, ingested seeds are much more complicated to track and recover.

The most controlled method of determining if seeds are destroyed or remain viable after rodent handling is to conduct feeding trials with caged rodents from wild populations (Estrada and Coates-Estrada 1991; Amarasekare 1994; Williams et al. 2000). The main limitation with such a method is that animals commonly behave differently in captivity than they do in their natural environment (Wilson 1982; Brent 1992). Therefore, a more accurate method to determine the outcome of seed handling by rodents is to combine field and captive feeding trials, and to assess the overlap in results between the two methods (Mendoza and Dirzo 2007).

Workplan—A combination of field trials and captive feeding trials will be used to assess diaspore harvest by rats, seed predation, and the likelihood of seed dispersal. The species of diaspores that will be used in the trials will be based on those that are readily available at each study site. The dominant trees (native and non-native) listed above (see "Study Site" section) will provide the minimum set that I propose to study.

Field trials— One of the greatest difficulties in studying the impacts of rats on plants is to show unequivocally that rats, rather than any other small vertebrate with overlapping diet and behavior (e.g., birds, mice, mongoose) are truly the animals responsible for the effects on the plant community. To resolve this, a combination of vertebrate exclosures (Inouye et al. 1980; Bowers and Dulley 1993) and photo documentation using motion-sensing cameras, (Karanth and Nichols 1998; Jansen and den Ouden 2005; Aliaga-Rossel et al. 2006) will be used to assess diaspore removal in single species trials. Field trials will occur at KHI, and possibly at MAK for fewer species.

Captive feeding trials—Adult black rats will be captured from wild populations in the Waianae Mountains, Oahu, including forest adjacent to KHI, and taken to laboratory facilities at the University of Hawaii in Honolulu. Each rat will be individually caged and allowed to acclimate for at least one week before beginning feeding trials, during which time the rats will be fed a diet of mixed seeds (e.g., corn, sunflower, wheat, barley, oats, sorghum) and occasionally wedges of fruit (tangerine). Rats will be checked daily to ensure there is ample food and fresh water, and to clean urine/fecal trays. Captive feeding trials will use the same plant species as those used in the field. For each feeding trial, fruits of a single species, collected fresh from the respective field site, will be placed in each cage with a rat for 24 hours. After 24 hours of exposure to each rat, diaspores will be visually inspected to estimate the proportion of pericarp (fruit material) mass and seed mass remaining, and to assess seed survival. A seed will be considered destroyed if the embryo is not intact or > 50% of the seed was eaten (Pérez et al. 2008). For the smallest seeds (< 3 mm length), it will be necessary to microscopically inspect rat droppings and extract seeds that had passed through the digestive tracts of rats. To test for viability of such seeds, they will be sown on agar, and their germination compared to conspecific, unconsumed seeds sown on agar.

Diaspore and seed characteristics will be measured for all chosen species, and these measurements will include: seed and diaspore mass, length, and width; as well as fruit fleshiness and the average number of seeds in each fruit.

Hypothesis 4: *Seed survival is inversely correlated with seed size, and the upper limit for survival is* ca. *2.5 mm.*

Background— Small seeds of fleshy-fruited species are commonly ingested and dispersed by animals via gut passage (Traveset 1998). The sizes of seeds that pass intact through digestive tracts of animals vary by species, and may be influenced by a number of characteristics of the seeds and their fruits such as shape and fruit fleshiness (Traveset

1998; Traveset et al. 2008). The body size of vertebrates may also correlate with the sizes of seeds that pass intact through digestive tracts (Wheelright 1985; Vander Wall 1990). In New Zealand, the maximum reported lengths of the seeds that passed through digestive tracts were 2.5 mm for introduced black rats, and 0.11 mm for introduced Pacific rats (Williams et al. 2000). No seeds, including those as small as 0.11 mm, passed intact through the house mouse in New Zealand (Williams et al. 2000).

If these findings are applied to Hawaiian flora, it could mean that small-seeded native species (e.g., *Cyrtandra* spp., *Clermontia* spp.) may be less vulnerable to seed predation than larger-seeded species that rats harvest; alternatively, rats may be spreading small-seeded non-native species in Hawaii by ingesting the seeds and dispersing them via gut passage. Rats could be limiting populations of non-native plants through seed predation if they destroy copious amounts of their (relatively large) seeds.

Workplan—See above section on "Captive Feeding Trials"; the same methodology will be applied to test this hypothesis.

CHAPTER TWO:

POPULATION ECOLOGY OF INTRODUCED RODENTS (*RATTUS RATTUS, RATTUS EXULANS, AND MUS MUSCULUS*) AND THEIR HABITAT USES IN HAWAIIAN MESIC FOREST

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Abstract

Introduced rats (*Rattus rattus* or black rat, *R. norvegicus* or Norway rat, and *R. exulans* or Pacific rat) and/or the house mouse (*Mus musculus*) occur on more than 80% of the world's islands groups and pose great threat to native species. Understanding the interactions between these introduced rodents and the habitats which they have invaded can assist in land management and conservation efforts on islands. In three mesic forests in Hawaii, rat and mouse abundances were estimated using mark-and-recapture, microhabitat use and den sites were determined using spool-and-line tracking, and rat home-ranges were estimated using radio-tracking. Black rats dominate these forests in abundance (7.1 indiv./ha) relative to the two smaller rodents, Pacific rats (0.3 indiv./ha) and mice (3.7 indiv./ha). Norway rats were absent from the three sites. Home-ranges of black rats (N = 19) averaged 3.8 ha and did not differ between sites or sexes. The single radio-tracked Pacific rat had a home-range of 1.8 ha. Most (> 88%) rodent activity occurred in areas where vegetation closely (10-30 cm above individuals) covered the rodent; 70% of the monitored movements of both mice and Pacific rats were on the ground surface, whereas black rats were mainly arboreal (32% ground, 64% arboreal) and were typically observed ca. 2.8 m height when aboveground. Except for one individual mouse, all den sites of Pacific rats and mice were belowground, whereas dens of black rats were both above- and belowground. There are ecological differences among the three rodent species that coexist in Hawaiian forests; the abundances and habitat uses of these sympatric rodents may be partially governed by the dominance of the primarily arboreal black rat, and perhaps additionally affected by microhabitat preference, predator abundance, and food availability.

Introduction

Three rat species (*Rattus rattus* or black rat, *R. norvegicus* or Norway rat, and *R. exulans* or Pacific rat) and the house mouse (*Mus musculus*) have been widely introduced to terrestrial environments across the planet; more than 80% of island groups have been invaded (Atkinson 1985; Towns 2009) and most insular invasions include more than one of these four species (Yom-Tov et al. 1999; Russell and Clout 2004). All four rodent species are voracious predators of a wide range of plants and animals, and are probably the invasive animals responsible for the greatest number of plant and animal extinctions on islands (Towns et al. 2006; Angel et al. 2009).

The extent to which introduced rodents have invaded island habitats is variable, and almost certainly depends upon numerous interacting factors, including temperature, precipitation, food availability, predator populations, vegetation structure, and the presence of other rodents (Chapter 3; King et al. 1996; Yom-Tov et al. 1999; Blackwell et al. 2003; Harper 2006; Atkinson and Towns 2005; Harris and Macdonald 2007; Stokes et al. 2009). Some of these introduced rodents are found only in distinct habitats even when adjacent habitats are rodent-free or have smaller-bodied rodents that are more likely to succumb to the larger species (Lindsey et al. 1999; Harper 2006). For example, the Norway rat is the largest of the four introduced rodents and it is often found near water (e.g., near streams, lakes, and oceans; Innes 2005a, Harper 2006) or in urban and agricultural settings (Kami 1966; Tobin et al. 1990), but it is relatively uncommon in forests (Lindsey et al. 1999; Innes et al. 2001). Despite the larger body size of the Norway rat, black rats are typically the dominant rodent of the four introduced species (Innes 2005a,b; Harper 2006), and as a result black rats are generally more abundant and occur in a wider range of habitats than the others (Innes 2005b). The Pacific rat, which is restricted to Pacific islands, is the smallest of the three introduced rats and may be outcompeted in most environments by the two larger rat species (Russell and Clout 2004; Atkinson and Towns 2005). Similarly, the house mouse may be suppressed by all three introduced *Rattus* spp. (Russell and Clout 2004; Angel et al. 2009), and in New Zealand mice are rarely known to occur with Pacific rats (Yom-Tov et al. 1999; Ruscoe and Murphy 2005). The presence of particular rodent species may therefore affect whether or not other rodent species can occur in a habitat (Yom-Tov et al. 1999); and if rodent species are sympatric then their relative abundances will likely be influenced through competitive interactions (Tobin et al. 1990; Harper 2006).

Sympatric rodents must partition resources, such as habitat, food, and space, in order to continue to coexist (Grant 1972). Habitat partitioning among coexisting introduced rats (Lindsey et al. 1999; Harper 2006) and food partitioning among introduced rats and the house mouse (Chapter 3) has been previously demonstrated. When modeling the distributions of the four introduced rodents on islands, Russell and Clout (2004) found that the distribution of the Pacific rat is limited by that of the black rat, and that the Pacific rat was not found to interact with the house mouse. However, on southern Stewart Island, New Zealand, black rats and Pacific rats were found to coexist in some inland habitats, whereas black rats and Norway rats coexisted along the shoreline (Harper 2006). Isotopic analysis revealed there was no obvious food partitioning, at least at the trophic level scale, between black rats and Pacific rats on Stewart Island, but black rats and Norway rats partitioned food resources in the near-shore environment (Harper 2006). Although introduced rats were sympatric on Stewart Island, Harper (2006) did not investigate the potential partitioning among microhabitats. In wet forest on Hawaii Island where all three introduced rats occurred (but Norway rats were 1% of the captures), Lindsey et al. (1999) found that black rats were the most abundant and dominant rat, and it utilized both the canopy and ground for foraging and nesting (denning), whereas the less abundant Pacific rat was confined to the ground for den sites and activity (Lindsey et al. 1999). Also in Hawaii, there was evidence of food partitioning among three introduced rodents in mesic forest, where Pacific rats had an intermediate diet between the primarily vegetarian black rat and the mostly carnivorous house mouse (see Chapter 3). Therefore, introduced rodents may partition food resources, habitats, or both where they coexist.

An understanding of niche partitioning may provide insight into distributions, abundances, and prey items commonly consumed by sympatric rodents, which may suggest improvements to strategies for control and removal of invasive rodents (Cox et al. 2000). The four most problematic invasive rodents on islands (black rats, Norway rats, Pacific rats, and house mice) are found in contemporary Hawaii, where they have been repeatedly documented as major threats to agriculture (Doty 1945; Hood et al. 1971; Tobin et al. 1990), human health (Tomich et al. 1984; Sugihara 2002), and native biota (Chapters 1, 3; Cole et al. 2000; VanderWerf 2001). The densities of these four rodents in Hawaii are not equivalent among sites, perhaps partially owing to variation in habitat and species composition. For example, density estimates for black rats in Hawaii are wide-ranging and include: 0.7 indiv./ha in high elevation shrubland (Amarasekare 1994), 3.6 indiv./ha in lowland wet forest (Beard and Pitt 2006), and 8-15 indiv./ha in lowland dry forest (Tamarin and Malecha 1971). Also in lowland Hawaii, the populations of

Pacific rats ranged from 1.5-8 indiv./ha in dry forest (Tamarin and Malecha 1971) to 5 indiv./ha in wet forest (Beard and Pitt 2006). There are very few studies in non-agricultural Hawaii that have measured mouse population abundance aside from two studies at high elevation (1600-3000 m): 3-7 indiv./100 trap nights (Sugihara 1997) and 11 indiv./100 trap nights (Banko et al. 2002). Studies of home-ranges of rats are less common than studies of their abundances, and in Hawaii the single home-range study from non-agricultural land occurred in a wet montane forest (Hakalau Forest National Wildlife Refuge) on Hawaii Island. There, the average home-ranges were estimated at 3.5 ha and 3.0 ha for black rats and Pacific rats, respectively (Lindsey et al. 1999).

Determining the extent of variation (i.e., patchiness) in rodent species composition, abundance, and habitat use within a given forest type or mountain range can help clarify the extent to which rodent ecology can be generalized. Furthermore, an understanding of the population dynamics and behavior of introduced rodents in natural and semi-natural habitats may be helpful for conservation and restoration of wildlife on islands where rodents have invaded. The primary objectives of this study, which occurred in three mesic forests in the Waianae Mountains, Oahu, were to: 1) Determine the rodent community composition at each site, 2) Estimate each rodent species' abundance, population fluctuation, microhabitat use, and den site location, and 3) Estimate home-ranges and determine the den types occupied by introduced rats.

Methods

Study site

This research occurred at three study sites in the Waianae Mountains, on the island of Oahu, Hawaii: Kahanahaiki Management Unit (KHI; 21^{o} 32′ N, 158^{o} 11′ W), Kaluaa Valley at Honouliuli Preserve (HON; 21^{o} 28′ N, 158^{o} 5′ W), and Makaha Valley (MAK; 21^{o} 30′ N, 158^{o} 10′ W). All three sites are in mesic forest spanning 500-660 m a.s.l. and have a similar, mixed flora that includes both native and non-native plant species. Vegetation surveys were conducted at the focal study site, KHI (Chapter 1; Appendix A, B), and at HON (Bakutis 2005) and MAK (T. Ticktin, unpublished data). All three sites have been fenced to exclude feral goats and pigs and are actively managed to protect native species by Oahu Army Natural Resources.

Two species of rat, the black rat and the Pacific rat, and the house mouse were previously identified at KHI and HON (Meyer and Shiels 2009; Shiels and Drake, in press). Potential predators of rodents at the study sites, all of which are non-native species, include: the small Indian mongoose (*Herpestes javanicus*; Appendix D), the domestic cat (*Felis catus*; Appendix D), and the barn owl (*Tyto alba*). Both the mongoose and the barn owl were intentionally introduced in Hawaii as a control agent against rats and mice in sugarcane fields (Tomich 1962; Staples and Cowie 2001). Domestic cats accompanied early European explorers to the Pacific, including those that voyaged to the Hawaiian Islands in the late 1700's, as a means of rat and mice control on their ships; however, the feral cats in contemporary Hawaii are most likely escaped pets (Staples and Cowie 2001). On one occasion the native owl, pueo (*Asio flammeus* subsp. *sandwicensis*), was observed at KHI (A. Shiels and S. Mosher, personal observation 1

June 2010), and although this native owl is relatively uncommon on Oahu it has been documented as a predator of introduced rodents (Mostello 1996).

Mark-and-recapture to determine rodent abundances at each site

Distribution and abundance of rats and mice were assessed every two months from February 2007-April 2009 at KHI and HON, and quarterly from July 2008-April 2009 at MAK, using Haguruma live-traps and standard mark-and-recapture techniques (Krebs 1999). Both KHI and HON had 60 traps (45 on the ground, 15 up to 4 m height on horizontal branches in trees), and MAK had 50 traps (45 on ground, five up to 4 m height on horizontal branches in trees). Traps were spaced 25 m apart and arranged along four to six transects per site, each 35-50 m from adjacent transects. Steep topography did not allow for a symmetrical grid design. The total trapping area for each site included a 12.5 m buffer (i.e., half the trap spacing interval) around the outer edges of transects, and was: 2.87 ha for HON, 2.81 ha for KHI, and 3.37 ha for MAK. All traps were baited with fresh chunks of coconut (each ca. 2 cm x 2 cm), and pre-baiting with shredded coconut took place 2 days prior to opening traps (Sugihara 1997; Lindsey et al. 1999). Traps were opened for four consecutive trap nights per sampling interval, and were checked each day just after sunrise and once again just before sunset. Abundance of each rodent species captured was determined by the number of individuals captured per 100 trap nights (corrected for sprung traps by subtracting 0.5 trap nights for each sprung trap; Nelson and Clark 1973; Beauvais and Buskirk 1996; Innes et al. 2001). A trap night is one trap set for one night. Sprung traps were usually a result of non-native slugs (*Deroceras* spp., *Limax maximus*; Appendix E, F) eating the coconut and triggering the trap; however, wind, branchfall, and the rosy wolf snail (*Euglandina rosea*) also caused traps to spring and would require trap-night correction. Birds (e.g., Red-billed Leiothrix, *Leiothrix lutea*, Northern Cardinal, *Cardinalis cardinalis*) and mongoose were also caught in the live-traps and these traps were excluded from the analysis. Fresh coconut chunks replaced old ones that no longer appeared fresh, such as those that were chewed, pecked, or slimed by animals, or those that were no longer moist or had obvious microbial growth. Traps that caught mongoose were immediately replaced with clean traps so their scent did not influence subsequent rodent capture success (Tobin et al. 1995). Because several studies report density (No. indiv./ha) instead of No. indiv./100 trap nights, I also calculated rodent species densities for each 4-day trapping interval by using the total trapping area for each site.

Upon capture, each rodent was identified to species, and the following was determined: sex, adult or juvenile (based on whether testes were scrotal or vaginas were perforated), mass (using a Pesola 300 g hanging balance), body length (distance from snout to base of tail), tail length, pelt color, and occurrence of obvious disease or infection (e.g., ear mites, boils, balding). A uniquely numbered ear tag was attached to the lower portion of each ear prior to releasing the rodent at < 50 cm distant from its point of capture. In order to safely handle and complete measurements for each rodent, each individual was gripped with a leather glove around the body just below the neck, or in most cases each rat was anesthetized using isoflurane until the point of unconsciousness. The advantages to anesthetizing animals prior to handling are that anesthesia may reduce stress and discomfort to animals, and anesthesia may reduce the risk that researchers are bitten and possibly infected by zoonotic diseases (Animal Use and Care Committee 1998; Douglass et al. 2000).

To confirm species identification in the field, a subset of live-captured rodents were sampled for blood or tissue and analyzed by restriction fragment length polymorphism of the mitochondrial D-loop region using Hae III and Dde I (Matisoo-Smith et al. 2001).

Application of tracking tunnels to estimate rat abundance

To better predict rat abundance without using the high-effort, live-trapping technique described above, tracking tunnels were set up to estimate the presence of rats. At all three sites from May 2008-April 2009, tracking tunnels (The Black Trakka Gotcha Traps LTD) were deployed approximately 1 week after the end of each live-trapping interval. Tracking tunnels (N = 25 per site), which were permanently stationed on the ground along two transects established for live-trapping at each site (25 m minimal spacing), consisted of a 50-cm-long black plastic tunnel with 10 cm x 10 cm (width x height) openings at both ends. On the day of measurement, each tunnel received a water-resistant white card, in the center of which were a patch of ink and a chunk (ca. 2 cm x 2 cm) of coconut bait. After 24 hours, each white card was collected and inspected to identify the species of animal responsible for any foot-tracks on the card. During 2008-2009, tracking tunnels were deployed six times (i.e., bi-monthly) for each of KHI and HON, and three times (quarterly) for MAK. Reference foot tracks of known rodent species were used to compare to those observed in the field. The proportion of tunnels that had rat tracks were correlated with the live-capture rat abundances (No. indiv./trap night).

Radio-telemetry to determine rat home-ranges

In order to estimate rat home-range and den site movements at KHI and MAK, a subset of the captured black rats were fitted with radio collars (N = 14 for KHI; N =10 for MAK). Additionally, four Pacific rats were radio-tracked at KHI, and one Pacific rat was radio-tracked at HON to determine its den site. Radio-collared rats were tracked 3 February-10 December 2007 at KHI, 9 July 2008-16 June 2009 at MAK, and 13-16 March 2009 at HON. Each radio collar (ATS model M1540, 40 ppm, 83 day battery life for black rats; ATS model M1510, 40 ppm, 40 day battery life for Pacific rats) was < 4.5% of the animal's average (adult) body weight (mean ± SE collar mass: black rats: 3.88 ± 0.06 g, N = 9; Pacific rats: 2.02 ± 0.01 g, N = 5), and was attached with a zip-tie plastic tubing collar. All individuals that had radio-collars attached had been caught in live-traps, anesthetized using isoflurane to safely attach the radio collar, monitored until fully conscious, and released at the point of capture. Radio-tracking did not occur for at least 24 hours after releasing a newly radio-collared animal. Nighttime radio telemetry was conducted using triangulation, where two or three people were stationed on ridges or slopes (100-300 m apart) and were outfitted with individual receiving equipment (a hand-held Communications Specialist, Inc. receiver and a three-element hand-held Yagi aerial) and a compass to indicate the bearing of each target animal. Bearings were simultaneously taken (fixes) at approximately 15 minute intervals. These fixes were considered to be independent of one another, based on the assumption that individuals could move between any two points in their home range within this period (White and Garrott 1990; Rooney et al. 1998). At each fix, the rat was scored as moving, as evidenced by erratic pulses in tone and intervals between tones, or as stationary if the tone and intervals between tones were constant. Bearings were converted to local coordinates using program LOCATE (Nams 2006). In order to determine the error associated with determining rat locations by radio telemetry, a blind test was conducted where a transmitter was stationed at a location unknown to three investigators. The degree of variation (error) from the true point of transmittance was calculated as 1.7^{o} ± 0.4 degrees (N = 12 readings) where each of the three investigators was measuring from ca. 200-300 m distant from the transmitter. Of the 10 adult black rats that were radio-collared at MAK from September 2008-May 2009, eight individuals (five females, three males) retained collars with functioning batteries long enough to record nighttime movements. For all radio-collared black rats, the average time that collars were retained on a rat was 63 ± 10 days (mean ± SE), though the minimum time was 6 days and maximum time was 195 days. The single Pacific rat measured for its home-range retained its collar for 19 days. Locations of each fix for all radio-collared rats were entered into program Hawth's tools in ArcMap version 9.3 to generate fixed kernel home-ranges. A smoothing parameter (i.e., bandwidth h) of 25 was used on each animal's average distance moved. Kernel home-range estimates were selected rather than minimum convex polygon estimates because the latter is known to cause greater unpredictable bias from small sample sizes (Borger et al. 2006; Nilsen et al. 2008). Both the 95% kernel home-range occurrence area and the 50% (core) occurrence area were reported for each radio-collared individual at KHI and MAK. Both 95% kernel home-ranges and core occurrence were analyzed in MANOVA to determine if there were significant differences between KHI and MAK, and between sexes. Values were log-transformed to meet ANOVA assumptions and significance was based on $P < 0.05$.

Characteristics of rat den sites and rat predation

During the daytime, radio-telemetry was used to determine the location of rat den sites. Den sites were measured for their distance to point of capture (i.e., where the radio-transmitter was attached), and the height above or below ground. The type of substrate (e.g., rock, soil, and species of plant) that comprised each den site was recorded. The cause of rodent death and the cause of radio collar detachment (e.g., neck bands that were slipped or chewed) were determined whenever possible. Radio-collared rats were checked for den locations opportunistically, usually at least once a week (range: each 1-36 days) from 3 February-10 December 2007 at KHI, 9 July 2008-16 June 2009 at MAK, and 13-16 March 2009 at HON.

To test whether black rat den site locations (tree or ground) differed between study sites (KHI and MAK) or between sexes, a two-way ANOVA was performed after transforming data by arcsin squareroot and meeting parametric assumptions (SPSS 1998). Additionally, the maximum distance from a black rat den site to the trap where originally captured was compared between sites and sexes using two-way ANOVA. Lastly, utilizing all radio-collared rats from all three sites, the two species (black rat and Pacific rat) were compared for their maximum distance to trap using one-way ANOVA. Significance for all comparisons was based on $P < 0.05$.

Rodent microhabitat use

Rodent microhabitat use was assessed at all three study sites by spool-and-line tracking (Cox et al. 2000). This method allows assessment of habitat use at a resolution not possible by using radio-telemetry/radio-tracking. For this method, fine-threaded spools (bobbins) were attached to rodents by first anesthetizing them using isoflurane, and then clipping their dorsal hairs to a length of ca. 2-5 mm before attaching the bobbin (2-ply nylon thread spool, wrapped in parafilm) with cyanoacrylate (superglue). Bobbins were ca. 3.5 g (ca. 300 m of thread), and upon weighing each rodent the bobbin's weight was decreased by removing thread if the bobbin was not already < 4.5% of the rodent's body weight. Approximate weights just prior to attaching bobbins were: 3.5 g for black rats, 1.0 g for Pacific rats, and 0.4 g for house mice. Once the bobbin was secured on the rodent's back (held 30-60 seconds so the glue fastened), one end of the bobbin thread was secured to a nearby tree and the rodent was placed next to the trap and observed until it regained consciousness and fled. Because the thread spools unravel from the inside of the bobbin, the animal's movement through vegetation is not impeded by the thread's drag (Fig. 3). In some cases, the amount of thread released from a bobbin was the full 300 m, yet bobbins were often shed prior to releasing all of its thread. This method has been used widely for animal tracking and assessing microhabitat use of small mammals (Jones and Barmuta 2000; Shanahan et al. 2007) including introduced rats (Cox et al. 2000; Hoare et al. 2007). Bobbins were applied opportunistically in ca. equal proportions of each sex to rodent species at all three sites (N = 20-24 for black rats at each of three sites; and N = 4-6 for Pacific rats at KHI and HON, and N = 6-11 for house mice at KHI and HON).

Figure 3. Black rat fitted with a bobbin for spool-and-line tracking.

After 24-96 hours following release of rodents with bobbins, a suite of microhabitat characteristics were assessed at 5 m intervals along the total length of the thread, including: location (on, above, or below the ground), substrate type (e.g., bare soil, rock, leaf litter, branch, stem), height above ground when recorded above ground, height above or below the ground, vegetation cover between 10-30 cm height above the rodent, canopy height and species, distance to trap (i.e., the shortest distance between the capture/release point and each 5 m interval), and the total amount of thread released. The first 10 m of thread was not included in the measurements because this length typically represents the flight response of the rodent (Cox et al. 2000). Animals were included in statistical analysis only if data from a minimum of five sampling points were collected (i.e., ≥ 30 m of thread before termination). On a subset of the rodents that did not have bobbins shed or threads broken (5-10 per site), the end location of the rodent, as evidenced by the terminus of the bobbin thread, was recorded after 24, 48, 72, and 96 hours in order to determine if the rodent moved with the bobbin after the first 24 hours. In all such cases the rodent had only moved with the bobbin during the first 24 hours; data collection using bobbins was therefore restricted to ≤ 24 hours after attaching each bobbin.

The three rodent species (black rat, Pacific rat, house mouse) were compared between KHI and HON (the two sites where spool-and-line tacking occurred for all three rodents) for average and maximum distance to trap site using two-way ANOVAs after square-root transforming both response variables to meet ANOVA assumptions; and non-parametric ANOVA (Kruskal-Wallis) allowed comparisons among rodent species for average height above ground and maximum height above ground for the recordings when the rodent was above ground. Variables relating to substrate type were compared among rodent species and study sites using MANOVA after square-root transforming each of the following response variables: surface, aboveground, leaf litter, branch, bare soil, stem. Post-hoc comparisons used Tukey's test, or Mann-Whitney U test, depending on whether parametric assumptions were met (SPSS 1998), and significant was based on $P < 0.05$.

To determine if aspects related to height (above ground) and distance to trap were different among the three study sites and sexes for black rats having bobbins attached, a MANOVA was performed using data from all three sites for the following dependent variables (each square-root transformed to meet ANOVA assumptions) related to distances moved following capture: average distance moved, average height above ground, maximum height above ground, average distance to trap, maximum distance to trap. A second MANOVA was performed on data relating to the substrate type used by black rats while fitted with bobbins. The dependent variables for the second MANOVA included the frequencies (%) of 5 m intervals on the following substrates (with appropriate data transformations): surface, aboveground. Several additional variables related to substrate type used by black rats were measured but not included in the MANOVA because they did not meet normality assumptions and/or because differences in the natural substrate types among sites would not be accounted for in such analyses. When significant differences ($P < 0.05$) were present for full-model MANOVA, the between-subject (ANOVA) effects were examined. If significant differences were revealed in the between-subject tests, post-hoc Tukey's test was used to tests for differences among the three study sites.

Results

Mark-and-recapture to determine rodent abundances at each site

In total, 821 individual rodents (561 black rats, 31 Pacific rats, and 229 house mice) were captured, marked, measured, and released during the February 2007-April 2009 trapping season for all three sites (KHI, HON, MAK) combined. Sizes of rodents followed the expected pattern: black rat > Pacific rat > house mouse (Table 2). Adult male black rats tended to be larger in mass and length than adult females at all three sites; yet this pattern was not evident for juvenile black rats, particularly at MAK (Table 3). When sex was not considered, the sizes (mass and length) of both adult and juvenile black rats tended to be lowest at HON relative to KHI and MAK (Table 4). The size pattern of males tending to be larger than females was less clear for Pacific rats because adult males tended to be larger than females at HON but not at KHI (Table 5). Although juvenile mice were not easily distinguished from adults, the average mass of males (juveniles and adults combined) tended to be larger than those of females (Table 6).

Table 2. Rodent size characteristics from all three mesic forests in the Waianae Mountains, Oahu. KHI = Kahanahaiki, HON = Honouliuli, and MAK = Makaha. Means (±SE) are based on all individuals (adults + juveniles) of a given species captured at respective sites. Body length was measured from the snout to the base of the tail. A single Pacific rat (juvenile male) was captured at MAK.

	KHI	HON	MAK
Black rat			
No. indiv.	315	177	69
Mass (g)	106.0 ± 2.3	101.8 ± 2.9	116.2 ± 4.0
Body length (cm)	15.7 ± 0.1	15.6 ± 0.2	16.3 ± 0.2
Tail length (cm)	18.3 ± 0.1	18.3 ± 0.2	19.0 ± 0.3
Pacific rat			
No. indiv.	8	22	1
Mass (g)	54.3 ± 3.6	40.7 ± 3.2	24
Body length (cm)	13.3 ± 0.3	11.6 ± 0.4	9
Tail length (cm)	13.5 ± 0.1	12.8 ± 0.4	10
House mouse			
No. indiv.	85	122	22
Mass (g)	10.8 ± 0.3	9.5 ± 0.3	10.6 ± 0.5
Body length (cm)	6.9 ± 0.1	6.6 ± 0.1	6.8 ± 0.1
Tail length (cm)	7.1 ± 0.1	7.4 ± 0.2	7.2 ± 0.1

Table 3. Size characteristics of each sex and age (adults and juveniles) of black rats captured at the three study sites (KHI, HON, MAK) in the Waianae Mountains, Oahu, from February 2007-April 2009. Means (±SE) are based on captured individuals from each site. Body length was measured from the snout to the base of the tail.

	KHI		HON		MAK	
	Male	Female	Male	Female	Male	Female
Adults						
No. indiv.	122	99	70	60	32	26
Mass (g)	130.6 ± 2.7	120.2 ± 2.7	126.7 ± 3.4	111.3 ± 3.1	130.8 ± 4.6	121.4 ± 4.3
Body length (cm)	17.0 ± 0.1	16.5 ± 0.1	17.0 ± 0.1	16.3 ± 0.2	17.1 ± 0.2	16.7 ± 0.2
Tail length (cm)	19.6 ± 0.1	19.2 ± 0.2	19.5 ± 0.2	19.2 ± 0.2	20.0 ± 0.2	19.8 ± 0.3
Juveniles						
No. indiv.	55	41	29	18	7	4
Mass (g)	61.4 ± 3.2	60.3 ± 3.1	55.3 ± 3.4	53.3 ± 4.9	58.4 ± 6.2	67.5 ± 3.4
Body length (cm)	13.3 ± 0.3	13.1 ± 0.3	12.8 ± 0.4	12.6 ± 0.6	13.0 ± 0.6	13.8 ± 0.3
Tail length (cm)	15.7 ± 0.4	15.7 ± 0.3	15.6 ± 0.4	15.0 ± 0.7	15.5 ± 0.7	16.3 ± 0.3

Table 4. Means ± SE of black rat size characteristics for adults and juveniles captured at the three study sites in the Waianae Mountains, Oahu (KHI = Kahanahaiki, HON = Honouliuli, and MAK = Makaha).

	KHI	HON	MAK
Adult			
No. indiv.	221	130	58
Mass (g)	125.9 ± 1.9	119.1 ± 2.4	126.6 ± 3.2
Body length (cm)	16.8 ± 0.1	16.7 ± 0.1	16.9 ± 0.2
Tail length (cm)	19.4 ± 0.1	19.3 ± 0.1	19.9 ± 0.2
Juvenile			
No. indiv.	96	47	11
Mass (g)	60.9 ± 2.2	54.1 ± 2.7	61.7 ± 4.2
Body length (cm)	13.2 ± 0.2	12.7 ± 0.3	13.3 ± 0.4
Tail length (cm)	15.7 ± 0.2	15.4 ± 0.3	15.8 ± 0.5

Table 5. Size characteristics of each sex and ages (adults and juveniles) of Pacific rats captured at the three study sites (KHI, HON, MAK) in the Waianae Mountains, Oahu, from February 2007-April 2009. Means (±SE) are based on captured individuals from each site. Body length was measured from the snout to the base of the tail. A single juvenile (male) was captured at KHI and at MAK, and there were no adults captured at MAK.

	KHI		HON		MAK	
	Male	Female	Male	Female	Male	Female
Adults						
No. indiv.	5	2	7	5		
Mass (g)	55.8 ± 3.7	57.5 ± 10.5	55.3 ± 3.1	48.8 ± 2.9		
Body length (cm)	13.6 ± 0.3	13.0 ± 0.0	13.3 ± 0.2	12.5 ± 0.3		
Tail length (cm)	13.8 ± 0.1	13.0 ± 0.0	14.3 ± 0.3	13.6 ± 0.3		
Juveniles						
No. indiv.	1		5	5	1	
Mass (g)	40.0		26.4 ± 2.0	26.6 ± 4.3	24.0	
Body length (cm)	12.0		9.0 ± 0.2	9.9 ± 0.7	9.0	
Tail length (cm)	12.5		11.2 ± 0.2	11.3 ± 0.7	10.0	

Table 6. Size characteristics of each sex of the house mouse captured at the three study sites (KHI, HON, MAK) in the Waianae Mountains, Oahu, from February 2007-April 2009. Means (±SE) are based on captured individuals from each site. Juveniles were not easily distinguished from adults so adults and juveniles are not divided here; only animals where sexes were readily distinguishable are reported here. Body length was measured from the snout to the base of the tail.

	KHI		HON		MAK	
	Male	Female	Male	Female	Male	Female
Adults						
No. indiv.	32	39	64	55	10	11
Mass (g)	11.9 ± 0.4	10.3 ± 0.3	9.9 ± 0.4	9.6 ± 0.4	11.2 ± 0.6	10.0 ± 0.8
Body length (cm)	7.1 ± 0.1	6.8 ± 0.1	6.6 ± 0.1	6.5 ± 0.1	6.9 ± 0.2	6.7 ± 0.2
Tail length (cm)	7.2 ± 0.2	7.0 ± 0.1	7.0 ± 0.1	6.9 ± 0.1	7.4 ± 0.2	6.9 ± 0.1

The black rat was the most abundant rodent at all sites, averaging (indiv./100 trap nights): 13.5 ± 2.7 at KHI, 7.9 ± 0.6 at HON, and 9.9 ± 2.3 at MAK (Fig. 4). Mice were the second most abundant rodent, averaging (indiv./100 trap nights): 7.9 ± 3.3 at KHI, 5.3 ± 0.8 at HON, and 3.0 ± 0.2 at MAK. Although few Pacific rats were captured (never exceeding 5 indiv./trap night in any month sampled), they were present at all sites (Fig. 4). The Norway rat was never captured at any of the study sites. The nearly 2-fold higher black rat abundance at KHI compared to HON was largely attributable to the high abundance of black rats and mice during April-June 2007. The Pacific rat was most abundant during the beginning of the two-year sampling at KHI, whereas at HON they were most abundant at the end of the two-year sampling, and only one Pacific rat was caught during sampling at MAK (Fig. 4).

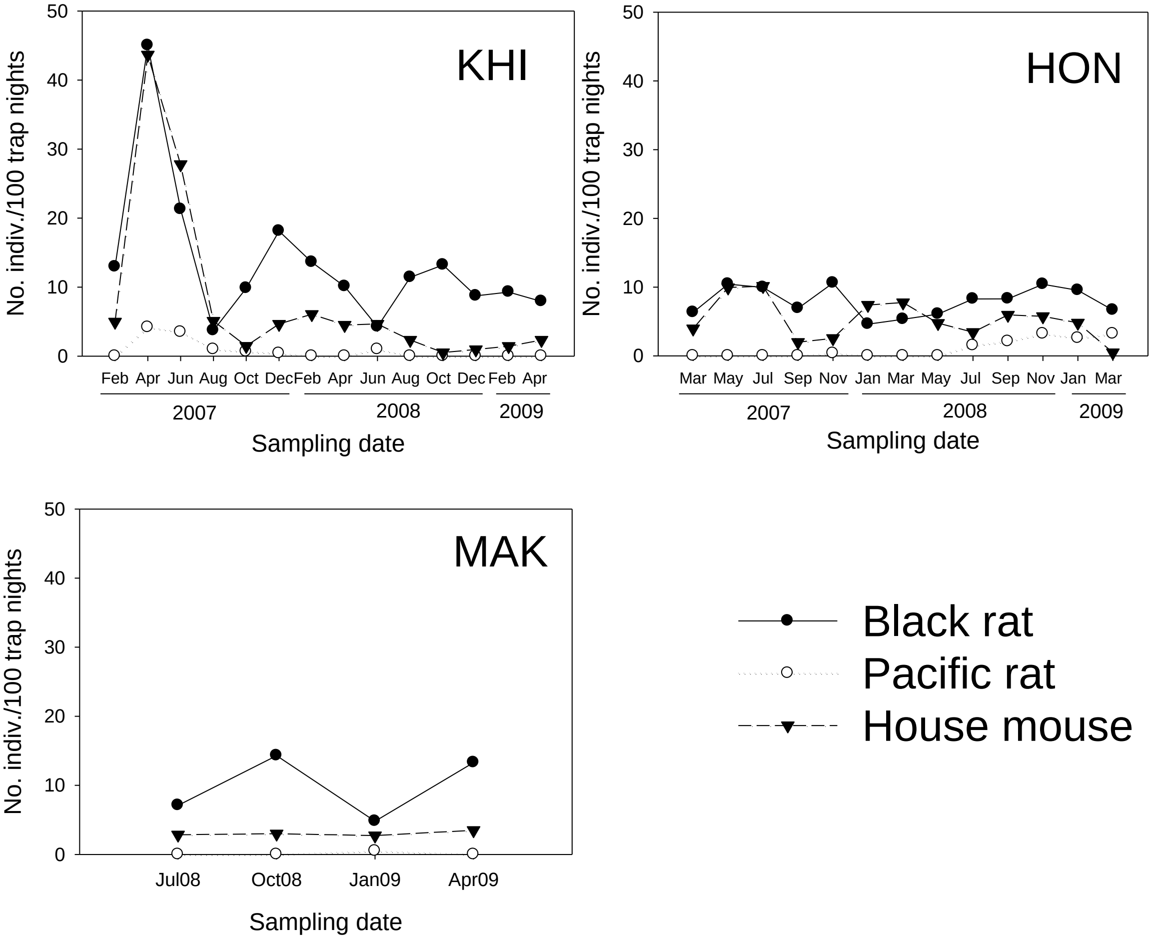

Figure 4. Abundances (No. indiv./100 trap nights) of the three rodent species at the three forest sites (KHI = Kahanahaiki, HON = Honouliuli, MAK = Makaha) in the Waianae Mountains, Oahu. All sampling was by live-trapping.

Rodent densities followed similar patterns as the aforementioned abundance measures. Black rats had average densities (No. indiv./ha) of: 9.8 ± 1.1 at KHI, 5.8 ± 0.5 at HON, and 5.8 ± 1.6 at MAK (Fig. 5). Average densities of mice were: 5.1 ± 1.9 at KHI, 4.4 ± 0.6 at HON, and 1.6 ± 0.1 at MAK; and average densities of the Pacific rat were: 0.2 ± 0.1 at KHI, 0.7 ± 0.3 at HON, and 0.1 ± 0.1 at MAK (Fig. 5). Rats were active only during the night; no rats but several mice were captured during the daytime at each site, particularly during samplings where total rodent abundances were relatively high (e.g., April and June 2007 at KHI). Rarely were Pacific rats or mice caught in traps in trees, yet on one occasion at HON a single Pacific rat was caught in a tree (ca. 2.5 m height), and one mouse at KHI was caught 4 m above the ground.

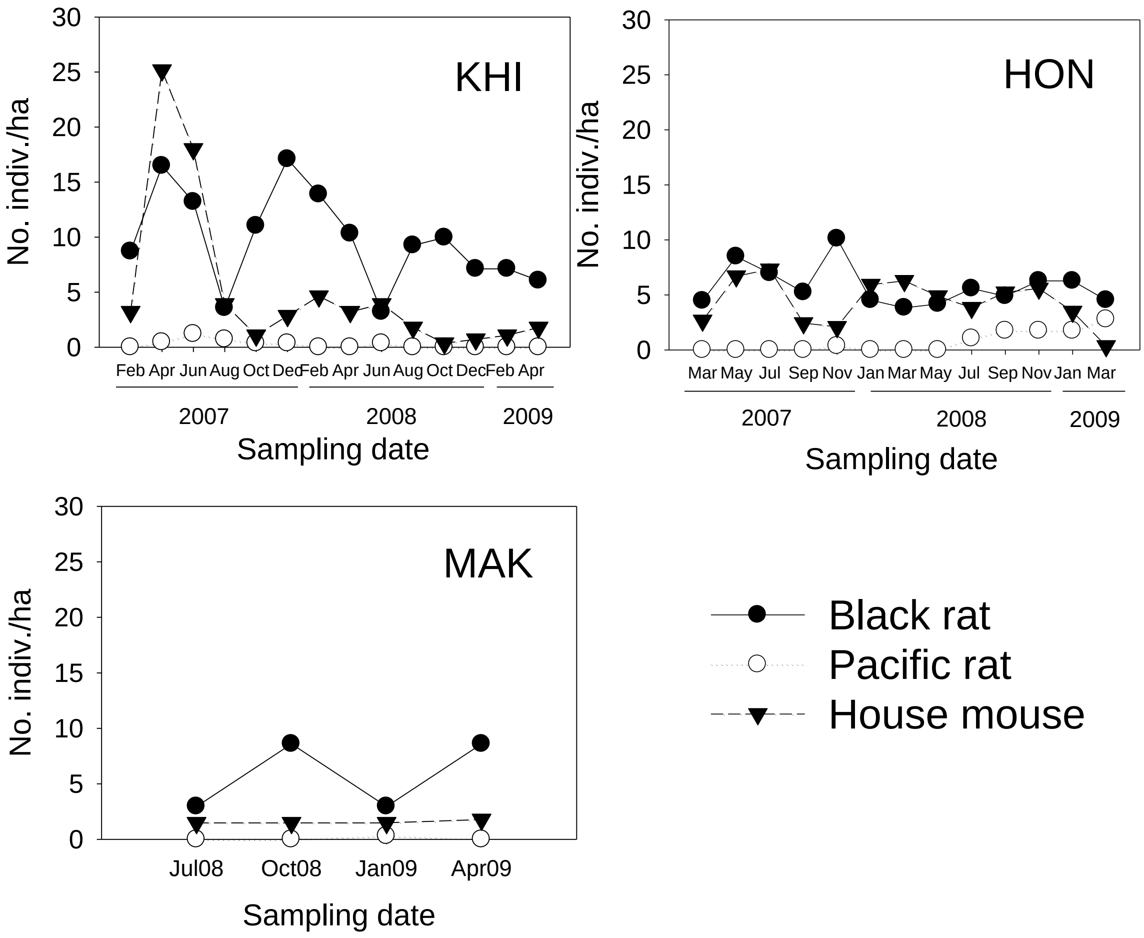

Figure 5. Densities (No. indiv./ha) of the three rodent species at the three forest sites (KHI = Kahanahaiki, HON = Honouliuli, MAK = Makaha) in the Waianae Mountains, Oahu. All sampling was by live-trapping.

At HON, from March 2007-March 2009, there were 177 black rats (73% adults and 27% juveniles), 22 Pacific rats (55% adults and 45% juveniles), and 122 mice (maturity level was not obvious) captured. The greatest numbers of juvenile black rats were caught in November of each year at HON (21 of 45, or 47% of all juveniles; Fig. 6). Approximately 15% of all captured black rats at HON had black pelts (13% of adults and 21% of juveniles), whereas the majority of black rats had brown pelts. All Pacific rats and mice had brown pelts. Pregnant female mice were observed in late September 2007, early February 2008, and mid-July 2008. Pregnant black rats were observed in each sampling month except May; and July 2008 tended to have the highest frequency of pregnant black rats of any sampling at HON. No pregnant Pacific rats were detected. Except for two black rats captured in July 2008, all of the black rats that were pregnant upon capture did not have noticeable ear mites and lesions. Disease and infection was relatively common for black rats captured at HON where ear mites and lesions (46 indiv. or 26%) were the most obvious infection for both adults and juveniles of both sexes. When individuals infected with ear mites and lesions were recaptured at a later sampling date (often several months after first capture), they retained these infections. These mites apparently colonize the ear tissue and appear as warts, especially on the ear fringes (Fig. 7). Dr. Thierry Work at the USGS Wildlife Health Center in Honolulu conducted a necropsy in May 2008 on one adult male black rat from HON (case# 21091) and confirmed that the ear lesions/infections were mites. Many of the rats with obvious ear mites and lesions also had what appeared to be fungus growing at the base of their tails. Additionally, two black rat individuals at HON had a boil and/or swelling on the pad of a rear foot, and one of these individuals also had a large boil or cyst on her abdomen just posterior to the urethra. There were no ear mites, lesions, or boils on any of the captured Pacific rats or house mice at any of the study sites.

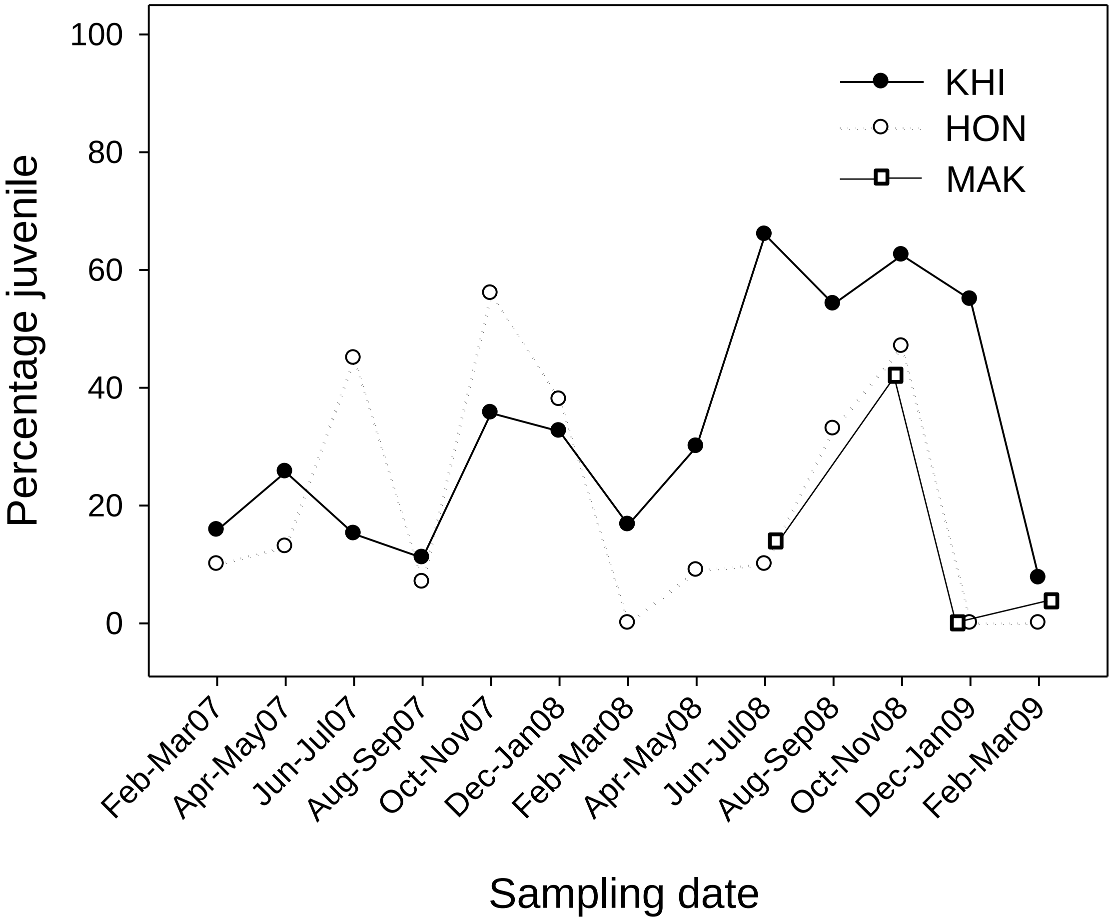

Figure 6. Percentage of captured black rats that were juveniles at the three study sites in the Waianae Mountains, Oahu, Hawaii. The MAK site had four sampling periods during July 2008-April 2009.

Figure 7. A black rat live-trapped at HON with ear mites and lesions. Mites apparently colonize the ear tissue and cause the wart-like appearance shown on the ear fringes.

At KHI, from February 2007-April 2009, 315 black rats were captured (70% adults and 30% juveniles), eight Pacific rats (88% adults and 12% juveniles), and 85 mice. The greatest numbers of juvenile black rats captured during the sampling was June-December 2008 (41 of 96, or 43% of all juveniles captured at KHI; Fig. 6). At KHI, ca. 15% of all captured black rats had black pelts (14% of adults and 16% of juveniles), whereas the majority of black rats, and all Pacific rats and mice, had brown pelts. At KHI, only five black rats that had ear mites and lesions like those observed at HON, and there were no other rodent species with such infections. The five black rats with ear mites included one female juvenile captured on 23 August 2007, two adult males (captured 24 August 2007 and 12 April 2009), one adult female captured in April 2009, and one adult female that was first caught in October 2007 without obvious ear mites and then 8 months later when recaptured she had ear mites. One juvenile female caught in December 2007 had a swollen foot pad on one hind foot. One black rat caught in April 2009 had balding around the rump, appearing like mange.

At MAK, from July 2008-April 2009, 69 black rats were captured (84% adults and 16% juveniles), one Pacific rat (a juvenile male), and 22 mice. The greatest abundance of juvenile black rats caught at MAK was during October (eight of 11 juveniles, or 73% of all juveniles captured at MAK; Fig. 6). Unlike KHI and HON, the majority (54%) of the black rats at MAK had black pelts (52% and 55% of the adults and juveniles, respectively). The remaining rodents had brown pelts. There was only one female that was pregnant when caught at MAK, and it was a black rat captured in January 2009. There were three black rats that had ear mites at MAK, including two adult males (captured in October 2008 and January 2009) and one juvenile female (captured in October 2008).

Application of tracking tunnels to estimate rat abundance

Both HON and KHI tracking tunnels were utilized on six occasions during 2008-2009, whereas MAK tracking tunnels were utilized on three occasions. There were no significant relationships between estimates of abundance based on live trapping vs. tracking tunnels when analyzed ($P > 0.05$; $r^2 < 0.01$ for each) on a site-basis or collectively (all three sites combined; $P > 0.05$; $r^2 = 0.01$). This indicated that the tracking tunnels do not provide a reliable index of rat abundance at these sites (Fig. 8).

Radio-telemetry to determine rat home-ranges

Nighttime locations of radio-collared rats at KHI were recorded for 19 nights (9 February 2007 – 30 July 2007) from hours 19:00-7:00, and the duration of each recording session was 125 ± 9 minutes (mean ± SE). The percentage of time that each rat was moving during recordings was 74 ± 6 (mean ± SE; N = 14 rats), and the females tended to move slightly more often (82 ± 2%; N = 7) than the males (67 ± 10%; N = 7). There were three black rats that were monitored from 28 May-18 June 2007 to determine the time of exiting their den sites (first movements around sundown). One female left her den site at sundown (three times) or 17 minutes prior to sundown (one time). The other two rats (both male) left their den sites 11-14 minutes, and 19-31 minutes, after sundown. For the single sampling to determine when black rats returned to den sites at KHI, four black rats were radio-tracked and all returned to dens within 3 minutes before sunrise (by 6:46 am, 23 February 2007). The one Pacific rat at KHI where nighttime radio-tracking was recorded (on 2 and 9 July 2007; at hours 19:30-0:30) revealed that this rat was moving during 25% of the recording times on 2 July and 83% of the recording times on 9 July. This Pacific rat began moving 105 minutes after sundown.

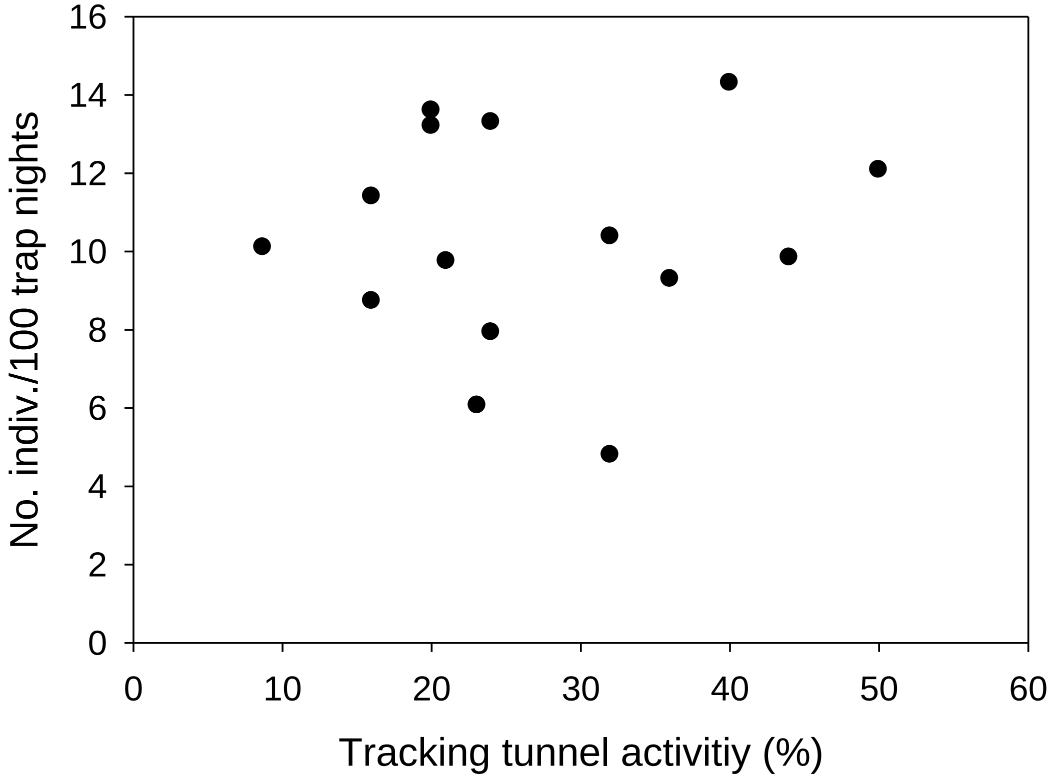

Figure 8. Scatterplot showing the rat (black rat + Pacific rat) observations (activity) in tracking tunnels that were sampled within one week of the rat abundance (No. indiv./100 trap nights) estimates from live-trapping at the three sites (KHI, HON, and MAK). There were no significant relationships present when analyzed with regression on an individual site-basis or collectively.

Nighttime movements and locations of radio-collared rats at MAK were recorded for seven nights (11 September 2008 – 25 May 2009) from hours 19:00-22:30, and the duration of each recording session was 93 ± 17 minutes (mean ± SE). Rats were moving during recordings 71 ± 9% of the time (mean ± SE; N = 8 rats), and the males tended to be moving slightly more often (77 ± 9%; N = 3) than the females (67 ± 13%; N = 5). There were two black rats that were measured on 18 September 2008, and three black rats measured on 25 May 2009, to determine the time of exiting their den sights (first movements around sundown). On 18 September, the female rat left her den 9 minutes after sundown while the male left his den 10 minutes after sundown. On 25 May, the male rat exited his den 12 minutes after sundown whereas one female left hers 28 minutes after sundown and one female whose den was in a 20 x 20 m clearing exited her den 47 minutes after sundown. There were no Pacific rats fitted with radio-collars at MAK.

Kernel home-range estimates (95% occurrence) for black rats at KHI were 4.01 ± 0.35 ha (mean ± SE) and 3.44 ± 0.65 ha for MAK (Table 7). The core area (50% occurrence) used by black rats was also similar between sites, and was 0.86 ± 0.07 ha for KHI and 0.70 ± 0.11 ha for MAK. These home-range estimates were based on approximately equal numbers of fixes, averaging 28 at KHI and 20 at MAK (Table 7). The black rats with the largest home-range at each site were both females (6.22 ha at KHI and 7.09 ha at MAK). There were no significant differences between home-ranges and core areas for site comparisons (MANOVA Wilks' lambda = 0.885; $F_{2, 14} = 0.908$; P = 0.426), sexes (Wilks' lambda = 0.760; $F_{2, 14} = 2.213$; P = 0.146), or site x sex interaction (Wilks' lambda = 0.976; $F_{2, 14} = 0.170$; P = 0.846). The only Pacific rat radio-tracked was at KHI and it had a home-range of 1.8 ha. Home-ranges (95% kernel) of black rats commonly overlapped with other individuals (Fig. 9).

Table 7. Home-ranges (95% kernel) for radio-collared rats from the two mesic forest sites (KHI and MAK) in the Waianae Mountains, Oahu, Hawaii. The core area represents the 50% area of occurrence for each rat. All rats are black rats except for one male Pacific rat at KHI.

Rat #	Sex	No. of night fixes	Core area (ha)	Home-range (ha)
Black rat				
KHI				
.1110	Male	28	0.54	2.13
.1717	Male	24	1.32	5.23
.2120	Male	85	1.00	4.34
.0524	Male	24	0.84	4.21
.0520	Male	17	0.59	2.74
.1520	Female	9	0.86	4.30
.1910	Female	10	1.06	4.51
.0130	Female	54	0.91	4.12
.1324	Female	32	1.08	6.22
.0725	Female	14	0.63	3.38
.07252	Female	14	0.60	2.98
Average		**28.3**	**0.86**	**4.01**
Pacific rat				
KHI				
.2693	Male	10	0.14	1.80
R. rattus				
MAK				
.3670	Male	13	0.65	2.54
.4560	Male	23	1.25	4.83
.9195	Male	26	0.87	4.12
.0172	Male	12	0.30	1.54
.4430	Female	14	0.74	2.94
.3800	Female	14	0.52	2.43
.4066	Female	35	0.34	2.00
.9420	Female	26	0.94	7.09
Average		**20.4**	**0.70**	**3.44**

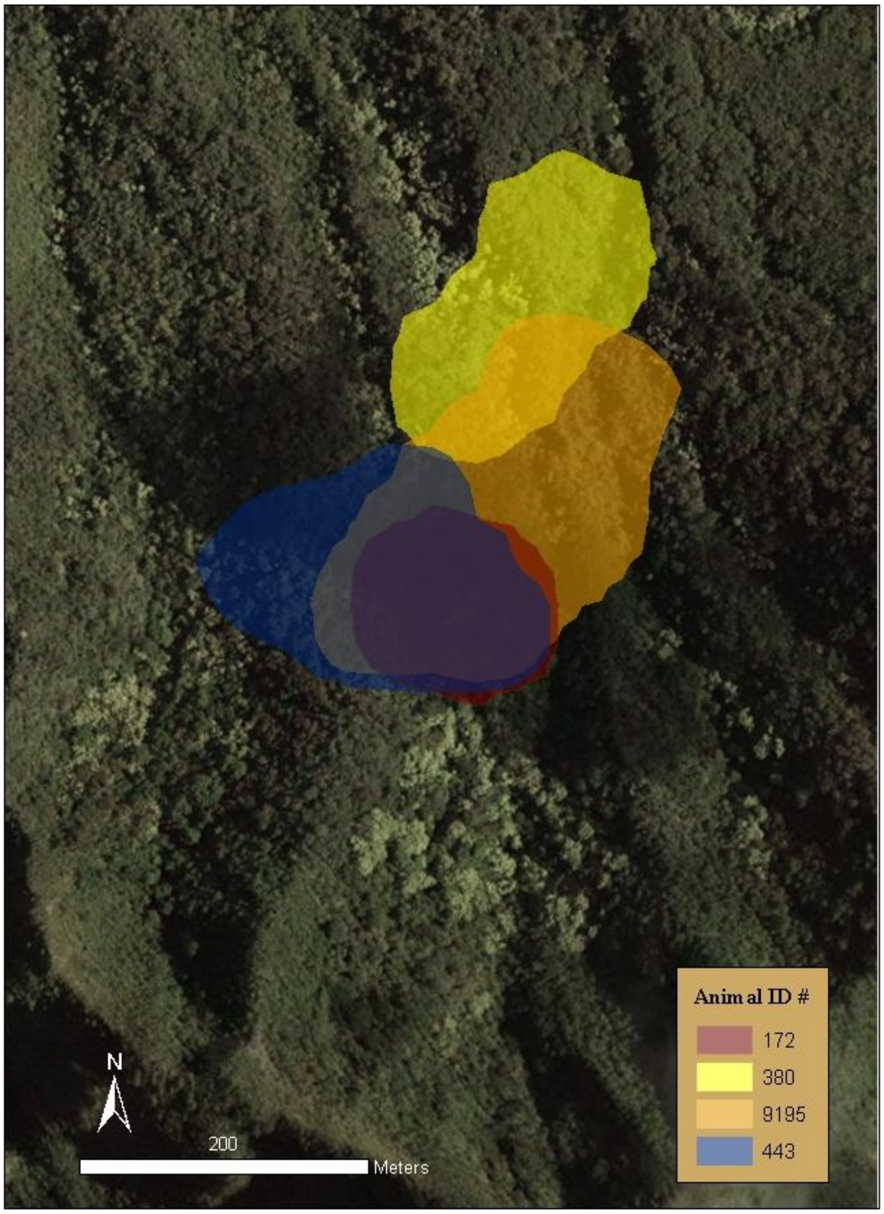

Figure 9. Home-range polygons (95% kernel) for four black rats at MAK, Waianae Mountains, Oahu. Rat 172 and 9195 were male, and 380 and 443 were female.

Characteristics of rat den sites and rat predation

Black rat den sites were in trees and in the ground. Of the 14 black rats radio-collared and followed at KHI, 43% had den sites both in the ground and in trees; whereas 36% denned only in trees and 21% (all females) denned only in the ground (Table 8). All but four rats changed den sites during the time intervals observed. The average number of times that den sites were changed was 2.9 ± 0.9 times (mean ± SE; N = 14 rats), and one male rat changed dens nine times whereas one female changed dens 11 times. There were no occasions where two collared rats with overlapping home-ranges shared the same den site. The substrates of dens in the ground were soil and/or fractured rock. The tree species that rats denned inside (above ground) were mostly non-native species such as *Grevillea robusta* and *Aleurites moluccana*, although two rats denned in the native *Metrosideros polymorpha*, and one rat denned in the native *Santalum freycinetianum* (Table 8). Most (ca. 60%) of the *Grevillea robusta* trees colonized by rats appeared partly or fully dead, whereas only one other individual tree (*Metrosideros polymorpha*) that a rat denned inside was dead. Aside from one female rat (number .0191) that occupied a den site 145 m from point of capture, male black rats tended to have a greater maximum distance from den sites to capture/recapture location; however, there was no significant difference for sex ($F_{1,20}$ = 4.247; P = 0.053) or sex x site interaction ($F_{1,20}$ = 0.640; P = 0.433; Table 8). Five of the 14 black rats (36%) were killed by predators at KHI, and four of those five were most likely killed by feral cats, as evidenced by a rat's stomach as the only remains next to its recovered radio-collar (Table 8). The predator of rat .0520 is unknown, and there was only some of the rat's pelt next to the recovered radio-collar. Stomachs from rats that were not collared were found on two occasions at

KHI, suggesting that the collars did not cause the mortality of radio-collared rats. Some black rats at KHI can live at least 19 months (Appendix G).

Table 8. The 14 black rats and four Pacific rats assessed for den sites and movements using radio-tracking at KHI mesic forest, Oahu, Hawaii. Den sites classified as rock were in fractured rock. The abbreviated tree species in which rats denned in include: *Grevillea robusta* (non-native), *Aleurites moluccana* (non-native), *Metrosideros polymorpha* (native), and *Santalum freycinetianum* (native). Approximately 60% of the *Grevillea robusta* trees colonized by rats appeared partly or fully dead. Evidence of predation upon each of the rats was likely feral cats except for .0520 (black rat) and .2693 (Pacific rat), whose predators were unknown. The number of den sites are distinct sites in the ground (G) or in trees (T).

Rat #	**Sex**	**Den site**	**Max distance from den to trap (m)**	**Tracking duration (days)**	**No. den sites (G: T)**	**Type of den site**	**Reason dis-continued**
Black rat							
.1110	Male	Tree	81	62	0: 3	*Grevillea; Aleurites*	Battery died
.1717	Male	Tree	89	65	0: 1	*Aleurites*	Battery died
.2120	Male	Ground & Tree	22	140	6: 1	In rock; *Metrosideros*	Unknown; not moving
.0524	Male	Ground & Tree	38	60	1: 1	In rock; *Grevillea*	Killed/ predation
.0906	Male	Tree	40	6	0: 1	*Grevillea*	Collar slipped
.0520	Male	Tree	60	50	0: 3	*Grevillea*; *Metrosideros*	Killed/ predation
.1520	Female	Ground & Tree	7	50	3: 1	Dead *Grevillea*	Killed/ predation
.1910	Female	Ground	145	40	1: 0	Under roots	Battery died
.0130	Female	Ground & Tree	31	195	4: 2	In soil; *Grevillea*	Battery died

Rat #	**Sex**	**Den site**	**Max distance from den to trap (m)**	**Tracking duration (days)**	**No. den sites (G: T)**	**Type of den site**	**Reason dis-continued**
Black rat							
.0320	Female	Ground	20	8	3: 0	Under log	Battery died
.1324	Female	Tree	26	34	0: 3	*Santalum*; *Aleurites*	Killed/ Predation
.0725	Female	Ground	39	14	1: 0	In rock wall	Killed/ Predation
.07252	Female	Ground & Tree	12	24	1: 1	In soil; in dead prone tree	Battery died
.09062	Female	Ground & Tree	26	120	2: 3	In rock & soil; *Aleurites*	Battery died
Pacific rat							
.2693	Male	Ground	43	19	2: 0	Under *Blechnum*	Killed/ predation
.2550	Male	Ground	23	2	1: 0	Under log	Collar chewed off
.2930	Male	Ground	25	2	1: 0	Under *Blechnum*	Collar slipped off
.3300	Female	Ground	4	43	2: 0	Under *Rubus* & *Oplismenus*	Battery died

All four Pacific rat den sites at KHI were in the ground, and were surrounded by a relatively thick ground layer of low-statured, non-native plants, including the fern *Blechnum appendiculatum*, the shrub *Rubus rosifolius*, and the grass *Oplismenus hirtellus* (Table 8). It proved difficult to radio-track the Pacific rat because the few that were caught and fitted with radio-collars were either killed by an unknown predator (1 rat), or the rats slipped off (1 rat) or chewed off (1 rat) their radio-collars (Table 8). The only additional Pacific rat fitted with a radio-collar was at HON, where it was observed daily for four days where it had denned under a large boulder 68 m from where it was captured (Table 9). The maximum distance from den sites to the respective traps where originally captured at KHI and HON for the Pacific rat was 33.0 ± 10.7 m (mean ± SE; N = 5), which was similar to that of the black rat (48.5 ± 6.7 m; N = 24) ($F_{1,27}$ = 0.990; P = 0.328).

Table 9. The 10 black rats at MAK and one Pacific rat at HON that were assessed for den sites and movements using radio-tracking in mesic forest, Oahu, Hawaii. The abbreviated tree species in which rats denned include: *Pouteria sandwicensis* (native), *Aleurites moluccana* (non-native), *Psidium guajava* (non-native), *Metrosideros polymorpha* (native), *Acacia koa* (native), *Sapindus oahuensis* (native), and *Szygium cumini* (non-native). Approximately one-third of the *Aleurites moluccana* trees colonized by rats were dead, whereas the other tree species used as den sites were living. The predator of rat .9580 is unknown. The number of den sites are distinct sites in the ground (G) or in trees (T).

Rat #	**Sex**	**Den site**	**Max distance from den to trap (m)**	**Tracking duration (days)**	**No. den sites (G: T)**	**Type of den site**	**Reason dis-continued**
Black rat							
.3670	Male	Tree	108	71	0: 2	*Pouteria* & *Aleurites*	Battery died
.4560	Male	Tree	62	115	0: 3	*Aleurites* & *Pouteria*	Battery died
.9195	Male	Tree	80	62	0: 1	*Aleurites*	Site was no longer visited

Rat #	**Sex**	**Den site**	**Max distance from den to trap (m)**	**Tracking duration (days)**	**No. den sites (G: T)**	**Type of den site**	**Reason dis-continued**
Black rat							
.0172	Male	Ground	52	10	2: 0	Under *Psidum* tree & dead branches	Collar slipped off
.4430	Female	Ground & Tree	36	69	1: 2	Under boulder; *Aleurites* & *Metrosideros*	Battery died
.3800	Female	Ground & Tree	27	71	2: 1	Soil & rock slope; *Acacia*	Battery died
.4066	Female	Ground & Tree	47	166	1: 2	Under boulder, *Aleurites*	Site was no longer visited
.9420	Female	Ground & Tree	18	60	2: 1	Under *Sapindus* & dead tree; *Syzigium*	Site was no longer visited
.9580	Female	Tree	42	13	0: 2	*Aleurites* & *Psidium*	Killed/ predation
.2310	Female	Tree	55	16	0: 2	*Aleurites* & dead tree	Collar slipped off
Pacific rat							
.3053	Female	Ground	68	4	1: 0	Under Boulder	Site was no longer visited

Of the 10 black rats radio-collared and followed at MAK, 40% had den sites both in the ground and in trees; whereas 50% denned only in trees and 10% (a male) denned only in the ground (Table 9). All but one rat changed den sites during the intervals when the radio-collared rats were observed; however, they tended to change dens less (1.4 ± 0.2 times, mean ± SE; N = 10 rats) than those at KHI; the most an individual rat changed dens at MAK was twice (by five rats; Table 9). The maximum distance from black rats den sites to their point of capture (trap) at MAK was not significantly different than that at KHI ($F_{1,20} = 0.533$; $P = 0.466$). Similar to KHI, the rats at MAK had terrestrial den sites in soil and in rocks, as well as beneath boulders (i.e., very large rocks) and trees. Aboveground, the tree species that black rats would most commonly den inside, of which ca. 33% were dead, was the common non-native *Aleurites moluccana*; however, four native trees were also den sites for rats at MAK, including *Pouteria sandwicensis*, *Metrosideros polymorpha*, *Acacia koa*, and *Sapindus oahuensis*. Black rats were also found denning in two additional non-native tree species, *Psidium guajava* and *Szygium cumini*. There was no significant difference in the frequency in which males vs. females occupied dens in trees either when KHI and MAK were combined ($F_{1,20} = 3.059$; $P = 0.096$), or separated (sex x site interaction: $F_{1,20} = 1.427$; $P = 0.246$). Additionally, there was no significant difference in the frequency of rat den sites in trees relative to the ground between the two sites ($F_{1,20} = 0.853$; $P = 0.367$). There was evidence of predation for one rat (.9580) at MAK, and the predator was unknown. At two different times (separated by nearly 6 months), a radio-collared black rat denned in the same den as occupied by a previously collared black rat. These den sites that were used by multiple rats on different times of the year included a living *Pouteria sandwicensis* tree and a dead standing tree; both dens were approximately 2 m above ground. The highest den site was used by a female black rat, and it was estimated at 20 m height in an *Aleurites moluccana* tree.

Rodent microhabitat use

The average amount of thread released for each rodent species during spool-and-line tracking was 90.1 ± 8.4 m (mean ± SE) for black rats, 109.5 ± 13.9 m for Pacific rats, and 52.4 ± 4.7 m for mice. Each rodent species was active in areas where cover was present at 10-30 cm above it. Averaged across all sites and 5 m intervals where spool-and-line tracking (bobbins) were recorded, black rats were under vegetative cover of 10-30 cm height 88.8 ± 0.2% (mean ± SE) of the monitoring time, although much of that time the black rats were aboveground in locations with vegetation cover 10-30 cm above them. Pacific rats and mice were under 10-30 cm tall vegetative cover 94.5 ± 4.1% and 89.4 ± 3.8% of the monitoring time, respectively, and such cover was typically represented by thick ground cover of ferns and grasses.

When the three rodent species (black rat, N = 48; Pacific rat, N = 10; house mouse, N = 17) at KHI and HON were compared for distance to trap ($\chi^2 = 11.57$, $P = 0.003$), average height above ground ($\chi^2 = 30.14$, $P < 0.001$), and maximum height above ground ($\chi^2 = 34.32$, $P < 0.001$), each of these variables had differed significantly among rodent species. Black rats occurred at a greater average height and maximum height above ground than did Pacific rats (Mann-Whitney U > 51.0 for each; P < 0.001 for each) and mice (Mann-Whitney U > 69.0; P < 0.001 for each; Fig. 10). The average height above ground and maximum height above ground were similar between Pacific rats and mice (P = 0.334 and P = 0.141, respectively) (Fig. 10).

When the three rodent species and two study sites (KHI and HON) were compared for the average distance to trap site, there was a significant difference among species ($F_{2,69}$ = 4.610; P = 0.013), but not site ($F_{1,69}$ = 0.927; P = 0.339), or species x site interaction ($F_{2,69}$ = 2.034; P = 0.139). The significant difference among species was due to the greater average distance to the trap for Pacific rats and black rats relative to mice (P = 0.003, and P = 0.037, respectively). Black rats had similar average distance from the trap as Pacific rats (P = 0.148) (Fig. 11A). Similarly, the maximum distance to trap site was significantly different among species ($F_{2,69}$ = 4.385; P = 0.016), where both rat species had a greater maximum distance to the trap site than mice (P = 0.003 and P = 0.038 for Pacific rats and black rats, respectively) (Fig. 11B). Black rats had similar maximum distance from the trap site compared to Pacific rats (P = 0.152) and there were no significant site ($F_{1,69}$ = 1.795; P = 0.185) or species x site interaction ($F_{2,69}$ = 1.970; P = 0.147) for maximum distance from trap site.

When the five black rat movement variables (average distance moved, average height above ground, maximum height above ground, average distance to trap, and maximum distance to trap) were compared among the three study sites, there were no significant differences (MANOVA Wilks' lambda = 0.903; $F_{10, 116}$ = 0.606; P = 0.806; Table 10). Similarly, there were no significant differences in sex (Wilks' lambda = 0.939; $F_{5,58}$ = 0.749; P = 0.591) or the interaction of sex and study site (Wilks' lambda = 0.802; $F_{10,116}$ = 1.355; P = 0.210) when comparisons were made using the same five black rat movement variables. Therefore, the distances from capture location and the height above ground were similar between male and female black rats, and similar among black rats measured at KHI, HON, and MAK.

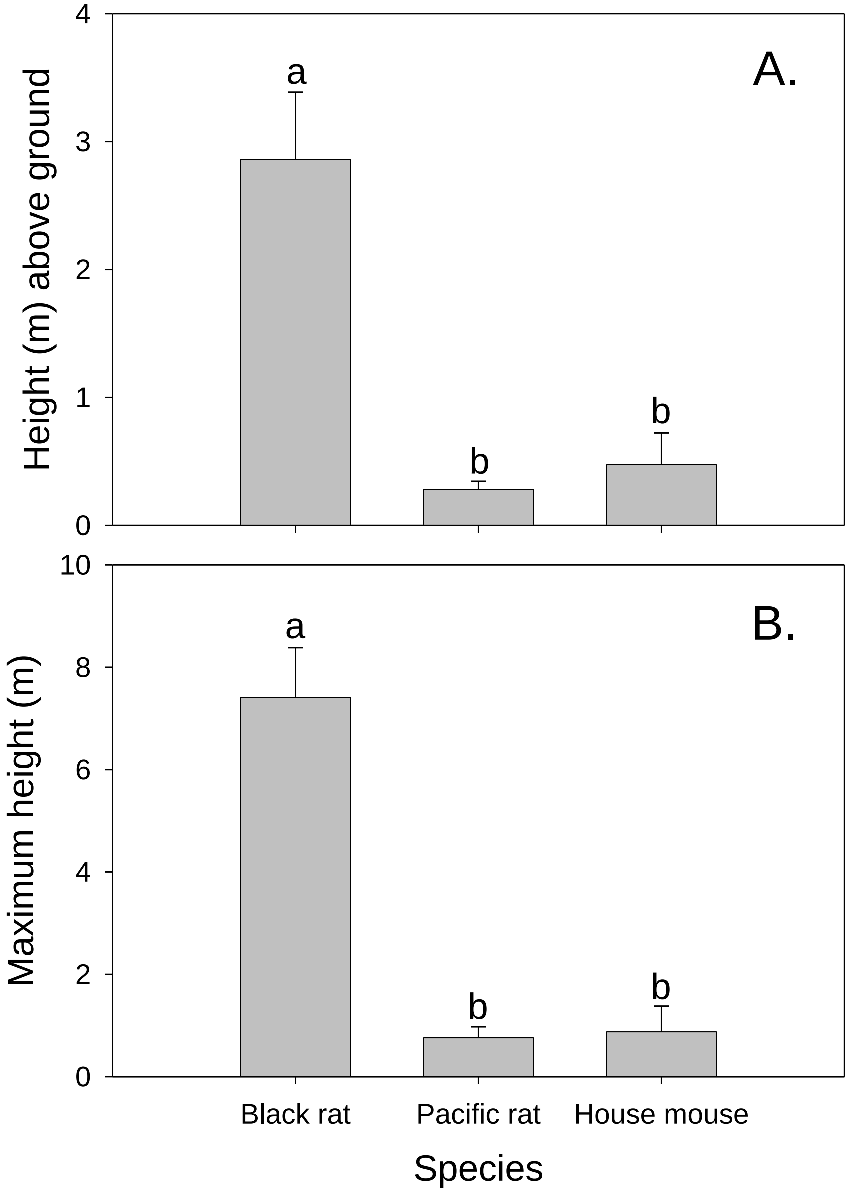

Figure 10. Mean ± SE average (A.) and maximum (B.) height (m) observed above ground after thread bobbins were attached to rodent species at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included because black rats were the only rodent species measured there. Different letters indicate significant ($P < 0.05$) differences among rodent species.

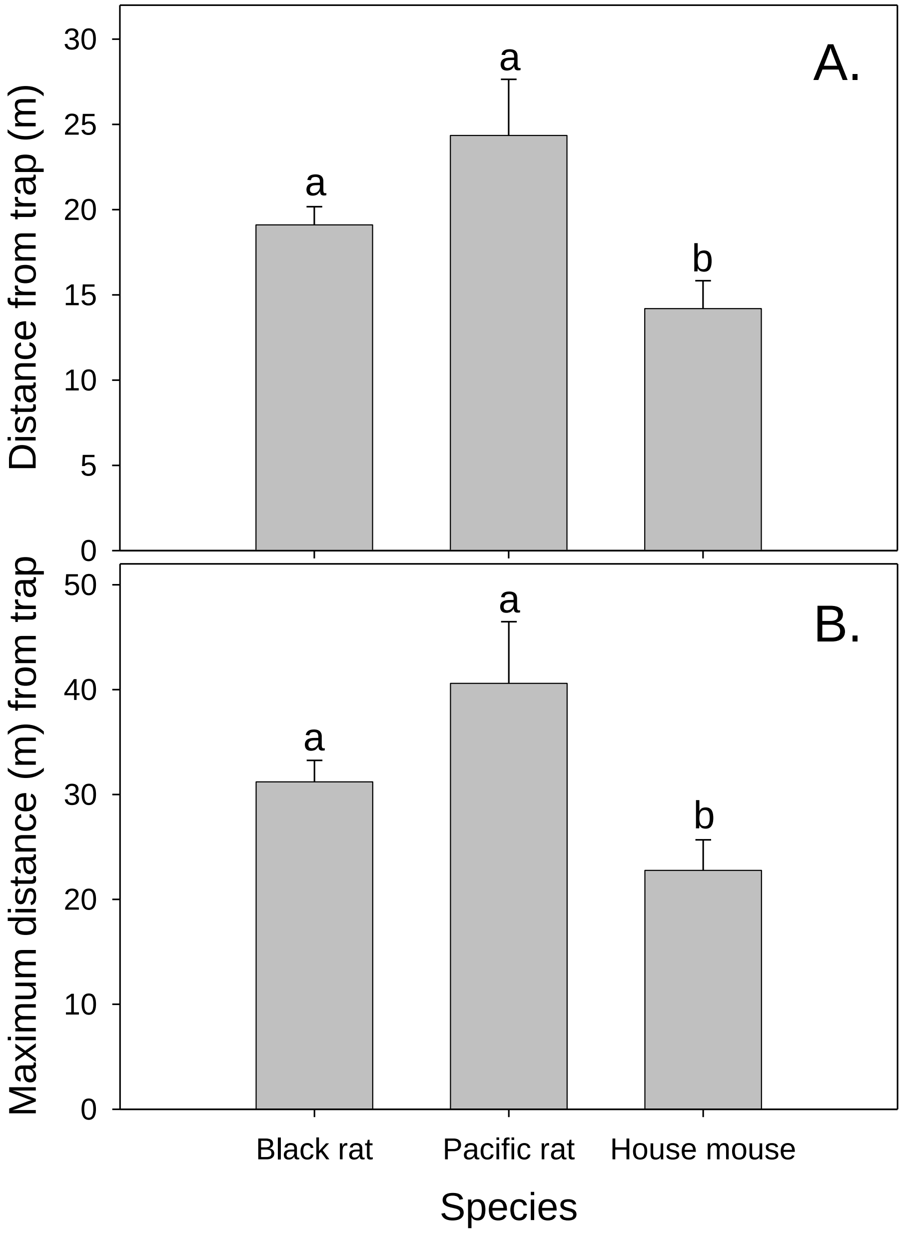

Figure 11. Mean ± SE average (A.) and maximum (B.) distance (m) from trap (point of capture) following bobbin attachment to rodent species at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included because black rats were the only rodent species measured there. Different letters indicate significant ($P < 0.05$) differences among rodent species.

Table 10. Mean ± SE distances (m) black rats were observed using spool-and-line tracking at the three study sites (KHI, HON, MAK) in the Waianae Mountains, Oahu, Hawaii. Average and maximum distance to trap accounted for the three-dimensions and was calculated by measuring the shortest distance between the trap and interval along the bobbin thread. There were no significant differences among sites for any of the measured variables ($P > 0.05$). N = 24 for KHI, N = 24 for HON, N = 20 for MAK.

Variable (m)	Site		
	KHI	HON	MAK
Total thread released	82.29 ± 8.46	97.92 ± 14.53	88.75 ± 12.51
Average height above ground	2.39 ± 0.41	3.33 ± 0.97	2.21 ± 0.35
Maximum height above ground	6.23 ± 0.99	8.58 ± 1.67	5.12 ± 0.70
Average distance to trap	20.45 ± 1.62	17.75 ± 1.38	19.18 ± 2.08
Maximum distance to trap	33.38 ± 3.51	29.04 ± 2.14	31.45 ± 4.03

There were significant differences among rodent species when the six variables related to substrate types (surface, aboveground, leaf litter, branch, bare soil, stem) were compared (Wilks' lambda = 0.523; $F_{12, 128} = 4.089$; $P < 0.001$), and individually, all six response variables were significantly different among rodent ($F_{2, 69} \geq 4.86$; $P \leq 0.012$ for each). Post-hoc comparisons revealed that the presence of Pacific rats on the surface and aboveground is similar to that of mice ($P = 0.999$ for surface; $P = 0.813$ for aboveground); yet, the black rat is found significantly less on the surface ($P < 0.001$) and significantly more aboveground ($P < 0.001$) than both the Pacific rat and the house mouse (Fig. 12). Black rat were also found less often on leaf litter, more often on branches, and more often on stems than both Pacific rats ($P = 0.014$, $P = 0.004$, and $P = 0.014$, respectively) and mice ($P < 0.001$, $P < 0.001$, and $P = 0.044$, respectively) (Fig. 13). The Pacific rat was observed on bare soil significantly more often than the black rat ($P = 0.009$). There were no further significant differences in pairwise comparisons of substrate type between rodents ($P > 0.05$). There were no significant differences between

KHI and HON for the six substrate variables (Wilks' lambda = 0.865; $F_{6, 64} = 1.659$; P = 0.146), or species x site interaction (Wilks' lambda = 0.749; $F_{12, 128} = 1.659$; P = 0.084). There were no significant differences when rodent species were compared for their uses of belowground (P = 0.069), rock (P = 0.583), root (P = 0.791), and dead log (P = 0.851; Fig. 13).

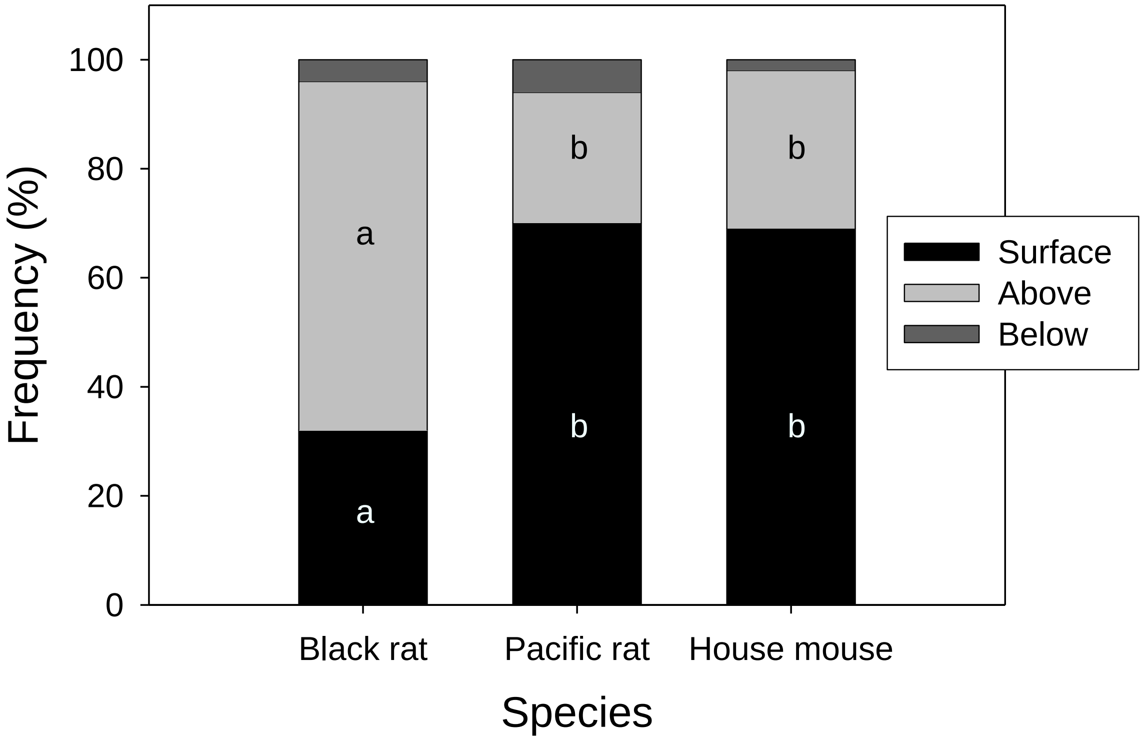

Figure 12. Mean ± SE frequency of each rodent in the three environments (surface-, above-, and belowground) when observed by spool-and-line tracking at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included because only black rats were measured there. Different letters within similar categories represent significant ($P < 0.05$) differences among rodent species.

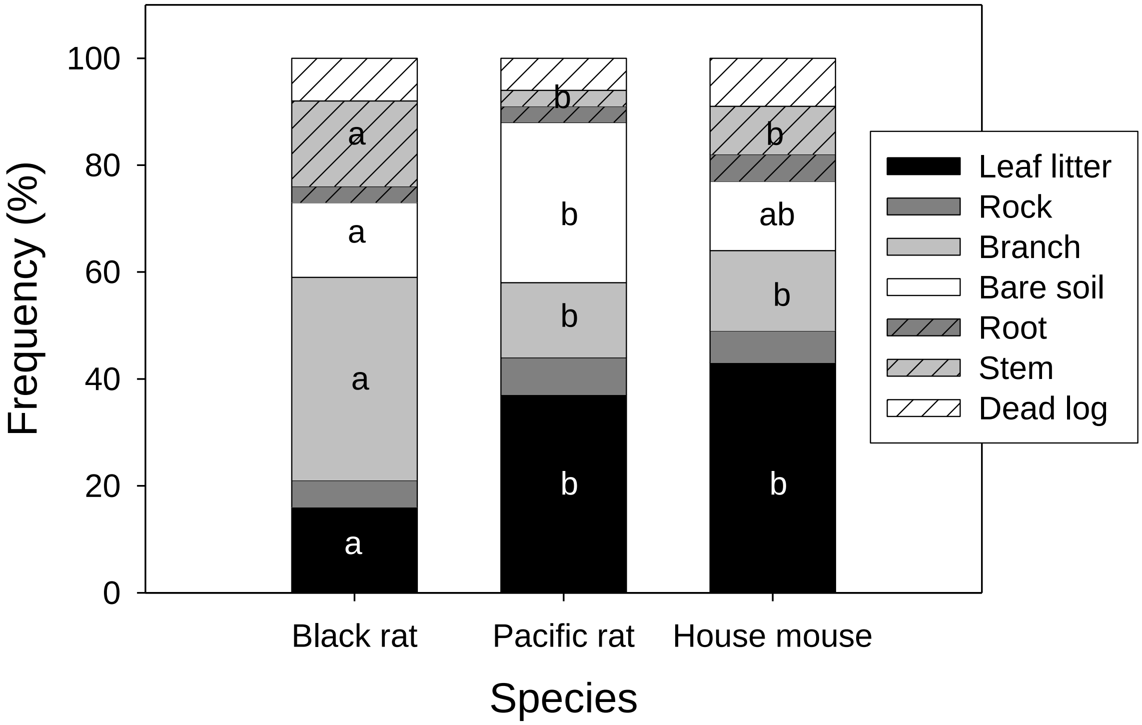

Figure 13. Mean ± SE frequency recorded on substrate types for each rodent at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included because only black rats were measured there. Different letters within similar categories represent significant ($P < 0.05$) differences among rodent species. Categories without letters were not significantly different among species.

There were significant differences when black rat's usage of surface ($F_{2, 62}$ = 4.472; P = 0.015) and aboveground ($F_{2,62}$ = 4.212; P = 0.019) were compared by site. Black rats at HON were observed less frequently on the surface (P = 0.011) and more frequently aboveground (P = 0.018) than black rats at KHI (Table 11). Black rats at MAK did not differ from rats at KHI or HON with respect to presence at the surface (P = 0.774 and P = 0.086, respectively) and aboveground (P = 0.874 and P = 0.083, respectively; Table 11). There were no significant differences when the interaction between black rat sex and study site was compared (P = 0.863).

Table 11. Mean ± SE frequency of observation on surface, aboveground, and belowground when black rats were tracked using the spool-and-line method at the three study sites (KHI, HON, and MAK) in the Waianae Mountains, Oahu, Hawaii. For a given variable, different letters next to mean values when sites are compared indicate significant differences ($P < 0.05$). N = 24 for KHI, N = 24 for HON, N = 20 for MAK. Belowground substrate was not compared.

Variable (%)	Site		
	KHI	HON	MAK
Surface	40.71 ± 5.10^{a}	23.00 ± 3.25^{b}	36.45 ± 4.49^{ab}
Aboveground	55.13 ± 5.46^{a}	73.10 ± 3.41^{b}	58.45 ± 4.94^{ab}
Belowground	4.13 ± 1.35	4.08 ± 1.29	5.20 ± 1.71

Following spool-and-line tracking, a subset of rats and the house mouse entered den sites as evidenced by the terminus of the bobbin’s string in a tree cavity or hole tunneling belowground. The frequency of each type of den site was recorded as soil, rock, living tree, and dead tree for individuals of the three rodent species (N = 28 black rats; N = 4 Pacific rats; N = 5 house mice). All Pacific rats and mice observed at KHI denned in soil, whereas black rats at KHI denned in all four categories of den sites (Fig. 14). At HON, ≥ 50% of each of the three rodent species were found denning in soil. At MAK, the majority of black rats observed were denning in trees (Fig. 14).

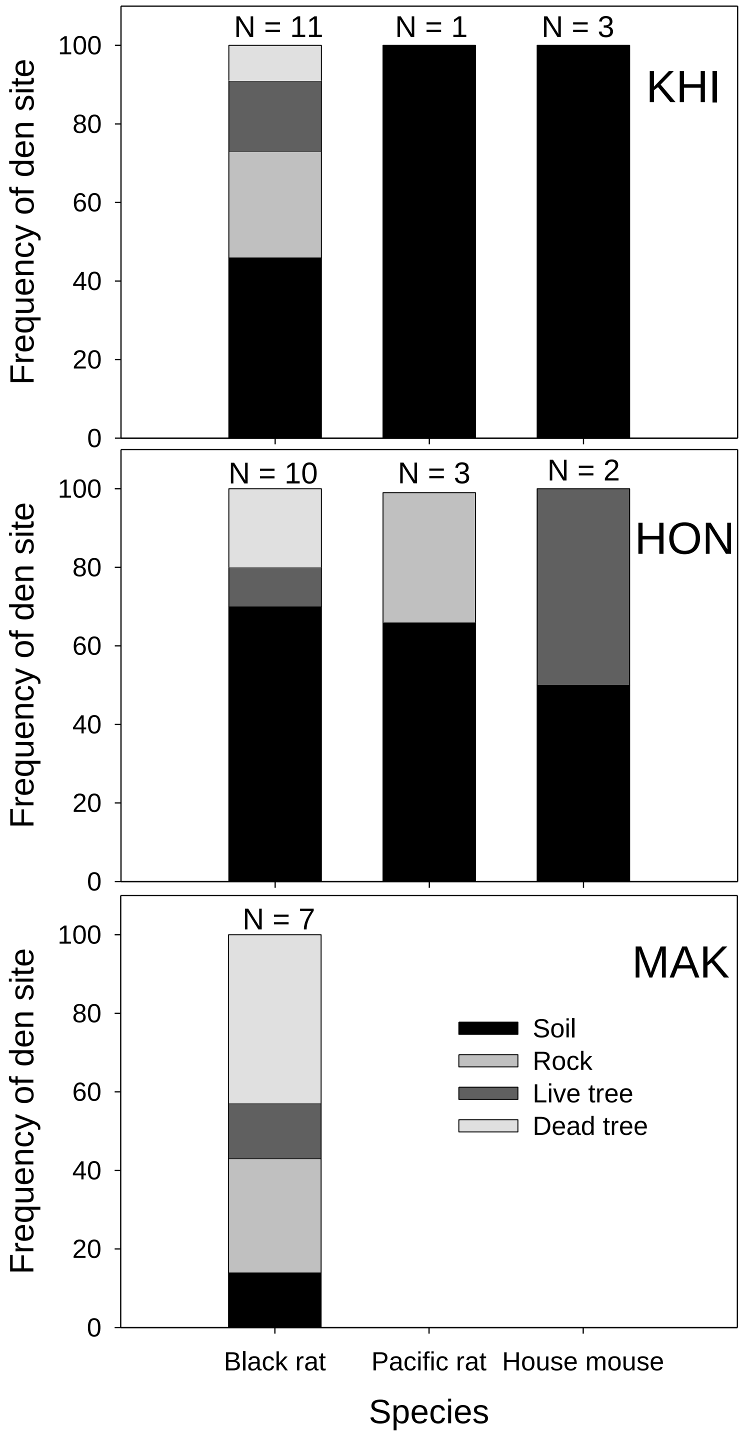

Figure 14. Mean ± SE frequency (%) of den sites occupied by each of the rodent species, as evidenced by the terminus of thread bobbins, at the three study sites in the Waianae Mountains, Oahu. Sample sizes are given above each species. Bobbins were only attached to black rats at MAK.

Discussion

Black rats are the most abundant rodent species in three mesic forest sites in Hawaii, yet both mice and Pacific rats are also present in lower abundances. Bi-monthly live-trapping at the three sites revealed that April-May and October-December tended to be the months with the greatest numbers of black rats, whereas the pattern of fluctuation across years was less distinguishable for Pacific rats and mice across sites. Black rat and mouse abundances were two- and four-times higher, respectively, during April-June 2007 at KHI than in any other sampling month. The rodents also differ in uses of microhabitat, including substrate types, height above the ground, and distances travelled from point of capture. Whereas the dominant rodent, the black rat, commonly uses both the canopy (especially above 2 m height) and the ground surface for both activity and denning, Pacific rats and mice are largely confined to the ground and Pacific rat dens were recorded only in the ground. In habitats studied in Hawaii, as well as elsewhere on islands where these three introduced rodents coexist, habitat partitioning and competition are possible explanations for the differences in relative abundance and habitat use among these coexisting species.

Factors influencing rodent abundances

Fluctuations in rodent species abundances were common to each of the three mesic forests in my study, and the highest overall abundances were typically for black rats at KHI. Determining the causes of such fluctuations and population differences has been one of the greatest challenges in animal ecology (Elton 1942; Krebs et al. 1973). For example, in New Zealand, dramatic seasonal increases in rat and mouse populations were explained by increased litter arthropods that fed on fallen beech (*Northofagus truncata*) flowers (Fitzgerald et al. 1996) only until it was revealed that additional factors also correlated with rodent densities, such flowering, fruiting and seed availability (Alley et al. 2001) as well as cat and stoat populations (Efford et al. 2006). Additional complications in indentifying factors that predict rodent abundance was shown when Ruscoe et al. (2004) demonstrated that one season's rimu (*Dacrydium cupressinum*) fruiting in a beech-dominated forest drove house mouse abundance. Therefore, mouse and rat population eruptions in beech forests in New Zealand are probably driven by a combination of several related factors that may not be constant from year-to-year and that cannot be easily separated without experimental manipulations (King et al. 1996; Alley et al. 2001), and the same conclusion is likely for my study sites in Hawaii.

Like the mast fruiting of beech forests in New Zealand, a pronounced increase in food supply may be one important factor that can influence rodent reproduction and abundance (Blackwell et al. 2003). At KHI, juvenile black rat abundance was highest in June-December, which overlaps with the heaviest fruiting and seed rain of *Psidium cattleianum* (June-October; unpublished data), and thus may influence black rat seasonal reproduction, natal care, and juvenile growth. According to laboratory studies, black rats reach sexual maturity at 2-4 months (Watts and Aslin 1981) and wean young at 21-28 days (Cowan 1981; Hooker and Innes 1995). In a study in dry coastal forest on Oahu, abundance of juvenile black rats was also highest during the July-November period (Tamarin and Malecha 1971). Similarly, juvenile black rats in New Zealand were more abundant in the autumn and winter after summer breeding (Innes et al. 2001). *Psidium cattleianum* is the most abundant tree with the most seed rain of all woody species at KHI

(Appendix A, C). Additionally, black rats readily consume *P. cattleianum* fruits and seeds (see Chapters 3, 4, 5). Because *P. cattleianum* is also abundant at HON and MAK, and the fruit ripen at all three sites at approximately the same time of year, the increased black rat abundance during October-December at each of the three sites may be partially due to the prior months' increase in this reliable food source. The greater abundance of black rats at KHI relative to HON may also be partially explained by *Psidium* spp. fruit and seed availability (both *P. cattleianum* and *P. guajava* are found at all three sites) because *Psidium* spp. seed rain at KHI is ca. 28 times greater than at HON (compare Appendix C and Bakutis 2005). Abiotic factors, such as rainfall can also be important drivers of rodent population fluctuations, and this was the case with rainfall correlating with house mouse abundance in Australia (Singleton 1989). At KHI, May-July are typically the months with the lowest precipitation (cited in Joe and Daehler 2008), and June through September are the warmest months (unpublished data). If such abiotic factors such as rainfall and temperature influence rodent abundance at KHI, it is unlikely that these factors are the sole influencing factors.

Predator abundance and disease are two important attributes that can influence rodent populations and these may partially explain differences in relative abundances of black rats between KHI and HON. Mongoose and cats are well known predators of rats in Hawaii (Mostello 1996; Staples and Cowie 2001; Appendix D), and observations of both of these predators during rodent trapping were more common at HON than KHI. Mongooses were incidentally captured in live-traps on five occasions (May 2007, July 2007, May 2008, November 2008, January 2009) at HON and just once at KHI (October 2008). A cat was observed agitating a captured rat in a live trap at KHI, and on three occasions at HON an unknown animal transported traps with recently captured rats for distances of 7 m, 9 m, and 20 m. Five radio-collared black rats were killed by cats at KHI, and at least three other rat stomachs (two at KHI and one at HON) were found on the forest floor and these appeared to also result from predation by cats. No predators were caught or observed at MAK, but one radio-collared black rat was killed by an unknown animal, and mongoose tracks in tracking tunnels indicated their presence at all three sites. Studies in New Zealand have suggested that stoats and cats are key predators that may partly regulate black rat populations (Innes et al. 2001; Blackwell et al. 2003; Efford et al. 2006), and cats and mongooses are two rodent predators in Hawaii that may have influenced the black rat populations at my sites. Disease can also influence population dynamics, and the incidence of disease was much more prevalent at HON than at either KHI or MAK, as evidenced by the greater ear mite infections in black rats at HON (26% of individuals), relative to the much lesser infection rates at KHI (2%) and MAK (4%). Additional evidence of less healthy black rats at HON relative to the other two sites included a higher frequency of boils, swelling, and possibly fungus growing on tails. It is unknown to what extent these infection affect black rat fitness and population dynamics.

Rodent species abundances at the three sites in the Waianae Mountains were within the ranges of other studies in Hawaii (Sugihara 1997; Lindsey et al. 1999); however, such generalizations should be interpreted cautiously because of the wide range of factors that are dissimilar among studies (e.g., habitat, trapping regime, species composition, abundance calculation). Black rat abundances were 8-14 indiv./100 trap nights in my study, which was nearly identical (8-17 indiv./100 trap nights) to a study in montane wet forest on Maui where the same three introduced rodents coexist (Sugihara 1997), but lower than in montane wet forest (11-25 indiv./100 trap nights) on the Island of Hawaii (Lindsey et al. 1999). In a study on South Island, New Zealand, Alterio et al. (1999) found abundances of black rats ranged from 1.8-5.6 indiv./100 trap nights. In a 5-year study of blacks rats in North Island, New Zealand, Innes et al. (2001) found that abundances were 1-20 indiv./100 trap nights (mean ca. 8-10). Other studies of black rats from North Island, New Zealand found that abundances ranged from 5-35 indiv./100 trap night (Dowding and Murphy 1994; Wilson et al. 2007). When density was calculated for black rats (7.1 rats/ha when averaged across my sites), it was within a suite of New Zealand forest studies (0.5-6.5 rats/ha; Dowding and Murphy 1994; Brown et al. 1996; Innes et al. 2010) but lower than estimates from dry forest on Oahu (8-18 rats/ha; Tamarin and Malecha 1971). Pacific rats were relatively uncommon in my study, never reaching abundances > 5 indiv./100 trap nights, and there were no Pacific rats captured during approximately half of the total trapping sessions across all three sites. Both Sugihara (1997), with 4-8 indiv./100 trap nights, and Lindsey et al. (1999) with 4-20 indiv./100 trap nights caught many more Pacific rats than in my study. When densities were compared, averages across my sites (< 1 rat/ha) were lower than those in dry forest on Oahu (1.5-8 rats/ha; Tamarin and Malecha 1971). Mouse abundance (No. indiv./100 trap nights) in Hawaii ranged from 3-8 (this study and Sugihara 1997) to 9-16 (Banko et al. 2002), and were comparable abundances to those of subantarctic New Zealand (7.4; Harper 2010), disturbed plantation understory (10; King et al. 1996), and logged native forest (4; King et al. 1996) in North Island, New Zealand.

There are typically more male rodents in a given population than females, and the males tend to be slightly larger in mass than females (Sugihara 1997; King et al. 1996; Innes et al. 2005a,b; Ruscoe and Murphy 1995). These patterns were observed with the three rodent species on Oahu except that at KHI the average masses of male Pacific rats were similar to those of females. Both black rats and Pacific rats were larger in Hawaiian wet forests (Sugihara 1997; Lindsey et al. 1999) than those adult rats caught in mesic forests on Oahu (black rats: males 126-131 g, females 111-121 g; Pacific rats: males 55-56 g, females 48-58 g; Table 2,3,5). For example, at Hakalau National Wildlife Refuge in Hawaii (1500-1650 m a.s.l.), Lindsey et al. (1999) found that male black rats were 152.6 ± 4.9 g (mean ± SE) and females were 124.7 ± 4.8 g, whereas male Pacific rats were 69.9 ± 0.7 g and females were 58.9 ± 0.6 g. Similarly, Sugihara (1997) trapped in wet forest at 1505-2125 m a.s.l. on Maui where adult black rats (male and female combined) averaged 145-172 g and adult Pacific rats averaged 64-72 g. The average mass of black rats over a five year period in New Zealand forest was 129 g, where males on average were larger (141 g, N = 824) than females (121 g, N = 613; Innes et al. 2001). Male house mice were over twice the mass on Auckland Island, New Zealand (23.1 ± 0.9 g), as on Oahu (9.9-11.9 g; Table 6), and the body length for both males (9.3 ± 0.2 cm) and females (9.0 ± 0.1 cm) were slightly larger for Auckland Island mice (Harper 2010) than those captured on Oahu (ca. 6.5-7.1 cm; Table 6). Both sexes of mice in forests on North Island, New Zealand, were larger (males: 16.4 ± 0.2 g, mean ± SE; females: 15.5 ± 0.3 g; King et al. 1996) than those on Oahu or on Hawaii Island at high elevation (11.3 ± 0.3 g, mean ± SE, N = 65; 2500-2935 m a.s.l.; unpublished data) and low elevation (7.9 ± 0.2 g, N = 64; 33-188 m a.s.l.; unpublished data). The sizes of mice on Auckland Island

and North Island were within the normal range for mice in New Zealand, where they average 16-26 g (Ruscoe and Murphy 2005), which implies that the mice in New Zealand are substantially larger than those on Oahu and Hawaii Island. This is in agreement with Bergmann's rule where the body sizes of mammals are larger at higher latitudes relative to lower latitudes. The black-colored variety of black rats comprised approximately the same proportion (13%) of the sampled populations (N = 1587 individuals) captured in New Zealand (Innes et al. 2001) as in KHI and HON (15%), but were much fewer than those captured at MAK (54%).

Tracking tunnels have been used in Hawaii and New Zealand to help assess activity levels and abundances of invasive rodents (Lindsey et al. 1999; Innes et al. 1995; Brown et al. 1996; Blackwell et al. 2002; Mosher et al. 2010). The potential use of tracking tunnels is promising because it requires much less effort than trapping, and it can provide an index of rodent activity when monitoring areas prior to and following rodent reduction and eradication attempts (Innes et al. 1995; Mosher et al. 2010). By using tracking tunnels in New Zealand, Innes et al. (1999) demonstrated that fledging success of the kokako (*Callaeas cinerea wilsoni*) bird decreases when rats are tracked in > 5% of tunnels. In my study, black rat tracking did not correlate with abundance estimates (i.e., indiv./100 trap nights) when the three sites were considered separately or collectively. A competitor or predator may alter the use of tracking tunnels (Brown et al. 1996), which may have been the case in my study as evidenced by frequent mongoose and occasional cat foot-prints appearing in the tracking tunnels. Without rat control in Podocarp forest in New Zealand, Innes et al. (1999) suggests that rat tracking in tunnels is typically 40-80% and rarely as low as 15%. Tracking at the three Waianae Mountain sites in my study ranged from 11% to 63%. Currently, tracking tunnels are being implemented at KHI where rodents are repeatedly kill-trapped bi-weekly (Mosher et al. 2010); yet, like in my study, the numbers of rats captured do not correlate with tracking tunnel activity. Blackwell et al. (2002) found that tracking tunnels do not correlate with trapping at low rodent abundances. Mouse abundances can often increase when black rats are trapped (Harper and Cabrera 2010) and may also interfere with rat tracking tunnel activity (Brown et al. 1996). Tracking tunnels can be a useful tool for estimating rodent activity in some areas (e.g., Innes et al. 1999); however, at my three study sites it does not appear to correlate with rat abundances.

Rat home-ranges and rodent habitat use

Home-ranges of black rats at the two mesic forests in the Waianae Mountains (1.5-9.1 ha) 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 black rat 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). The only other published home-range study of black rats and Pacific rats in non-plantation forest in Hawaii was by Lindsey et al. (1999), where, like in my study, locations of radio-collared rats were determined by triangulation. In the study by Lindsey et al. (1999) in montane wet forest, they found that black rat home-ranges averaged 4.2 ha for three males and 1.8 ha for one female. Only one Pacific rat's home-range was calculated in my study on Oahu (1.8 ha), yet Lindsey et al. (1999) determined that Pacific rat home-ranges ranged from 2.8 ha (two males) to 3.4 ha (one female). Male black rats can often have larger home-ranges than females (two times larger in Whisson et al. 2007; three times larger in Hooker and Innes 1995; > 9 times larger in Pryde et al. 2005), yet home-ranges did not differ between sexes in my study or that of Dowding and Murphy (1994). However, Dowding and Murphy (1994) found that one male black rat quadrupled its home-range within 7 days, and the authors suggest that such erratic changes in the distance travelled and home-range increase probably correlates with the breeding season. Additionally, Dowding and Murphy (1994) caution that such a large change in home-range size within a short time could greatly affect the precision of rat density estimates. While there is less seasonal shift in weather in Hawaii than in New Zealand, the unpredictable movements and behavior of rats at my study sites may be one explanation for the absence of an obvious relationship in home-range area and rat abundance.

Black rats were more active in trees than on the ground when compared to Pacific rats and mice in the Waianae Mountains, and the average height black rats were observed above ground (ca. 2.8 m) was similar to findings by Hooker and Innes (1995) in New Zealand forest where radio-collared black rats were primarily arboreal and 73% of the radio locations were > 2 m above ground. In wet forest on Hawaii Island, 44 rats were captured in trees and 43 of those were black rats and one was a Pacific rat (Lindsey et al. 1999). Using spool-and-line tracking on a New Zealand off-shore island, Hoare et al. (2007) found that 85% of Pacific rat activity occurred on the ground, and aboveground ventures (10% of observation time) were usually to the tops of 3.5 m trees that were in fruit at the time of measurement. Pacific rats used mainly surface habitat, which averaged 70% of the recordings in my study. Also in agreement with findings from my study, Lindsey et al. (1999) observed all radio-collared Pacific rats (N = 4) had den sites belowground. Radio-collared black rats in the Waianae Mountains occupied dens in both canopy and the ground, yet Lindsey et al. (1999) with nine radio-collared black rats, and others in New Zealand forests (Dowding and Murphy 1994; Hooker and Innes 1995), found black rats occupied den sites only aboveground. However, despite the black rat denning in trees, they spent ca. 90% of the night on the ground (Dowding and Murphy 1994). Lindsey et al. (1999) also observed most black rats on the ground when active at night. Perhaps differences in the relative abundances of rodent species, a shorter canopy forest at my sites relative to that of Lindsey et al. (1999), or more favorable ground-habitat for den sites in the Waianae Mountains, may partly influence the black rat's choice of den site. Additionally, aboveground den sites may be favored over belowground sites to better escape predators, especially daytime predators like mongoose in Hawaii and stoats in New Zealand. Seemingly more frequent observations of predators at HON may also partially explain the greater frequency that black rats were observed in the arboreal habitat there than at the other sites.

Rodents are often in areas of relatively high vegetation cover presumably to limit their exposure to predators (King et al. 1996; Cox et al. 2000; Atkinson and Towns 2005; Arthur et al. 2005). King et al. (1996) found that house mouse abundance was greater in densely vegetated areas, such as disturbed sites along roads or plantations, than in the more open understory of the forest interior. In Australia, Arthur et al. (2005) conducted experiments in 50 m x 50 m outdoor enclosures and found that house mouse abundances were greater in areas having reduced exposure to predators resulting from increased habitat cover (grass and downed logs). Dickman (1992) determined that house mouse abundance roughly correlates with vegetation density in Western Australia. In eastern

Australia, Cox et al. (2000) found that black rats preferred densely vegetated understories. In New Zealand, Pacific rats are well known to restrict their activity to areas of dense ground cover (Atkinson and Towns 2005), unless they are the top predator at a site, in which case they commonly occupy open spaces (Hoare et al. 2007). All three rodents in the Waianae Mountains were under 30 cm vegetation cover at least 88% of the time when they were out of their dens. While Pacific rats and house mice may be largely restricted to the ground by the more dominant black rat (Lindsey et al. 1999; this study), the activity of these two smaller rodents under the cover of ground vegetation may be a predator avoidance behavior.

Sympatric rodent species may use different substrate microhabitats, as they did in the Waianae Mountains. Leaf litter was a common substrate in which the Pacific rat and the house mouse were active, but it was less used by black rats. This finding differed from that discovered by Cox et al. (2000) where black rats tracked by the spool-and-line method were most active in microhabitats containing litter, especially deep litter, as well as in dense understory cover that included an abundance of stems. However, experimental manipulation of leaf litter showed a significant attraction to habitats with increased leaf litter only when the black rat population was relatively high (Cox et al. 2000). There are four other rodents (including the house mouse) that are potential competitors of black rats at the study site of Cox et al. (2000), which may further influence the black rat’s use of leaf litter microhabitat. Leaf litter may provide an important substrate for rodents to find arthropod prey, and both Pacific rats and mice consume significantly more arthropods at KHI, and possibly the other two sites, than do black rats (Chapter 3). While leaf litter may not be a preferred habitat for the dominant black rat in the Waianae Mountains, the use of leaf litter could be influenced by rodent density (Cox et al. 2000) where times of higher local density may shift the smallest rat (Pacific rat) to a proportionally greater use of bare soil microhabitat than that of leaf litter. The greater activity of black rats on branches and stems compared to the other two rodent species is not surprising given that black rats spends significantly more time aboveground than at the surface.

Spool-and-line tracking in the Waianae Mountains revealed that the den sites of all of the monitored Pacific rats and all but one of the monitored mice were belowground, whereas black rats had den sites aboveground, in cavities of living or dead trees, and belowground. Most of the living trees where black rat den sites were located by radio-tracking were observed in some of the tallest trees at the study sites, especially the non-natives *Aleurites moluccana* and *Grevillea robusta*, and to a lesser extent the natives *Acacia koa* and *Metrosideros polymorpha*. Lindsey et al. (1999) found the majority of the dens of black rats were in large *A. koa* and *M. polymorpha* trees, which were the dominant trees at their site, and one black rat nest consisted of dried leaves in the top of a tree fern (*Cibotium splendons*). Similarly, Hooker and Innes (1995) found that all of the black rats radio-collared in their study had dens in trees and that the den sites were too high to pinpoint from the ground; yet one black rat nest that was recovered was a “loosely woven structure in a small rimu (*Dacrydium cupressinum*) tree.” Innes (2005b) suggested that nests made of leaves like the one observed by Lindsey et al. (1999) and Hooker and Innes (1995) are built if other microsites, such as tree cavities, are not available. Unlike other studies where black rats were typically found denning only in trees, all of the black rats followed on a 797 ha offshore island in southern New Zealand had dens belowground despite the presence of a short-statured forest (Rutherford et al. 2009); many of the dens were in seabird burrows and beneath logs and branches. Although the frequency and time intervals in which rats are checked for den site locations will influence the reported number of den site changes, it is interesting to note that black rats do not typically occupy just one den site during the period that they are monitored. Black rats changed den sites to different trees 1-3 times at Hakalau Forest on Hawaii Island, 3-5 times in the Rotoehu Forest, North Island New Zealand, and 2-9 times in Puketi Forest, North Island, New Zealand. In the Waianae Mountains, black rats changed dens 1-11 times, yet these rats differed from aforementioned studies in Hawaii and New Zealand because individuals in my study commonly changed between dens above- and belowground. Similar to the study of Hooker and Innes (1995), there were no occasions where two radio-tagged individuals in the Waianae Mountains were observed sharing a single den site. However, two individual black rats of opposite sex were observed sharing den sites in other New Zealand and Hawaiian forests (Dowding and Murphy 1994; Lindsey et al. 1999; Rutherford et al. 2009), and Dowding and Murphy (1994) observed at least one pairing (four occasions at three sites within overlapping home-ranges) with two adult males in the same den, and three females shared the same den on four occasions.

Conclusion

The black rat is the most abundant rodent at the three study sites in the Waianae Mountains, and it is most frequently recorded in arboreal habitats > 2 m high. The two smaller rodents, the Pacific rat and the house mouse, are generally surface-dwelling in these forests when they are not in their belowground dens. Pacific rats occur infrequently and unpredictably during the year and may therefore be missed by land managers that do not trap enough throughout the year. Additionally, mouse eruptions can be episodic and extend for short periods (e.g., two months at KHI), during which time they can outnumber black rats. The observed dissimilarity in microhabitat use for these three sympatric rodent species is evidence that they differ ecologically and occupy different niches. There are at least three possible, non-mutually exclusive, explanations for these differences in microhabitat use. One is that the black rats competitively exclude the two smaller rodents from trees. A second is that the Pacific rat and the house mouse prefer the surface habitat, perhaps because it offers greater concealment from predators in thick surface cover, preferred terrestrial prey items, or closer proximity to belowground den sites. A third potential explanation for the observed variation may be that these rodent's behaviors are the ultimate effects of past ecological interactions that have occurred over long (evolutionary) time periods. Whatever the mechanism, it is clear that these three invasive rodent species are able to coexist, at least to date, in mesic forests in the Waianae Mountains.

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CHAPTER THREE:

NICHE PARTITIONING BASED ON DIET ANALYSIS OF THREE INTRODUCED RODENTS IN HAWAIIAN MONTANE FOREST

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Abstract

Determining the diets of sympatric rodents can uncover patterns of resource partitioning and competitive interactions. Prey items that appear in the stomachs of introduced rodent predators can provide insight into trophic divisions and disruptions and help to assess the vulnerability of native prey. In the Hawaiian Islands, where rodents were absent prior to human arrival ca. 1000 years ago, three rodents (*Rattus rattus* or black rat, *Rattus exulans* or Pacific rat, *Mus musculus* or house mouse) are common to forests and are voracious predators of plants and animals. These three rodents were trapped in mesic montane forest from February 2007 to September 2009 to determine their short-term diet by analyzing stomach contents and their long-term (life-time) diets by extracting bone collagen for $\delta^{15}N$ and $\delta^{13}C$ isotopic analysis. For all three rodents > 75% of individuals had plants and > 90% had arthropods in their stomachs. Mean relative abundance of the major items in stomachs was 81% plant and 14% arthropod for black rats, 60% plant and 38% arthropod for Pacific rats, and 36% plant and 57% arthropod for mice. Rodents may be dispersing some native and non-native seeds, including the highly invasive *Clidemia hirta*, because intact seeds were found in some of the stomachs of all three species. Fruit pulp comprised 55% of the black rat diet, 41% of the Pacific rat diet, but only 11% of the house mouse diet. Caterpillars were particularly common in Pacific rats and mice, and aside from a native spider, a cricket, and two species of beetle, the majority of identifiable arthropods in all three rodents were non-native species. None of the stomachs contained evidence of birds, snails, or lizards, all of which are common at the study site. The $\delta^{15}N$ and $\delta^{13}C$ signatures revealed that the Pacific rat and house mouse occupy the same trophic level, whereas the slightly lower

$\delta^{15}N$ values of black rats reflect a proportionally more vegetarian diet compared to the two smaller rodents. Therefore, the strongest evidence of food resource portioning among the three rodents is between the black rat and house mouse; the Pacific rat has an intermediate diet that partly overlaps with the two other rodent species.

Introduction

How closely related species coexist in a community has long intrigued ecologists. Numerous factors influence a species niche, including biotic and abiotic attributes, resource use, and competition (Elton 1927; Hutchinson 1957). Niche partitioning reflects competitive interactions among species and can be determined by diet analysis of sympatric animals (Biró et al. 2005; Purnell et al. 2006). Animals with similar life-history traits and close phylogenetic associations, such as different species of rodents in the same habitat, must partition resources across time and space in order to coexist (Gause 1934).

Introduced animals can disrupt food webs by consuming native prey and by altering the niches of native competitors (Fritts and Rodda 1998; Fukami et al. 2006). Identifying prey consumed by introduced predators provides insight into native species' vulnerability and can help improve strategies of native and non-native species management (Stapp 2002; Caut et al. 2008a). Rodents (*Rattus rattus* or the black rat or ship rat, *R. norvegicus* or the Norway rat, *R. exulans* or the Pacific rat or Polynesian rat, and *Mus musculus* or the house mouse) are omnivorous predators that have been introduced to many ecosystems worldwide and are among the most widespread and problematic invasive animals affecting islands (Towns et al. 2006; Angel et al. 2009;

Drake and Hunt 2009). Introduced rodents may consume a wide variety of prey, including plants (e.g., fruits, seeds, vegetative material) and animals (e.g., arthropods, mollusks, birds; Sugihara 1997; Campbell and Atkinson 2002; Stapp 2002), and their diets can shift depending upon a number of factors, including the availability of food items, the chemical and nutritional quality of the food items, and the rodents' competitive ability relative to other animals that coexist in the environment (Clark 1982).

Predation by introduced rodents is rarely observed directly, perhaps because they are nocturnal and often forage in the canopy or burrow belowground (Lindsey et al. 1999; Towns 2009). Consequently, field observations of partially consumed prey items (e.g., seeds, mollusks, arthropods; Norman 1970; Campbell et al. 1984; McConkey et al. 2003) or captive-feeding trials (Williams et al. 2000; Pérez et al. 2008; Meyer and Shiels 2009) have been used to determine the species suffering from predation by introduced rodents. Additionally, stomach content analysis has been used to identify rodent's prey and assess their diets (e.g., Clark 1982) despite this method reflecting one to a few meals.

Stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) have been widely used to determine the trophic levels at which animals have fed during tissue development (Peterson and Fry 1987; Lajtha and Michener 1994); however, interpretations of diet using stable isotopes are restricted by the tissue type analyzed and tissue turnover rates. For example, liver tissue has a higher turnover rate than blood cells or muscle, and bone collagen is deposited and reworked during the lifetime of an animal, so its isotopic values represent a long-term average of an animal's diet (Lajtha and Michener 1994; Caut et al. 2008b). The difference in isotopic composition between a predator and its prey (discrimination values) is presumed to average ca. 3‰ and 1‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively; however, the discrimination values can differ widely depending on the species of prey involved, as demonstrated by Post (2002) where the majority of the δ^{15}N discrimination values in lake organisms were 2-4.5‰, and Caut et al. (2008c) determined from lab trials that the δ^{15}N discrimination values for black rats ranged from -1.46‰ to 4.59‰. Applying isotope mixing models enables quantification of each prey item's contribution to a predator's diet (Phillips and Gregg 2003). However, without isotopic signatures for all prey items consumed by the predator, collected from the specific habitat of the predator (Flaherty and Ben-David 2010), interpretations of mixing models can be problematic (Martínez del Rio et al. 2009). Combining δ^{15}N and δ^{13}C to assign trophic-level feeding of coexisting predators and prey (Peterson and Fry 1987; Lajtha and Michener 1994) with stomach content analysis of predators can provide an understanding of the diet and trophic level occupancy of similar, coexisting predators.

In the Hawaiian Islands the first rodents (the Pacific rat) arrived with humans ca. 1000 years ago (Athens et al. 2002), and later arrival of two additional rats (the Norwary rat and the black rat) and the house mouse occurred upon European settlement ca. 230 years ago (Tomich 1986). In contemporary Hawaii, the Norway rat has rarely been found in forests. The black rat appears to be the most common rat in forests, and both black rats and mice are distributed from sea level to nearly 3000 m (Amarasekare 1994; Lindsey et al. 1999; unpublished data). The Pacific rat is the smallest of the three introduced rats and may be outcompeted in many environments in Hawaii and other Pacific islands by the European-introduced rats (Russell and Clout 2004). Similarly, the house mouse may be suppressed by all three introduced rats (Russell and Clout 2004; Angel et al. 2009), such as in New Zealand where mice are rarely known to occur where Pacific rats are present (Yom-Tov et al. 1999; Ruscoe and Murphy 2005). It has been established that these introduced rodents consume plants and animals in Hawaii, as evidenced by field trials (VanderWerf 2001; Shiels and Drake, in press), captive feeding trials (Pérez et al. 2008; Meyer and Shiels 2009; Shiels, in press), and two high elevation studies that analyzed stomach contents (Sugihara 1997; Cole et al. 2000). However, the short- and long-term diets and potential resource partitioning of three introduced rodent species has not been established in Hawaii or elsewhere. The objectives of this study are to 1) determine the short- and long-term diets of black rats, Pacific rats, and mice where they coexist in mesic montane forest in Hawaii, 2) identify some of the native and non-native prey species that are vulnerable to these three rodents, 3) determine if there is evidence of niche partitioning that may result from differential feeding and trophic level occupancy for each of the three rodent predators relative to their dominant prey.

Methods

Study site

Rodents were obtained from Kahanahaiki Management Unit (21^o 32′ N, 158^o 11′ W), a 36 ha segment of mesic forest in highly dissected terrain (500-660 m a.s.l; Gagné and Cuddihy 1999) in the northern Waianae Mountains, on the island of Oahu, Hawaii. Kahanahaiki is managed for native species preservation by the U.S. Army, and the forest was fenced in 1996 to exclude feral goats and pigs. Daily air temperature at the site ranges from 16-24^oC (unpublished data) and monthly rainfall varies from 50 mm to 170 mm (cited in Joe and Daehler 2008).

Two species of rats, the black rat (133 ± 3 g; mean ± SE) and Pacific rat (47 ± 2 g), and the house mouse (10 ± 1 g) are present at Kahanahaiki (Meyer and Shiels 2009; Shiels and Drake, in press). Average estimated relative abundance measures using bi-monthly mark-and-recapture sampling over 15 months during 2007-2008 were 17 indiv./100 trap nights for black rats and 1 indiv./100 trap nights for Pacific rats. No Norway rats were captured at the study site and the house mouse was captured at ca. 6 indiv./100 trap nights (Shiels and Drake, in press).

Stomach content analysis

Rodents (black rats, Pacific rats, mice) were collected from kill-traps (Victor® rat traps) from February 2007 through September 2009. Traps, each spaced 10-25 m apart, were established along a single 300 m transect and at two 50 x 50 m plots where native snails (*Achatinella mustellina*) were relatively abundant. Each month, 15-32 traps were baited with coconut chunks or peanut butter and set for 2-5 consecutive days and checked each 24 hours. From May-September 2009, approximately 400 kill-traps were added to the site and arranged along multiple transects that circled the core interior and were spaced ca. 25-50 m apart. I used the same bait and trap spacing as described above, and traps were checked each 1-7 days. Only rodents that were freshly (< 24 hours) killed, evidenced by lack of obvious decay, were used in this study. Upon capture, each rodent was weighed and its sex was determined whenever possible. Carcasses were stored in a freezer for later analysis.

Rodent stomach contents were extracted from the stomach cavity, swirled for 5 min in water and mild detergent (Joy® brand) to separate contents and dissolve gastric juices and oils, and then sieved through a No. 35 US Standard sieve (0.4 mm opening; Sugihara 1997). Recovered contents were preserved in 95% ethanol and analyzed for: 1) frequency (percent) of occurrence of each food type, and 2) relative abundance (percent) of each food type for each individual. For each sample, a transparent grid (5 x 5 mm for rats; 3 x 3 mm for mice) was positioned beneath a Petri dish that contained the stomach contents of the sample. Samples were inspected using a dissecting microscope with 10-20x magnification. Rodent stomachs that were more than half-filled with intestinal worms were excluded from this study (Sugihara 1997). Relative abundance of each food type was determined for each individual sample by scoring the number of grid-boxes containing a given food type and dividing by the total number of grid-boxes (i.e., 40 grid-boxes). If more than one food type was in a grid-box, the item closest to the center of the grid-box, or the centermost item on top when overlapping items were present, was recorded (Cole et al. 2000). Plant food types included fruit, seed, and other plant material (including leaves, flowers, stems, wood); whereas arthropod food types included caterpillar, ant, bug, spider, and other arthropod material. Rodent hair and flesh, and other/unknown (i.e., material that did not fit any of the listed categories), represented the final two major food type categories. Food items were classified to the lowest taxonomic level whenever possible using voucher specimens collected from the study site. Frequency of occurrence for each food type was calculated by the presence of each of the food types in a given sample divided by the total number of samples.

Stable isotope analysis

To augment the short-term diet assessment from stomach contents, the long-term diets of each of the rodents was determined using stable isotope analysis. On a subset of the trapped rodents (N = 20 black rats, N = 12 Pacific rats, and N = 11 mice), bone collagen was extracted and analyzed for $\delta^{15}N$ and $\delta^{13}C$ values. Bone collagen was extracted using methods described in Lajtha and Michener (1994) where the femur bone (plus tibia and fibia bones for mice) of each individual was excised, cleaned of flesh, and soaked in 0.5 M HCl for 48 hours at 4^o C; the remaining sample (now collagen) was rinsed with deionized water and allowed to dry at 60^o C for 5 days before grinding to a fine dust. Prey items (fruit, seed, arthropod) were collected from the study site and were chosen based on similar species (or life forms) identified in the rodent stomachs and those found to be attractive to rodents at this site using field trials (Shiels and Drake, in press). For plant-prey items (N = 5), one sample from each of the following species was collected for analysis: *Alyxia stellata* (seed), *Clidemia hirta* (fruit + seed), *Diospyros hillebrandii* (seed), *Psidium cattleianum* (seed), and *Pouteria sandwicensis* (fruit). Three samples of each of the three herbivorous arthropods were analyzed: caterpillar, isopod, and amphipod. Three predatory arthropods (spiders) were analyzed, including *Steatoda grossa* and two unknown species. Samples were dried at 60^o C, ground to homogenize either multiple individuals of the same species (e.g., plants, herbivorous arthropods) or single individuals (e.g., spiders), and, like the rodent bone collagen, analyzed isotopically using a Carla Erba elemental analyzer (model NC2500) with an attached mass spectrometer (Finnegan DeltaS with source upgrade). Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from international standards.

Statistical analysis

The relative abundances of each of the major food types were compared among the three rodents by parametric and non-parametric ANOVAs. The major food types were grouped into three general categories: 1) Plants, which included fruit, seed, and other plant material, 2) Arthropods, which included caterpillar (i.e., Lepidoptera larvae), ant, burrowing bug, spider, other arthropod material, and 3) Other, which included rodent hair + flesh, and unknown (unidentifiable) items. Because these data were percentages, all data were arc-sin square-root transformed prior to assessment of meeting ANOVA assumptions. Fruit and seed were the two major food types that met parametric assumptions of ANOVA; whereas the remaining comparisons used Kruskall-Wallis tests to assess significant differences among rodents for each major food type. Significance was based on $P < 0.05$, and if significant differences occurred when all three rodents were compared, post-hoc Tukey's test (for fruit and seed) or Mann-Whitney U tests were applied to assess significance between rodent species (SPSS 1998).

To test whether the diet of black rats changed during the time period when few (February 2007-April 2009), and the majority (May-September 2009), of Pacific rats and mice were trapped, ANOVAs, after square-root transformations to meet normality assumptions, were used to compare the two time periods for the three dominant food types (fruit, seed, arthropod).

Results

The black rat was the most commonly trapped rodent at the study site and 95 stomachs were analyzed for short-term diets. Forty-seven mouse stomachs were analyzed, and 12 stomachs were analyzed from the less common rat, Pacific rat. There were roughly equal numbers of males and females analyzed for each rodent, and the sizes of the rodents were 124 ± 5 g (mean ± SE) for black rats, 52 ± 4 g for Pacific rats, and 12 ± 1 g for mice.

Stomach content analysis

All major food types were found in stomachs of some individuals of all three rodents (Table 12). There were significant differences among rodents for most major food types found in stomachs, and burrowing bugs were the only major food type that was not significantly different among rodents (Table 12). Plant relative abundance in stomachs significantly differed among rodents ($P < 0.001$; $\chi^2 = 56.7$, d.f. = 2), and was highest for black rats, intermediate for Pacific rats, and lowest for mice ($P < 0.015$ for each post-hoc comparison; Fig. 12). Fruit comprised the majority of the plant material for both rats, but seed was the most abundant plant material in mice (Table 12). Arthropod mean relative abundance also differed significantly among rodents ($P < 0.001$; $\chi^2 = 56.7$, d.f. = 2), and was highest for mice, intermediate for Pacific rats, and lowest for black rats ($P < 0.035$ for each post-hoc comparison; Fig. 15). Caterpillars (Lepidoptera larvae) comprised the majority of the identifiable arthropods found in each of the rodents, and were > 50% of the mouse's arthropod diet (Table 12). Rodent hair, which dominated the 'other' category in Fig. 15, was found in most stomachs of each rodent (69% of black rat individuals, 67% of Pacific rats, and 57% of mice), and mean relative abundance for rodent hair was highest for mice and lowest for black rats (Table 12; Fig. 15). Rodent flesh (with rodent hair attached) was found only in black rats (N = 1) and Pacific rats (N

= 1). There was no evidence of birds, reptiles, or other vertebrates in any of the stomachs, and there were no snails or fungi.

Table 12. Mean ± SE relative abundances (%) of major food types identified in stomachs of invasive rodents in Hawaiian mesic forest. The P-value reflects the comparison among species, and different letters represent significant ($P < 0.05$) differences from post-hoc comparisons between each rodent species. When no amount of food item was present for a rodent (i.e., unknown), that rodent was not included in the statistical analysis. Rodent flesh was only found in rats, and comprised < 5% of rodent hair + flesh.

Food type	Black rat (N = 95)	Pacific rat (N = 12)	House mouse (N = 47)	P-value
Plants				
Fruit	55.1 ± 2.4^{a}	40.6 ± 5.7^{a}	10.8 ± 2.7^{b}	< 0.001
Seed	24.9 ± 2.2^{a}	15.9 ± 4.3^{a,b}	19.0 ± 3.3^{b}	0.037
Other plant material	1.1 ± 0.4^{a}	2.5 ± 0.8^{b}	5.8 ± 1.5^{b,c}	< 0.001
Arthropods				
Caterpillar	3.2 ± 0.7^{a}	28.8 ± 3.8^{b}	53.8 ± 4.9^{c}	< 0.001
Ant	1.7 ± 0.3^{a}	1.3 ± 0.8^{a}	0.5 ± 0.2^{b}	0.007
Burrowing bug	0.9 ± 0.3	0.2 ± 0.2	0.7 ± 0.5	0.110
Spider	0.4 ± 0.1^{a}	0.2 ± 0.2^{b}	0.1 ± 0.1^{b}	0.016
Other arthropod material	7.4 ± 1.4^{a}	7.4 ± 2.7^{a}	2.1 ± 1.0^{b}	0.002
Other				
Rodent hair + flesh	4.9 ± 0.7^{a}	4.2 ± 1.4^{b}	7.2 ± 1.5^{b,c}	< 0.001
Unknown	0.4 ± 0.2	0.0 ± 0.0	0.1 ± 0.1	0.528

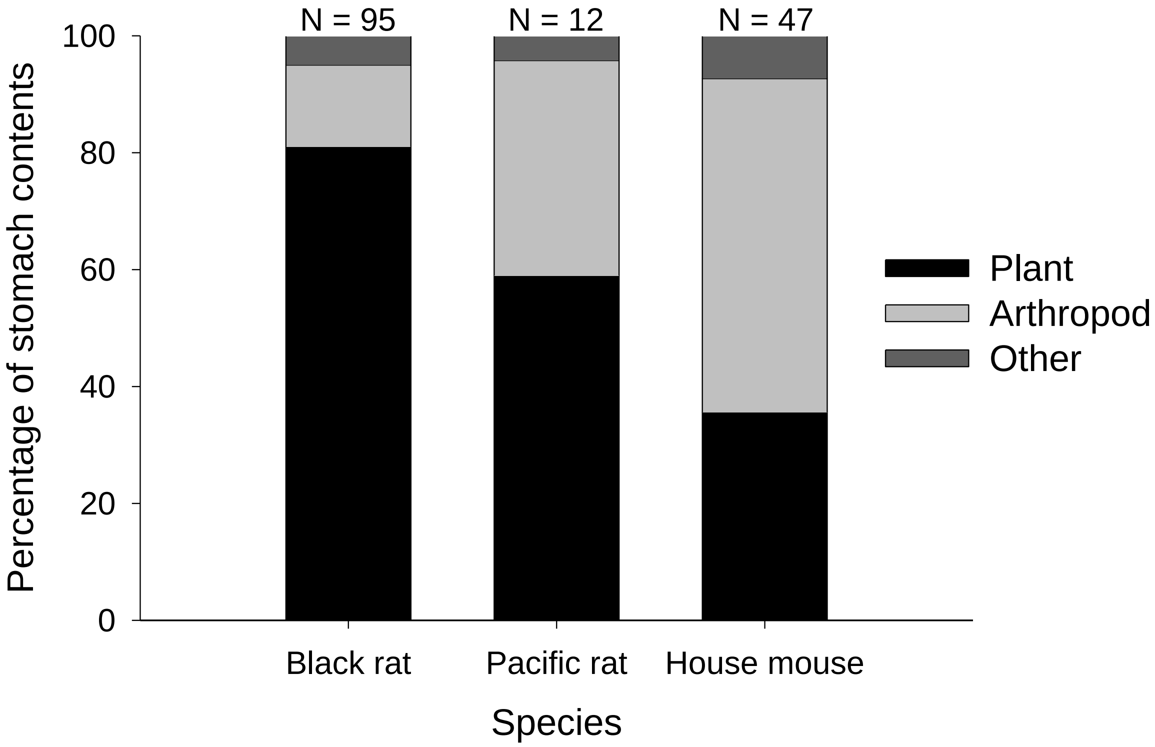

Figure 15. Mean relative abundances (%) of the three major items found in stomachs of black rats, Pacific rats, and house mice in Hawaiian mesic forest. The 'other' category is dominated by rodent hair, which was most likely a result of grooming rather than cannibalism (see Table 12 for minimal presence of rodent flesh in stomachs). For each of the three major items, there were significant ($P < 0.05$) differences between each species.

In each rodent species > 75% of individuals had plants and > 90% had arthropods in their stomachs (Table 13). All individuals of black rats and Pacific rats had fruit in their stomachs, and > 90% also had seed. The frequency of mouse stomachs with fruit (40%) tended to be less than those containing seed (64%). The majority of seed in all three rodents appeared chewed and was probably destroyed, but intact seeds of some native and non-native species were found in black rats and all three rodents had intact seeds of the non-native weed *C. hirta*. The frequency of other plant material, which mostly included stems and leaves, tended to be highest in Pacific rats, intermediate in mice, and lowest in black rats.

Table 13. Frequency (%) of rodent stomachs with identifiable seed, fruit, and arthropod taxa in Hawaiian mesic forest. Both *Cyrtandra dentata* and *Delissea subcordata* are federally endangered species in Hawaii. Many food items were damaged such that they could not be classified more specifically than fruit, seed, plant, or arthropod.

Species or group	Life form	Native or non-native	Black rat (N = 95)	Pacific rat (N = 12)	House mouse (N = 47)
Plants			100	100	76.6
Intact seeds					
Clidemia hirta	Shrub	Non-native	30.5	25.0	6.4
Rubus rosifolius	Shrub	Non-native	7.4	0	0
Paspalum conjugatum	Grass	Non-native	2.1	0	0
Cyrtandra dentata	Shrub	Native	1.1	0	0
Delissea subcordata	Shrub	Native	1.1	0	0
Unknown #1	-	-	1.1	0	0
Unknown #2	-	-	1.1	0	0
Unknown #3	-	-	2.1	0	0
Total intact seeds			42.1	25.0	6.4
Total seed			93.7	91.7	63.8
Fruit fragments					
Clidemia hirta	Shrub	Non-native	33.7	50.0	6.4
Rubus rosifolius	Shrub	Non-native	7.4	8.3	0
Psidium cattleianum	Tree	Non-native	25.3	2.1	0
Total fruit			100	100	40.4
Other plant material			16.8	58.3	34
Arthropods			91.6	100	95.7
Solenopsis papuana	Ant	Non-native	36.8	16.7	10.6
Rhytidoporus indentatus	Burrowing bug	Non-native	16.8	8.3	4.3

Species or group	Life form	Native or non-native	Black rat (N = 95)	Pacific rat (N = 12)	House mouse (N = 47)
Balta spp.	Cockroach	Non-native	6.3	0	0
Platyzosteria sorer	Cockroach	Non-native	1.1	8.3	0
Steatoda grossa	Spider	Non-native	3.2	8.3	0
Mecaphesa sp.	Spider	Native	0	0	1.1
Blackburnia sp.	Beetle	Native	1.1	0	0
Rhyncogonus sp.	Beetle	Native	1.1	0	0
Araecerus fasciculatus	Beetle	Non-native	1.1	0	0
Xylosandrus compactus	Beetle	Non-native	1.1	0	0
Stelidota geminata	Beetle	Non-native	2.1	0	0
Pantomorus cervinus	Beetle	Non-native	0	0	1.1
Banza sp.	Cricket	Native	1.1	0	0
Apis mellifera	Honey bee	Non-native	2.1	0	0
Hemiptera	Aphid	Non-native	1.1	0	0
Phthiraptera	Louse/lice	-	2.1	0	0
Orthoptera	Cricket	-	1.1	0	0
Lepidoptera larvae	Caterpillar	-	33.7	100	83.0
Diptera larvae	Maggot	-	2.1	0	8.5
Araneida	Spider	-	11.6	0	0
Other arthropod material	-	-	9.5	75	23.4

Arthropods, which mostly appeared as fragments rather than intact animals, were found in nearly all (> 90%) of the rodents examined. Only four species of arthropod were found intact in rodent stomachs, and these were *Solenopsis papuana* (Papuan thief ant), *Xylosandrus compactus* (black twig-borer), *Stelidota geminate* (strawberry sap beetle), and Phthiraptera (rat lice) (Table 13). The two arthropod species that were found in some individuals of all three rodents were *S. papuana* and *Rhytidoporus indentatus* (burrowing bug, Hemiptera). Most identifiable arthropods were non-native species; the only native arthropods found in stomachs were *Banza* sp. (bush cricket/katydid, Orthoptera), *Blackburnia* sp. (beetle, Coleoptera), and *Rhyncogonus* sp. (weevil, Coleoptera) in black rats, and *Mecaphesa* sp. (crab spider, Araneae) in mice. Unknown species of caterpillars were found in all 12 Pacific rats, 83% of mouse individuals, and 34% of black rat individuals (Table 13).

There was no evidence indicating a dietary shift in black rats between seasons when few (February 2007-April 2009), and the majority (May-September 2009), of Pacific rats and mice were trapped (P = 0.709 for fruit; P = 0.860 for seed; P = 0.549 for arthropod; Fig. 16).

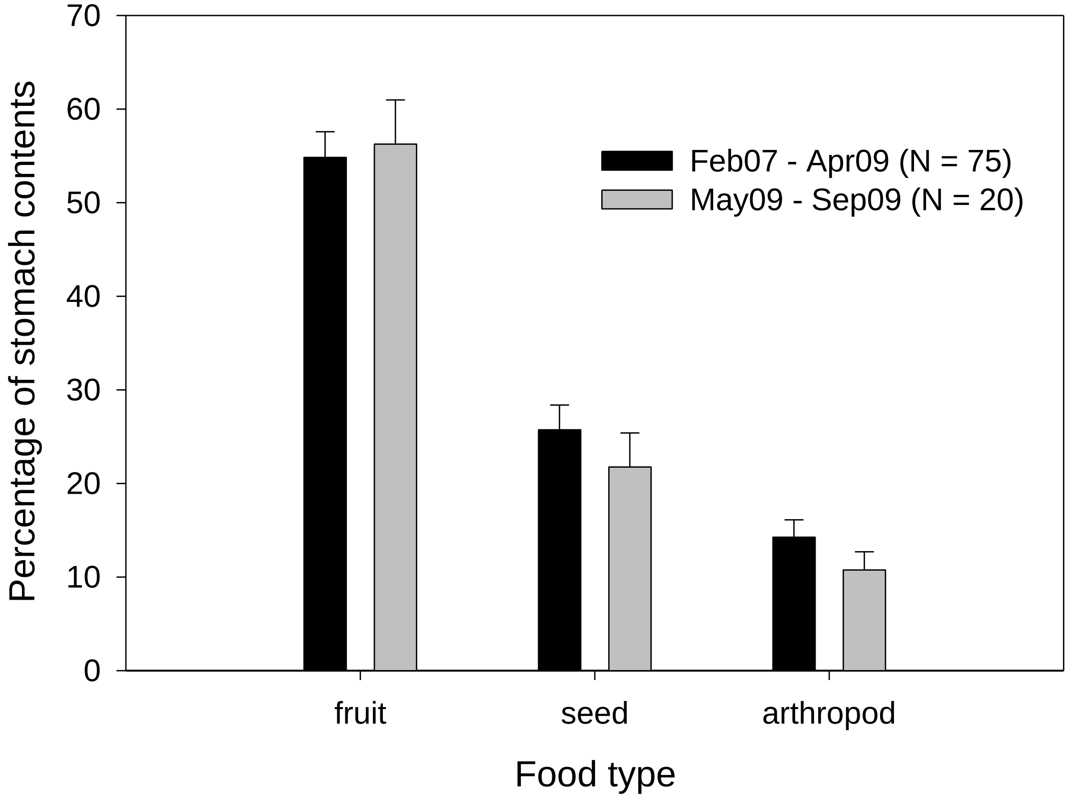

Figure 16. Mean ± SE relative abundances (%) of major food items in stomachs of black rats for the time periods when few (February 2007-April 2009), and the majority (May-September 2009), of Pacific rats and mice were trapped. There were no significant differences ($P > 0.05$) between time periods for any of the major food items.

Stable isotope analysis

Examining long-term diets via stable isotopes shows that black rats have lower $\delta^{15}N$ values than Pacific rats and mice (Fig. 17). Assuming that a ca. 2‰ discrimination value in $\delta^{15}N$ indicates a difference of one trophic level, black rats appear to be feeding at a lower trophic level than Pacific rats and mice. The Pacific rat and mouse have similar $\delta^{15}N$ signatures. Spiders, which are arthropod predators and are not known to consume plants, appear to be feeding at a higher trophic level than all three rodents. While all three rodents consume plants and animals as part of their diets, the $\delta^{15}N$ findings complement the short-term stomach content findings that depict black rats as mainly vegetarian and Pacific rats and mice as slightly more carnivorous.

A difference of ca. 1‰ in $\delta^{13}C$ is typically indicative of a difference between organisms in trophic-level, and the three rodents appear to form a distinct grouping from their potential prey (Fig. 17). Although there is a relatively high amount of variability among Pacific rat and mouse samples for $\delta^{13}C$, these two rodents are nearly equal in $\delta^{13}C$ and appear slightly higher than the $\delta^{13}C$ signature of the black rat (Fig. 17). The herbivorous insects are about 1.5‰ from plants, but surprisingly the spiders are also aligned with the insects for $\delta^{13}C$ (Fig. 17).

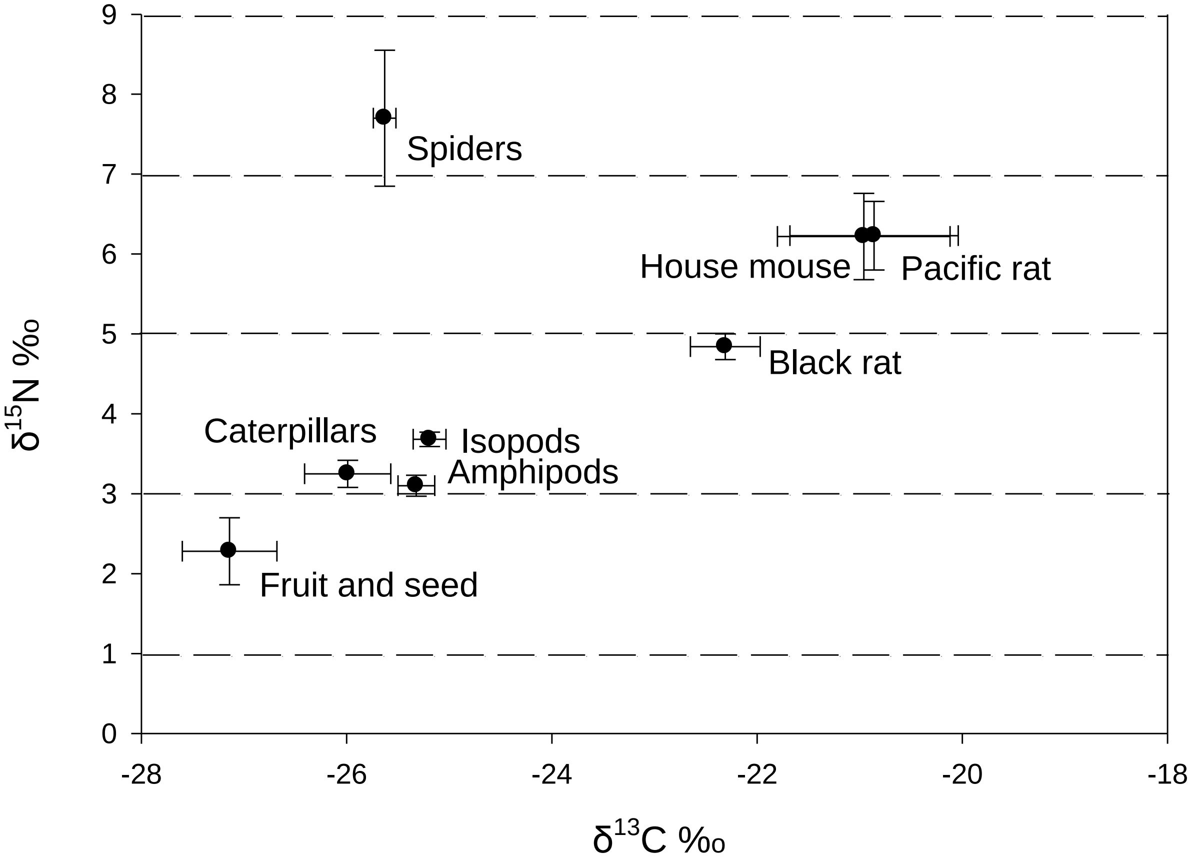

Figure 17. Mean ± SE δ^{15}N and δ^{13}C values for black rats (N = 20), Pacific rats (N = 12), and the house mouse (N = 11), and some of their potential prey items (spiders N = 3; isopods N = 3; amphipods N = 3; caterpillars N = 3; fruits and seeds N = 5), from Kahanahaiki forest, Oahu. Isotopic values were determined from bone collagen for rodents, whole individuals for arthropods (caterpillars, isopod, amphipod) and spiders, and multiple seeds and/or fruit from five common plant species. Dashed lines divide the proposed trophic levels.

Discussion

The findings from this study reveal that black rats, Pacific rats, and house mice each consume a variety of plant and animal prey, and that where these three introduced rodents coexist they appear to partition food resources such that the house mouse is primarily carnivorous and feeds mainly on arthropods, the black rat is primarily vegetarian and feeds mainly on fruit and seed, and the Pacific rat has an intermediate diet that, over its life-time, is more closely related to the house mouse than to the black rat. An understanding of the trophic dynamics involving these introduced rodents, as evidenced by stomach contents and stable isotope analysis, should help identify the types of species and trophic levels that may be vulnerable to rodent predation and deserving of conservation attention.

Habitat and resource partitioning are complementary mechanisms for coexistence of different species. While all three rodents consumed the main types of prey (e.g., arthropods, seed, fruit) on Oahu, the relative abundances and identifiable species of prey were different among rodent species. A similar finding occurred with these same three sympatric rodents in gulches adjacent to sugarcane fields on Hawaii island (Kami 1966). There, insects were a small part of both rat diets, but black rats fed heavily on fruit and grass stalks, Pacific rats ate mainly sugar cane stalks, and mice consumed mainly seeds and insects (Kami 1966). Habitat partitioning has been previously observed for these three rodents when sympatric; in New Zealand the Pacific rat is often restricted to grassland or thick ground cover when other introduced rodents are present (Atkinson and Towns 2005), and in Hawaii, Lindsey et al. (1999) used radio tracking to determine that black rats (N = 9) nested in trees or treeferns whereas Pacific rats (N = 4) nested belowground. In Hungary where diets of three species of cat (*Felis* spp.) were analyzed, small mammals dominated their diets but the species compositions and microhabitats of the consumed prey differed among cat species (Bíro et al. 2005). Additional evidence of partitioning habitats and feeding were demonstrated by Sala and Ballesteros (1997) where fish in the same genus partitioned the near-shore zone, and by Chapman and Rosenberg (1991) where four species of Amazonian woodcreepers partitioned forest habitats and feeding substrates. Therefore, habitat partitioning by coexisting and closely related species can result in consumption of similar types, but often different species and abundances, of prey.

In addition to resource competition, interference competition can be reduced through habitat partitioning. Experimental evidence of habitat partitioning between black rats and Pacific rats was demonstrated by Strecker and Jackson (1962) where several rats of each species were confined in 3 x 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, then 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). Stokes et al. (2009) in Australia, and Harris and MacDonald (2007) in the Galápagos Islands, demonstrated that native rats (*Rattus fuscipes* and *Nesoryzomys swarthi*, respectively) suffered from interference competition rather than resource competition with non-native black rats. There have not been, to my knowledge, competition trials conducted with the house mouse and *Rattus* spp.; however, increased house mouse abundance following black rat reduction has been recorded in the

Galápagos Islands (Harper and Cabrera 2010) and in New Zealand (Ruscoe and Murphy 2005). If aggressive confrontation occurred among the three rodent species at Kahanahaiki, it apparently did not result in much rodent consumption or cannibalism because there were only two rats with rodent flesh in their diets, and this probably originated from their scavenging from the kill-traps as indicated by past studies (Norman 1970; Clark 1980; Sugihara 1997). The presence of rodent hair in the majority of the stomachs of all three rodents may be explained by grooming, which is a common behavior of these rodents (personal observation). The degree to which competition occurs among the three rodents in Hawaiian forest is unknown, yet it is probable that the larger and more abundant black rat is the most dominant of the three rodents (Yom-tov et al. 1999; Russell and Clout 2004; Chapter 2). Past findings of habitat partitioning between *Rattus* spp., and partitioning of potential prey demonstrated in my study, is evidence that these three rodents adjust their habits and realized niches when sympatric.

The species composition and relative abundances of plants and arthropods in rodent-occupied environments directly affects rodent diets. Based on past studies of rodent stomach contents in Hawaii, the habitats dominated by non-native plants and arthropods have mostly non-native prey in stomachs (Beard and Pitt 2006; this study), whereas native-dominated habitats have mostly native prey in stomachs (Cole et al. 2000). Strong seasonal patterns common to temperate environments can also alter resource availability and perhaps the proportion of animal and plant material consumed by rodents. In parts of New Zealand, wetas, which are large, flightless Orthoptera, were the dominant food found in black rat stomachs, probably because they were available throughout the year and are high in protein (Innes 1979; Gales 1982; Miller and Miller

1995). On Green Island, Tasmania, Norman (1970) found that 58% of the 77% plant material in black rat stomachs was monocotyledons that were present all year and encompassed > 70% of the total plant cover. In general, invasive rodents' diets will in part reflect their surrounding environment, and these rodents seem to survive well in areas with native, non-native, or a mixture of both types of these prey.

Fruit was a large part of both rat diets, and the relative abundance of fruit in black rat stomachs was similar in my study (55%) to that in a wet Hawaiian forest (23-53%; Sugihara 1997) and in an arid Hawaiian shrubland (44%; Cole et al. 2000). However, fruit in Pacific rat stomachs in my study (41%) was greater than in other habitats where Pacific rats were also sympatric with black rats (3-16% seasonal averages; Sugihara 1997). On 37 Tokelau islands where the Pacific rat was the only rodent, the stomach contents of Pacific rats consisted of 88% plant material (mostly coconut, *Cocos nucifera*) and 4% arthropod (Mosby et al. 1973). Similarly, the stomach contents of Pacific rats on Kure Atoll, Hawaii, consisted of 62% plant material and 30% arthropods and there were no other rodents present (Wirtz 1972). Fruit fragments of *C. hirta*, *R. rosifolius,* and *P. cattleianum*, which are all problematic invasive species in Hawaii, were found in both rat species trapped in Kahanahaiki forest, and ripe fruit of all three of these species were available at the site during the May-September time period (unpublished data). Fruit of *Rubus* spp. (Sugihara 1997) and *R. rosifolius* and *C. hirta* (Beard and Pitt 2006) were also found in stomach of black rats and Pacific rats in Hawaiian wet forests. Interestingly, fruit of *R. rosifolius* and *P. cattleianum* were not found in any of mouse stomachs at Kahanahaiki despite the availability of these common fruits during the time period when the bulk of mice were trapped. The amount of fruit (11%) in mouse stomachs was much less than in both rat species in my study, but was almost identical to the 10% determined by Cole et al. (2000). Fruit was absent from the 25 mouse stomachs analyzed from gulches adjacent to sugar cane fields on Hawaii island (Kami 1966). From studies within and outside Hawaii, it appears that the house mouse consumes relatively small portions of fruit (especially fleshy fruit) compared to seed, vegetative material, and arthropods (Kami 1966; Cole et al. 2000; Angel et al. 2009; this study). It is unclear why fruits and seeds from other species that are present in Kahanahaiki were not observed in any of these rodent stomachs; however, it may be a result of food preference or simply a reflection of the difficulty with microscopically identifying chewed fragments in rodent stomachs.

Most seeds consumed by rodents appeared highly vulnerable to predation as evidenced by chewed and fragmented seed tissues. However, there were several native and non-native seeds that were intact and would possibly be dispersed by these rodents. Because the black rat is the largest of the three rodents studied and body sizes of vertebrates often positively correlate with the sizes of seeds that pass intact through digestive tracts (Wheelright 1985; Vander Wall 1990), black rats pass intact seeds of a greater size range than the smaller rodents in my study (Williams et al. 2000). Intact seeds of eight plant species, including at least two natives, occurred in black rat stomachs in my study. Two of these, *C. hirta* and *R. rosifolius*, are among the most problematic invasive plants in the Hawaiian Islands, and their small seeds (≤ 1.5 mm length) pass intact through the rat’s digestive tract and germinate (Chapter 5; Shiels, in press). Some individuals of all three rodents had intact *C. hirta* seeds in their stomachs, suggesting that they may be capable of dispersing this and other small-seeded species.

Arthropods comprise a substantial portion of the diet of introduced rodents, as evidenced by > 90% of all stomachs examined in this study containing arthropods. In a recent review by Angel et al. (2009), arthropods were found to be the prey of choice for the house mouse on islands in the Southern Ocean, and this pattern may be supported at Kahanahaiki where arthropods accounted for an average of 57% of their stomach contents. However, in high elevation (2000-3000 m) shrubland in Hawaii, plant material (mainly seeds) was the dominant food type for mice and arthropods comprised 33% of their diet. Relative to mice, arthropods were a much smaller component of black rat stomach contents in my study (14%) and that of Cole et al. (2000) where stomachs contained 16% arthropods. There were no arthropods in black rat stomachs and only trace amounts of caterpillars in Pacific rat stomachs in lowland wet forest in Hawaii (Beard and Pitt 2006). The arthropod composition of Pacific rats in my study was 37% and was therefore intermediate between black rats and mice. There was no report of Pacific rats captured in the study by Cole et al. (2000), but Sugihara (1997) compared invertebrates, which were mostly arthropods but included slugs, snails, and earthworms, and found that stomachs contained 67-96% and 34-45% invertebrates for Pacific rats and black rats, respectively. Despite the presence of native and non-native snails (Meyer and Shiels 2009) and non-native slugs and earthworms (Joe and Daehler 2008) at Kahanahaiki, there was no evidence of any of these organisms in rodent stomachs.

Several of the same taxonomic groups of arthropods that were consumed by rodents in my study are similar to those found in black rat and mouse stomachs by Cole et al. (2000) from higher elevations in Hawaii, including bugs, spiders, and ants. The non-native ant *Solenosis papuana* is ca. 1 mm in length and was present in at least 10%

of individuals of each rodent species, but it is unlikely, due to its small size, that these ants were consumed intentionally. Although crickets and beetles are common components of both black rats and mice in New Zealand (Innes 2005b; Ruscoe and Murphy 2005), as well as in the study by Cole et al. (2000), they were only found in black rats in my study. Two groups that were found in my study but not that of Cole et al. (2000) were cockroaches (Blattaria) and lice (Phthiraptera). Cole et al. (2000) found that the majority of the arthropods in rodent stomachs were native; however, ca. one-third of the identifiable arthropod groups or species in black rats were native in my study, and only one native species (*Macaphesa* sp.) was found in the house mouse. Caterpillars (larvae of Lepidoptera) appear to be a vulnerable food item to all three rodents studied in Hawaii because some individuals of all species studied had caterpillars in their stomachs in high elevation environments (Sugihara 1997; Cole et al. 2000), and 100%, 83%, and 34% of individuals of Pacific rats, mice, and black rats, respectively, had caterpillars in their stomachs in Kahanahaiki. The proportion of stomach contents that contained caterpillar was greatest in mice (54% in my study; 22% in that of Cole et al. 2000) and least in black rats (3% in my study; 4% in Cole et al. 2000). In New Zealand, caterpillars are generally the most common arthropod eaten by mice (Badan 1986; Ruscoe and Murphy 2005), and one of the most common groups eaten by Pacific rats (Bunn and Craig 1989; Atkinson and Towns 2005).

Although the stomach contents revealed that Pacific rats had an intermediate (short-term) diet between those of black rats and mice, the greater amount of caterpillar and unknown arthropod material that was consumed by Pacific rats and mice relative to black rats may partially account for the slightly higher δ^{15}N and δ^{13}C for the two smaller rodents compared to black rats. Additionally, Pacific rats may be more similar to mice than to black rats in lifetime average diet because of differences in foraging microsites when the black rat is present (Lindsey et al. 1999; Stapp 2002; Atkinson and Towns 2005; Chapter 2) or assimilation rates of different prey types (Gannes et al. 1997).

Rather than using isotopes to assign trophic levels to introduced rodents that are sympatric in forests, most past isotope studies involving introduced rodents examined effects on seabirds and the proportion of the rodent diet attributable to marine and terrestrial feeding (Strapp 2002; Caut et al. 2008a; Quillfeldt et al. 2008). Isotopic analysis shows that the black rat is a substantial predator of seabirds on some islands (e.g., Strapp 2002; Caut et al. 2008a) but not others (Cassaing et al. 2007). Evidence of bird consumption by rodents was absent at Kahanahaiki despite an abundance of introduced passerines and game birds at the study site (personal observation). Marine inputs to rodent diets are unlikely at Kahanahaiki because the site is > 3 km from the ocean and home-ranges are typically < 4 ha for each rodent (Chapter 2). Therefore, $\delta^{13}C$ differences in my study are more likely to involve unequal consumption of C_3 and C_4 plants (Gannes et al. 1997), which may help explain the slightly higher $\delta^{13}C$ values for Pacific rats and mice relative to black rats. In an interior forest habitat on Stewart Island, New Zealand, Harper (2006) determined $\delta^{15}N$ and $\delta^{13}C$ values and found that the diets of Pacific rats and black rats were similar. The only isotopic study available with wild house mice was by Quillfeldt et al. (2008) in the Falkland Islands where $\delta^{13}C$ were similar to those in my study (-21‰ and -24‰); yet the $\delta^{15}N$ for mice ranged from 12-31‰ and were indistinguishable from potential prey, including terrestrial plants ($\delta^{15}N$ 8-35‰), terrestrial invertebrates ($\delta^{15}N$ 14‰), and upland birds ($\delta^{15}N$ 16-19‰) (Quillfeldt et al. 2008). Therefore, using isotopes to study diets and differentiate trophic feeding among predators may not always give a clear depiction of predator-prey interactions without supplemental dietary analysis such as stomach contents (Strapp 2002; Caut et al. 2008a; Quillfeldt et al. 2008; Flaherty and Ben-Davis 2010; this study).

The three rodents in this study appear to occupy two different trophic levels and their dietary patterns provide evidence of niche differentiation resulting from unequal consumption of types and quantities of prey. When these three rodents coexist in Hawaiian forest, the larger-bodied black rat appears to dominate fruit and seed consumption. The house mouse, which eats some seed and even less fruit, feeds primarily on caterpillars. The Pacific rat, which has been in Hawaii for ca. 1000 years but may be outcompeted by black rats because it is sparsely abundant in contemporary Hawaii (Chapter 2), has an intermediate diet between the other two rodent species and its $\delta^{15}N$ and $\delta^{13}C$ signatures suggest that this small rat has a lifetime diet more like the house mouse than the black rat. The relative effects of each of the rodent species on their prey cannot be determined without further understanding of prey abundances in the presence and absence of each rodent predator (e.g., using removal experiments). Conservationists working in island habitats containing these three introduced rodents should not overlook the range of arthropods that may be at risk to rodent predation, and that all three rodents typically chew, and probably destroy, most consumed seeds > 2 mm in length. The degree to which prey species and trophic levels are exploited by each introduced rodent in Hawaii and elsewhere may depend upon the assortment of rodent species that are present at a given site.

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CHAPTER FOUR:

ARE INTRODUCED RATS (*RATTUS RATTUS*) BOTH SEED PREDATORS AND DISPERSERS IN HAWAII?

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Abstract

Invasive rodents are among the most ubiquitous and problematic species introduced to islands; more than 80% of the world's island groups have been invaded. Introduced rats (black rat, *Rattus rattus*; Norway rat, *R. norvegicus*; Pacific rat, *R. exulans*) are well known as seed predators but are often overlooked as potential seed dispersers despite their common habit of transporting fruits and seeds prior to consumption. The relative likelihood of seed predation and dispersal by the black rat, which is the most common rat in Hawaiian forest, was tested with field and laboratory experiments. In the field, fruits of eight native and four non-native common woody plant species were arranged individually on the forest floor in four treatments that excluded vertebrates of different sizes. Eleven species had a portion (3% to 100%) of their fruits removed from vertebrate-accessible treatments, and automated cameras photographed only black rats removing fruit. In the laboratory, black rats were offered fruits of all 12 species to assess consumption and seed fate. Seeds of two species (non-native *Clidemia hirta* and native *Kadua affinis*) passed intact through the digestive tracts of rats. Most of the remaining larger-seeded species had their seeds chewed and destroyed, but for several of these, some partly damaged or undamaged seeds survived rat exposure. The combined field and laboratory findings indicate that many interactions between black rats and seeds of native and non-native plants may result in dispersal. Rats are likely to be affecting plant communities through both seed predation and dispersal.

Introduction

Three rat species (black rat or ship rat, *Rattus rattus*; Norway rat, *R. norvegicus*; Pacific rat, *R. exulans*) and the house mouse (*Mus musculus*) are perhaps the most widespread and problematic invasive mammals affecting islands (Lowe et al. 2000; Drake and Hunt 2009; Traveset et al. 2009). Through mostly unintentional introductions by humans, these rodents occupy > 80% of the major islands worldwide (Atkinson 1985; Towns 2009). As a consequence of their omnivorous diet and large incisor teeth, introduced rats (*Rattus* spp.) are probably the invasive animals responsible for the greatest number of plant and animal extinctions on islands (Towns et al. 2006). *Rattus* spp. can affect plant communities directly by destroying or dispersing seeds; however, on islands these rats are viewed mainly as seed predators (Campbell and Atkinson 2002; Towns et al. 2006; Meyer and Butaud 2009; Traveset et al. 2009; Towns 2009).

In continental environments where native rodents have evolved with the local native flora, seed dispersal by rodents commonly occurs when they transport intact seeds but then fail to eat them (Forget 1993; Hulme 1997) or they partially consume transported seeds without ingesting whole seeds or damaging their embryos (Steele et al. 1993; Dalling et al. 1997; Koptur 1998; Vallejo-Marín et al. 2006; Mendoza and Dirzo 2009). Seed dispersal can also occur by endozoochory, when rodents consume seeds that are small enough to pass intact through their digestive tracts (Williams et al. 2000; Bourgeois et al. 2005). A key feature for characterizing animals as seed predators versus seed dispersers is based on their seed hoarding (storing) behavior, and rodents that hoard seeds are generally viewed as seed dispersers (Vander Wall 1990). Introduced rats are not known to hoard seeds, which supports prior views that these rats are generally seed predators (Towns et al. 2006; Meyer and Butaud 2009). However, introduced rats do transport food to nearby sheltered areas (e.g., husking stations) for consumption, which allows for the possibility of dispersal of seeds that were not destroyed following collection (Campbell et al. 1984; McConkey et al. 2003; Abe 2007).

The Hawaiian Islands, like many others, lost the majority of their avifauna following human colonization (Steadman 1995) and many of those birds were frugivores and seed dispersers (James and Olson 1991; Olson and James 1991). It is unknown if introduced rats disperse seeds of Hawaiian plants and whether, by doing so, they have replaced some of the functions of the extinct native seed dispersers. The first rats (Pacific rats) in the Hawaiian Islands were introduced by the first human colonists approximately 1000 years ago, and for the next ca. 800 years Pacific rats were the only rats to consume native biota (Athens et al. 2002). Following European arrival in the late 1700's, three additional rodents were introduced, including the black rat, the Norway rat, and the house mouse (Tomich 1986). In contemporary Hawaii, all four rodents may coexist in a given habitat, though Norway rats rarely occur in forests. The black rat appears to be the most common rat in forests and it is distributed from sea level to nearly 3000 m (Amarasekare 1994; Lindsey et al. 1999; Meyer and Shiels 2009; Chapter 2). Black rats and Pacific rats are significant predators of numerous native species in Hawaii, including rare and endangered birds (VanderWerf 2001), snails (Hadfield et al. 1993), arthropods (Cole et al. 2000) and plants (Athens et al. 2002; Pérez et al. 2008).

Determining seed fate is a critical component of understanding how rats affect plants. Because assessing seed fate is very challenging (see Forget et al. 2005 and citations therein), most quantitative studies of the effects of introduced rats on seeds are limited to seed removal trials (Moles and Drake 1999; Grant-Hoffman et al. 2010; Chimera and Drake, in revision), or examination of gut contents (Clark 1981; Sugihara 1997; Sweetapple and Nugent 2007; Chapter 3), droppings (Medeiros 2004; Bourgeois et al. 2005), or husking stations (Campbell et al. 1984; McConkey et al. 2003). In New Zealand, Williams et al. (2000) determined seed fates by conducting laboratory feeding trials with *Rattus* spp. and performing germination trials with seeds that had passed through rat digestive tracts. Combining fruit/seed removal trials in the field with captive feeding trials can help overcome challenges of assessing seed fate and rat impacts on plants (Mendoza and Dirzo 2007). The following questions are addressed in this study in order to investigate how the black rat, which is probably the most significant vertebrate seed predator in Hawaii, may be altering plant community composition through effects on native and non-native plants: 1) Which of the dominant species in a Hawaiian mesic forest have their fruits removed from the forest floor by rats? 2) To what degree do rats damage seeds of these species? 3) Are any of these species' seeds dispersed by rats?

Methods

Field Site

This research occurred at Kahanahaiki Management Unit (21^{o} 32′ N, 158^{o} 11′ W), a 36 ha segment of mesic forest in highly dissected terrain (500-660 m a.s.l; Gagné and Cuddihy 1999) in the northern Waianae Mountains, on the island of Oahu, Hawaii. Kahanahaiki is managed for native species preservation by the U.S. Army, and the forest was fenced in 1996 to exclude feral goats and pigs. Daily air temperature at the site ranges from 16-24^{o}C (unpublished data) and monthly rainfall varies from 50 mm to 170 mm (cited in Joe and Daehler 2008). A recent plant inventory at the site documented at least 35 tree species (Appendix A). I studied 12 of the most common woody plants, including eight native and four non-native species (trees, shrubs, and lianas; Table 14). Botanical nomenclature follows Wagner et al. (1999) with recent updates for two species (Middleton 2002; Terrell et al. 2005). The five most common trees at the study site include the non-native *Psidium cattleianum* and *Schinus terebinthifolius*, and the native *Diospyros hillebrandii*, *Psydrax odorata*, and *Sapindus oahuensis* (Table 14). The two most common shrub species are the non-native *Clidemia hirta* and the native *Alyxia stellata* (Table 14). Plant species are hereafter referred to by genus.

Two species of rats, the black rat (133 ± 3 g; mean ± SE; N = 92 adults) and Pacific rat (47 ± 2 g; N = 6 adults), are present at Kahanahaiki (Meyer and Shiels 2009; Chapter 2). My average estimated relative abundance measures using bi-monthly mark-and-recapture sampling over 15 months during 2007-2008 were 17 rats/100 trap nights for black rats and 1 rat/100 trap nights for Pacific rats. No Norway rats were captured at the study site and the house mouse (10 ± 1 g; N = 26) was captured at ca. 6 mice/100 trap nights.

Field Trials

Each of the 12 most abundant woody species at Kahanahaiki (Table 14) were tested for their vulnerability to rats by placing fruits in one of four exclosure treatments on the forest floor: 1) no-vertebrate-access, which consisted of a wire metal mesh (1.2 cm aperture) open-bottom cage (30 x 30 x 30 cm; length x width x height) that excluded all potential vertebrate seed predators and dispersers (e.g., rodents, cats, birds, mongoose

Table 14. Characteristics of the 12 fleshy-fruited woody plants (values expressed as mean (SE)) used in field trials and captive feeding trials.

Species[a]	Family	Life form	Fruit length (mm)[b]	Fruit mass (mg)	Number of seeds per Fruit	Seed mass (mg)	Seed length (mm)
Native							
Alyxia stellata	Apocynaceae	Shrub, liana	14.9 (0.4)	983 (38)	1.0 (0.0)	459 (36)	12.9 (0.6)
Coprosma foliosa	Rubiaceae	Shrub	9.3 (0.3)	352 (24)	2.0 (0.0)	42 (3)	6.2 (0.1)
Diospyros hillebrandii	Ebenaceae	Tree	21.3 (0.4)	2567 (188)	2.7 (0.2)	715 (43)	17.7 (0.7)
Kadua affinis	Rubiaceae	Tree	7.1 (0.3)	164 (25)	9.8 (0.7)	0.7 (0.1)	1.2 (0.1)
Nestegis sandwicensis	Oleaceae	Tree	16.1 (0.4)	1361 (39)	1.0 (0.0)	604 (33)	15.7 (0.4)
Pouteria sandwicensis	Sapotaceae	Tree	34.2 (0.9)	16050 (1910)	2.6 (0.5)	1787 (955)	17.9 (0.4)
Psydrax odorata	Rubiaceae	Tree	8.3 (0.5)	255 (32)	2.0 (0.0)	93 (20)	6.6 (0.7)
Sapindus oahuensis	Sapindaceae	Tree	29.0 (1.0)	5420 (440)	1.0 (0.0)	1509 (90)	18.0 (0.4)
Non-native							
Aleurites moluccana	Euphorbiaceae	Tree	46.7 (1.9)	46855 (2371)	1.4 (0.1)	8995 (542)	30.3 (0.5)
Clidemia hirta	Melastomataceae	Shrub	6.9 (0.3)	214 (21)	360 (57)	< 0.1	0.5 (0.0)
Psidium cattleianum	Myrtaceae	Tree	31.3 (0.9)	7516 (562)	6.9 (0.8)	51 (4)	5.2 (1.6)
Schinus terebinthifolius	Anacardiaceae	Tree	4.7 (0.2)	33 (5)	1.0 (0.0)	5.9 (0.0)	3.6 (0.1)

[a] The yellow-fruited form of *Psidium cattleianum* was used for all measurements and field and laboratory trials

[b] For fruit and seed measures, N = 8-15 fruits for each species were collected from 3-12 individuals. Lengths of fruit and seed are the longest axial lengths. Mass of fruit and seed are reported on a fresh-mass basis

(*Herpestes javanicus*)) and acted as the control to compare subsequent treatments, 2) small-vertebrate-access, which had the same dimensions as the no-vertebrate-access but had an 8 x 8 cm opening on each side that allowed small vertebrates such as rodents to access the interior but excluded larger vertebrates (e.g., cats, most birds), 3) open ground, where all vertebrates were able to freely access the station, and 4) open-cage-control, which had three sides of mesh and allowed all vertebrates access; this tested the influence of the caging material on fruit removal. Invertebrates were able to access all treatments. Three transects, each 310 m long and at least 30 m distant from the nearest adjacent transect, were established. Along each transect, eight replicates of each of the four treatments were positioned at 10 m intervals. Treatments were assigned randomly with the condition that no more than two of the same treatment could occupy consecutive stations. Each mesh exclosure was pushed into the ground ca. 1 cm and held in place using 8-cm-long turf staples. Each plant species was tested individually, in a single trial run, along one of the three transects, such that each species occupied 32 treatment stations (4 treatments x 8 replicates). To reduce bias from the influence of previous trials within a transect, each fruit trial was separated by at least 1 month since the previous trial ended. Placing fruits systematically along transects was favored over placement solely beneath adult conspecifics because the limited and clumped distribution of adult plants of some species would likely have restricted trials to areas within a single rat's home-range (Chapter 2).

To determine the animal responsible for fruit removal, motion-sensing cameras (Bushnell Sentry 2.1 MB or Multrie model L DSG-200 trail cameras) were placed at a random subset of the vertebrate-accessible treatment stations (i.e., small-vertebrate-access, open ground, and open-cage-control). Typically, two cameras were used for each species (mean ± SE: 2.0 ± 0.4) for the duration of each trial, except for three species (*Clidemia*, *Kadua*, *Schinus*) tested when cameras were unavailable.

Ripe fruits for each of the 12 species were collected from 3-12 individuals or from the ground below conspecific individuals if they had fallen within 24 hours. Large fruits (> 10 mm along longest axis; seven species; Table 14) were placed within each treatment singly, while small fruits (< 10 mm along longest axis; five species; Table 14) were placed as a cluster of up to three. Trials were held from July 2007 to January 2009 and scheduled to coincide with the fruiting season of each species. For each trial, fruits were checked for their presence at each station 24 hours after beginning the trial, and then subsequently every 1-7 days. The duration of each trial was species-specific (range = 6-43 days; Table 15) and was limited by natural decomposition (rotting and mold) of the pericarp (Hoch and Adler 1997). For each species the percentage of fruit remaining in each treatment was compared using a Kruskal-Wallis test (SPSS 1998) where significance was based on $P < 0.05$. When significant differences among treatments were present for a given species, a second Kruskal-Wallis test identified significant differences among the three vertebrate-accessible treatments.

Captive Feeding Trials

Adult black rats were captured from wild populations in the Waianae Mountains, Oahu, including forest adjacent to Kahanahaiki, and taken to laboratory facilities at the University of Hawaii in Honolulu. Each rat was held in an individual 38 cm x 22 cm x 18 cm metal-mesh (8 mm) cage. Rats were allowed to acclimate for at least one week before beginning feeding trials, during which time the rats were fed a diet of mixed seeds (e.g., corn, sunflower, wheat, barley, oats, sorghum) and occasionally wedges of fruit (tangerine). Rats were checked daily to ensure there was ample food and fresh water, and to clean urine/fecal trays. Approximately every four months from August 2007 through January 2009, a new set of rats (7-12 individuals; mean ± SE: 9.7 ± 0.6, in roughly equal proportions of females and males) was captured from the Waianae Mountains to replace the previous set of rats. A total of 51 rats were used during this study.

Captive feeding trials used the same 12 plant species as those used in the field. For each feeding trial, fruits of a single species, collected fresh from Kahanahaiki, were placed in each cage with a rat for 24 hours. The number of fruits offered to each rat matched the quantity used (N = 1-3) for each treatment in the field. Water was always available in each cage. After 24 hours of exposure to each rat, fruits were visually inspected to estimate the proportion of pericarp (fruit material) mass and seed mass remaining. When multiple fruits or seeds were offered to a rat, the proportion of mass remaining was determined by averaging visual estimates of each fruit's or seed's unconsumed mass. For seven of the 12 species, trials were continued an additional 24 hour period and inspected, but there was no significant difference ($P > 0.05$ for each; Mann-Whitney U tests) in pericarp or seed mass remaining from 24 to 48 hours, so all data presented for each of the 12 species are for the initial 24 hours of rat exposure. Additionally, for all but the two smallest species (*Clidemia* and *Kadua*), the proportion of surviving seeds was determined by inspecting all remaining seeds and seed parts for intact embryos. A seed was considered destroyed if the embryo was not intact or > 50% of the seed was eaten (Pérez et al. 2008; Shiels, in press). For *Clidemia* and *Kadua*, it was necessary to inspect rat droppings microscopically and extract seeds that had passed through the digestive tracts of rats. To test for viability of such seeds, they were sown on agar, and their germination was compared to conspecific, unconsumed seeds sown on agar. The proportion of seeds surviving rat exposure was determined from the ratio of surviving seeds to the average number of seeds per fruit for each species (see Table 14). Rats were returned to their regular diet for at least 48 hours between feeding trials.

Results

Field Trials

The percentage of fruit remaining after exposure to animals in the field varied by plant species, and ranged from 0% to 100% (Table 15). Seven of the 12 species had significantly fewer fruits in the three treatments that allowed access to vertebrates (i.e., small-vertebrate-access, open ground, and open-cage-control) relative to the no-vertebrate-access treatments, and there were no significant differences ($P > 0.05$) among the three vertebrate accessible treatments for each of these seven species (Table 15). Both *Nestegis* and *Kadua* had 50-60% of their fruit remaining in the open ground treatment, but substantial variation among vertebrate accessible treatments resulted in a lack of significant differences when all four treatments were compared ($P > 0.05$ for each; Table 15). The largest fruit and seed tested, *Aleurites*, had no fruit removed from any treatment station. Two additional species that appeared relatively unattractive to animals and did not differ significantly among treatments were the common non-native tree *Schinus*, which had 97% of its fruit remaining, and the large-seeded native tree *Sapindus*, which had 83% of its fruit remaining (Table 15).

Table 15. Mean (SE) percentage of fruits remaining at the end of each trial for exclosure treatments at Kahanahaiki forest, northwest Oahu, Hawaii.

Species	Trial days[a]	NVA (%)[b]	SVA (%)	OPA (%)	OCC (%)	P-value[c]	Rat photo-graphed?[d]
Native							
Alyxia	36	100 (0)	37.5 (18.3)	12.5 (12.5)	37.5 (18.3)	0.005	Yes
Coprosma	10	100 (0)	62.5 (15.7)	43.8 (18.9)	37.5 (15.7)	0.014	Yes
Diospyros	36	100 (0)	37.5 (18.2)	50.0 (18.9)	56.3 (17.5)	0.044	Yes
Kadua	10	100 (0)	83.5 (8.8)	58.3 (17.5)	79.3 (14.0)	0.144	Not tested
Nestegis	37	100 (0)	62.5 (18.3)	50.0 (18.9)	87.5 (12.5)	0.091	Yes
Pouteria	43	62.5 (18.3)	12.5 (12.5)	12.5 (12.5)	0.0 (0.0)	0.015	Yes
Psydrax	27	100 (0)	25.0 (13.4)	56.3 (17.5)	31.3 (13.2)	0.003	No
Sapindus	34	100 (0)	100 (0)	87.5 (12.5)	62.5 (18.3)	0.084	Yes
Non-native							
Aleurites	25	100 (0)	100 (0)	100 (0)	100 (0)	1.000	No
Clidemia	12	100 (0)	25.0 (16.3)	50.0 (18.9)	12.5 (12.5)	0.003	Not tested
Psidium	6	100 (0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	< 0.001	Yes
Schinus	37	100 (0)	91.6 (8.4)	100 (0)	100 (0)	0.392	Not tested

[a] The duration of each field trial was limited to an interval where fruit decomposition was minimal

[b] Treatments included: NVA = no-vertebrate-access, SVA = small-vertebrate-access, OPA = open ground, access for all animals, OCC = open-cage-control. N = 8 for each treatment

[c] Significant differences ($P < 0.05$) among treatments for each species are based on chi-square values from Kruskal-Wallis tests

[d] The final column indicates whether a rat was photographed by motion-sensing cameras at a treatment station concurrently with fruit removal at any point during its field trial. Three species were not monitored by cameras

The dominant non-native tree in the forest, *Psidium*, appeared to be the most attractive species as evidenced by removal of 100% of its fruit within 6 days in the vertebrate accessible treatments (Table 15; Fig. 18). Two native species were highly attractive to vertebrates (12.5% fruit remaining in open ground treatment): *Alyxia* and *Pouteria* (Fig. 18). *Pouteria* fruits were removed from three of the eight no-vertebrate-access treatments; in each case a rodent-sized tunnel had been dug under the cage wall. This was the only species that had any of the no- vertebrate-access treatment replicates compromised (Table 15). Six out of 12 species had ≤ 50% of their fruit remaining in open ground treatments, including: *Alyxia*, *Clidemia*, *Coprosma*, *Diospyros*, *Nestegis*, *Pouteria*, and *Psidium* (Table 15; Fig. 18). Besides *Psydrax*, which declined steadily to 56% remaining by the end of the 27 day trial, the majority of fruit removal for all species in open ground treatments occurred during the first 10-12 days of each trial (Fig. 18).

The motion-sensing cameras photographed black rats during intervals when fruits were removed for seven of nine species (Table 15). A total of 17 photographs of rats were associated with fruit removal (an average 1.9 ± 0.6 rat photographs for each of the nine species). Rarely were animals other than the black rat captured in photographs at the treatment stations, and the few times that they were (including a cat, a mongoose, and three bird species) the fruits at the treatment station where the camera was triggered were not removed. This gives me confidence that most fruit removal was attributable to black rats.

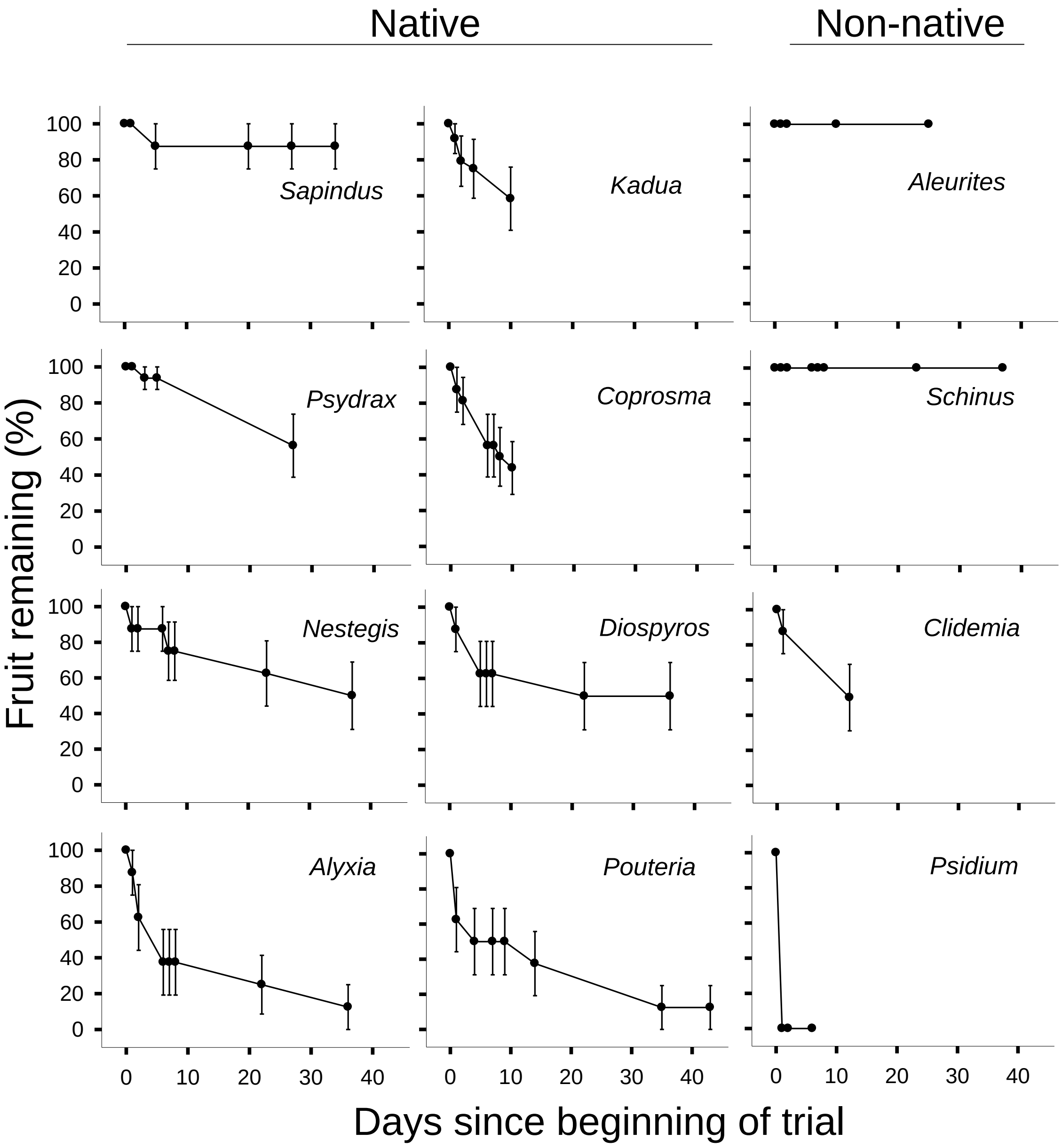

Figure 18. Mean (SE) percentage of fruit remaining at each sampling period for each species in open ground treatment (N = 8 stations per species, except *Psidium* had N = 6) at Kahanahaiki forest, northwest Oahu, Hawaii, where the duration (days) of each trial was restricted to an interval where fruit decomposition was minimal (see Table 15 for trial duration for each species). Species ordering is based roughly on the amount of fruit remaining at the end of the trials.

Captive feeding trials

After determining the degree of fruit removal by rats in the forest, the possible post-removal seed fates of these species were assessed through captive feeding trials. For each of the 12 woody species, rats ate both the pericarp and the seeds, but the amount eaten (Fig. 19) and the number of seeds destroyed (Fig. 20) varied by species. As in the field, *Aleurites*, the species with the largest seeds, appeared to be the least attractive of the 12 species offered; 77% of the pericarp and 99% of the seed mass remained after 24 hours. Also matching the field trials, the large-seeded native, *Sapindus*, and the non-native, *Schinus*, seemed relatively unattractive to captive rats, because an average of 83% and 93%, respectively, of both species' pericarp and seed mass remained after rat exposure. *Pouteria* experienced among the highest fruit removal by rats in the field and captive rats ate all but 36% of the pericarp but they left 86% of the seed mass uneaten (Fig. 19).

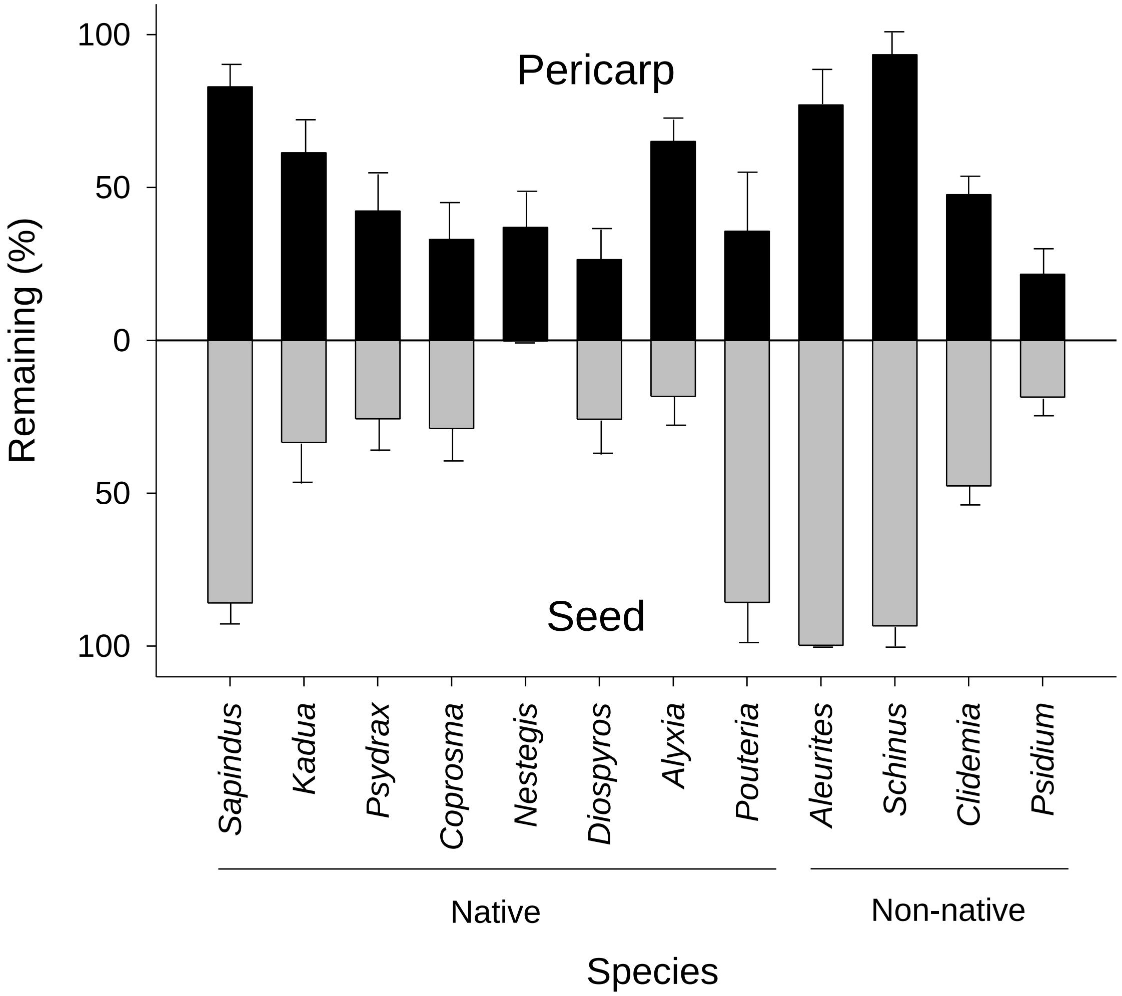

Figure 19. Mean (SE) estimated percentage of pericarp (fruit tissue) mass and seed mass remaining when fruits were offered to black rats in captivity (N = 7-12 rats) for 24 hours.

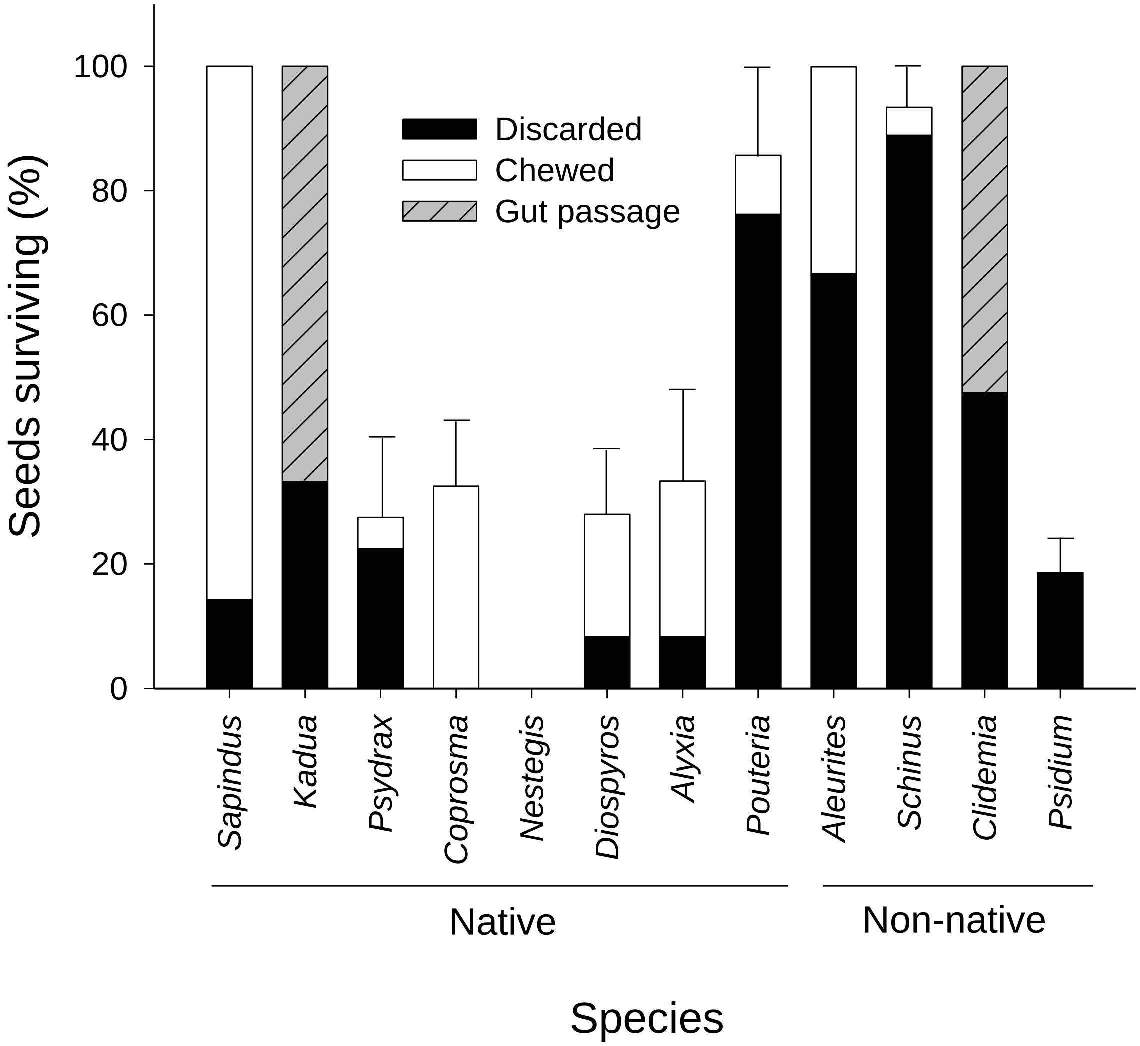

Figure 20. Mean (SE) percentage of seeds surviving 24 hour exposure to captive black rats (N = 7-12 rats) where the total number of seeds per fruit for each species was based on mean values described in Table 14. The three categories of seed survival include: discarded (not chewed or ingested), chewed, and gut passage. Error bars reflect total survival (all three categories combined).

Eight out of the 12 species had < 50% seed mass remaining after 24 hours. The most attractive species to captive rats was *Nestegis*, for which the majority of the seed masses were consumed by most (11 of 12) of the rats and only a few pieces of chewed seed remained in a single cage (Fig. 19). Most of the pericarp of *Nestegis* was also eaten, but the outermost part of the pericarp (the exocarp) was left uneaten in most cages. In addition to the particularly vulnerable seeds of *Nestegis*, both *Alyxia* and *Psidium* each had an average of < 20% seed mass remaining (Fig. 19).

Seed survival varied widely, but appeared to group into two levels: high survival (mean ≥ 85%; six species) and low survival (0-35%; six species) (Fig. 20). Several species, including *Aleurites*, *Clidemia*, *Kadua* and *Sapindus*, had no seeds destroyed by rats. The three categories of seed survival following rat interaction include: discarded (not chewed or ingested), chewed (but only partially damaged), and gut passage. For both of the very small-seeded species (*Clidemia* and *Kadua*), rats consumed the fruits partially or fully and seeds survived passage through the rat's teeth and digestive system as evidenced by only intact seeds and no seed fragments detected in droppings, and seed germination percentages equal to those of seeds not consumed by rats. While *Aleurites*, *Sapindus*, and *Schinus* had high seed survival resulting from unattractiveness of their fruit (pericarp + seed; Fig. 19), *Pouteria* had high seed survival because its seeds were less attractive than its pericarp (Fig. 19, 20). Of the five species with low seed survival (< 35%), *Psidium* had just 18% survival (Fig. 20), which amounts to an average of ca. one surviving seed per fruit.

Discussion

My findings are consistent with the widely held view that introduced rats are seed predators (Campbell and Atkinson 2002; Towns et al. 2006; Howald et al. 2007; Athens 2009; Towns 2009; Traveset et al. 2009), but I also demonstrate another facet of rat-plant interactions: fruit removal by black rats can sometimes result in seed dispersal. Rats in the forest removed fruits of 11 species, and for six of those, ≥ 50% of the fruits were removed before the pericarp decomposed. Seed predation was relatively high (< 35% survival) for five of the eight native species and one of the four non-natives (*Psidium*). The six species that had > 85% seed survival had a wide range of seed sizes, including the smallest and largest seeds. Rats disperse the smallest seeds (*Clidemia* and *Kadua*) by gut passage. They can also disperse relatively large seeds if the pericarp is the only food item of interest (e.g., *Pouteria*), or if some seeds that are normally eaten are discarded or only partially consumed during feeding, as observed for at least half of the species tested. Because rats disperse and destroy seeds of common native and non-native plant species, there is potential for them to have altered forest composition and structure in the Waianae Mountains, and elsewhere, since their colonization (ca. 200 years in Hawaii), and these potential alterations are likely to continue in ecosystems where rats are present.

Fruits of native and non-native species were removed by rats in Hawaiian mesic forest, and all but one native species (*Sapindus*) had ≥ 44% fruit removal. In New Zealand, introduced rodents (probably *Rattus* spp.) removed much lower proportions of 11 native seeds (4-24% removal; Moles and Drake 1999) than in my study. For example, removal of *Coprosma* by black rats in my 10 day trial was at least double that for local species of *Coprosma* that were removed by rodents in New Zealand (*C. grandifolia* after 15 days, Moles and Drake 1999; *C. macrocarpa* after 5 days, Grant-Hoffman et al. 2010). Similarly, whereas Hawaiian *Nestegis* had approximately two-thirds of its fruits remaining after 15 days (or half after 37 days) following exposure to vertebrates, Moles and Drake (1999) found that the New Zealand *Nestegis* (*N. cunninghamii*) had 95% of its seeds remaining after 15 days. Many factors can affect fruit and seed removal by rodents, including rodent densities, food availability, and various characteristics of the fruits and seeds (e.g., size, defenses). In my study, removal of non-native fruits ranged from no removal (*Aleurites*) to 100% within 6 days for *Psidium*, which is one of the most problematic invasive plants in Hawaii (Medeiros 2004; Uowolo and Denslow 2008).

Many factors contribute to the attractiveness and subsequent removal of fruits and seeds (see review by Janzen 1971), and seed removal in field trials is an important first step in determining seed fate (Forget et al. 2005). Larger seeds are often preferentially selected by rodents over smaller seeds (Abramsky 1983; Hulme 1998), perhaps owing to the greater nutritional reserve and the relative ease with which larger seeds are located (Mack 1998). However, the three largest seeds in my study (*Aleurites*, *Pouteria*, *Sapindus*; 17.9-30.3 mm longest axial length) were among the most unattractive to black rats. Intermediate-sized seeds (5.2-17.7 mm) suffered from a high level of predation by rats, whereas the smallest seeds (0.5-1.2 mm) were ingested but not destroyed. In wet forests in both Indonesia (Blate et al. 1998) and Mexico (Mendoza and Dirzo 2007), smaller-seeded species were more attractive and more heavily depredated by rodents than were larger-seeded species. Palm fruit of *Lepidorrhachis mooreana* had high fruit removal by black rats on Lord Howe Island, but a sympatric palm (*Hedyscepe canterburyana*) that has fruits 18 times larger suffered little removal by black rats (Auld et al. 2010). Additionally, relatively small seeds were the most commonly reported seed size consumed by introduced rats when a suite of New Zealand studies were reviewed (Grant-Hoffman and Barboza 2010). The physical and chemical defenses in seeds and fruits complicate generalizations of seed-size preference to mammals (Steele et al. 1993; Mendoza and Dirzo 2009). The possible chemical defenses in *Aleurites*, *Sapindus* and

Schinus (Wagner et al. 1999) and the physical defenses of a hard and thick seed coat in *Aleurites* (Wagner et al. 1999) may have influenced the very low attraction and predation of these common species. In contrast, *Nestegis* and *Psidium* suffered the highest predation levels in the captive feeding trials, suggesting limited defenses against black rats for seeds of these two species. Despite the high levels of predation for *Nestegis* in the laboratory and 50% fruit removal from the open ground treatment in the field, the accessible fruit in the field were not removed in greater proportions than in the no-vertebrate-access treatment. Seed fragments and rodent-chewed seeds from unripe and ripe fruits were common below parent plants of *Nestegis*, perhaps indicating seed predation prior to natural fruit fall (personal observation) and providing one possible explanation for the discrepancy between field and laboratory trials for *Nestegis*. Seed size preference and seed defensive traits are just two of the many possible characteristics that may influence seed removal and predation by rats.

There were at least two types of seed dispersal observed in black rat interactions with the woody species in this study and these can be distinguished by the degree of pericarp consumption and seed damage (Fig. 21). The first type (occasional dispersal in Fig. 21) occurs when a rat transports fruits or seeds, presumably with the intention to eat them (Herrera and Pellmyr 2002), but some of the chewed seeds are not destroyed. At least six of my studied species showed evidence of this pattern, where entire seeds were not damaged or were partially damaged, but with the embryos left intact such that the seeds potentially remained viable (e.g., *Alyxia*, *Coprosma*, *Diospyros*, *Psidium*, *Psydrax*). There are many examples of rodents in continental ecosystems that scatterhoard seeds, thereby dispersing those that they transport and then neglect to eat (Vander Wall 1990;

Forget 1993; Wang and Chen 2009), but there is no evidence of such seed caching for the black rat (Vander Wall 1990). Additionally, partial seed damage is tolerated by several tropical species (Dalling et al. 1997; Mack 1998) and even accelerates germination in others (Vallejo-Marín et al. 2006) including two endemic Hawaiian palm species that were experimentally damaged to simulate black rat gnawing (Pérez et al. 2008). Another pattern of behavior could involve removing and discarding the unwanted pericarp prior to chewing seeds (rare dispersal in Fig. 21), but no species followed this pattern in my study.

A second type of seed dispersal (via gut passage or endozoochory; Herrera and Pellmyr 2002) was observed for *Clidemia* and *Kadua*, and resulted from rats consuming the pericarp but not chewing the small seeds prior to gut passage (frequent dispersal in Fig. 21). Although this type of dispersal is much more common with birds than rodents (Herrera and Pellmyr 2002; Forget et al. 2005), it has been demonstrated with captive black rats for two small-seeded species (< 2.5 mm length) from New Zealand (Williams et al. 2000). Elsewhere, intact *Clidemia* seeds were found in rodent droppings in a wet forest on Maui, Hawaii (Medeiros 2004), and intact *Carpobrotus* spp. seeds were found in black rat droppings on Mediterranean islands (Bourgeois et al. 2005). Finally, the interaction of black rats with *Pouteria* fits none of the dispersal categories described by Herrera and Pellmyr (2002) because rats consumed only the fleshy pericarp and discarded the large seeds (frequent dispersal, Fig. 21). Other vertebrates are known to harvest and transport fruits prior to eating pericarps and discarding seeds, including native flying foxes (*Pteropus tonganus*) in the South Pacific with *Pouteria grayana* (McConkey and Drake 2006), and native jays (*Cyanocorax cyanomelas*) in Bolivia with *Guettarda*

		Pericarp (fruit tissue)	
		Eaten	Not eaten
Seed	Chewed	**Occasional dispersal** Through incomplete feeding	**Rare dispersal** Through incomplete feeding
	Not chewed	**Frequent dispersal** Large seeds: discarded Small seeds: gut passage	**No dispersal**

Figure 21. The four scenarios by which black rats may interact with fruits and disperse seeds.

viburnoides; the latter interaction increases plant population growth more than in nearby populations where seeds were dispersed by gut passage through other birds (Loayza and Knight 2010). My results indicate that rats interact with fruit differently depending on the species, and that a range of seed sizes (varying 36-fold in length and > 1500-fold in mass if *Clidemia* is compared to *Pouteria* or *Sapindus*) can be dispersed by black rats.

With the loss of most native seed-dispersing fauna in Hawaii after human arrival, some introduced animals, such as birds, have apparently filled the seed-dispersal role of some extinct native birds (Cole et al. 1995; Foster and Robinson 2007; Chimera and

Drake 2010). By contrast, several large-seeded species on Pacific islands may no longer experience bird dispersal because of the loss of particular native fauna (Meehan et al. 2002; Traveset and Richardson 2006), and consequently some of these plant species may not be dispersed beyond the canopies of the parent plants (Chimera and Drake 2010). Although I found that black rats may be important dispersal agents of some species common in Hawaiian mesic forests, it is unclear if black rats are increasing native plant recruitment through such seed dispersal. However, with the exception of *Alyxia*, most of the native species that I tested are uncommon in the seedling layer in Kahanahaiki (Appendix B), and suffer relatively high predation (< 35% survival) by black rats. Introduced rats may accelerate the spread of non-native plant species through dispersal of small seeds (e.g., *Clidemia*), and potentially create a positive feedback that further benefits the rats (Bourgeois et al. 2005; termed ‘invasional meltdown’; Simberloff and Von Holle 1999; Gurevitch 2006; Simberloff 2006), though rats may also partially limit the spread of non-native species by depredating their seeds. While a number of factors may influence seedling establishment, growth, and survival at a given site (Wang and Smith 2002; Joe and Daehler 2008; Cordell et al. 2009), the effects of black rats on native and non-native seeds may be both negative and positive.

Combining field trials with captive feeding trials using wild black rats represents a discontinuity between fruit removal and seed fate that may not be as realistic as if each fruit that a rat interacted with in the field was followed to its ultimate fate. However, it is notoriously difficult to elucidate all steps of a seed’s fate (Forget et al. 2005). A common shortcoming of seed fate trials conducted in the field is the uncertain identity of the animal responsible for seed damage (Abramsky 1983; Forget 1993; Mendoza and Dirzo

2007). Additionally, even if photographs capture the species responsible for seed or fruit removal, it is often uncertain whether the animal that removed the fruit or seed is responsible for all or part of the condition in which it is later recovered (Forget et al. 2005; Vander Wall et al. 2005). Although I was able to identify the animal removing fruits from the forest floor, I combined field trials with captive feeding trials to determine seed fate because it is very difficult to unobtrusively mark small seeds (like those that passed intact through the rat's digestive system) so they can be recovered in the field. Because the sites where rats defecate or deliver seeds (Abe 2007; e.g., husking stations, McConkey et al. 2003) may not always be suitable for germination or establishment, the conclusions using the methodology in this study are limited to seed survival after interaction with the black rat and prior to the germination and establishment stage of recruitment.

Introduced rats are selective in their removal of fruits from the forest floor, and I have shown that fruit removal does not always result in seed predation by black rats. Black rats directly affect seed fates and potentially influence the recruitment patterns of both native and non-native plants. Most past studies indicate that black rat interactions with seeds are antagonistic, but my study demonstrates the extent to which black rats may be seed predators and seed dispersers of a wide range of species. Through such interactions, rats will likely continue to influence plant communities in Hawaii and elsewhere; and by understanding these interactions we can focus management efforts on plant species and fruiting seasons that are most likely to experience negative effects from introduced rats.

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CHAPTER FIVE:

FRUGIVORY BY INTRODUCED BLACK RATS (*RATTUS RATTUS*) PROMOTES DISPERSAL OF INVASIVE PLANT SEEDS

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Abstract

Oceanic islands have been colonized by numerous non-native and invasive plants and animals. An understanding of the degree to which introduced rats (*Rattus* spp.) may be spreading or destroying seeds of invasive plants can improve our knowledge of plant-animal interactions, and assist efforts to control invasive species. Feeding trials in which fruits and seeds were offered to wild-caught rats were used to assess the effects of the most common rat, the black rat (*R. rattus*), on 25 of the most problematic invasive plant species in the Hawaiian Islands. Rats ate pericarps (fruit tissues) and seeds of most species, and the impacts on these plants ranged from potential dispersal of small-seeded (≤ 1.5 mm length) species via gut passage (e.g., *Clidemia hirta*, *Buddleia asiatica*, *Ficus microcarpa*, *Miconia calvescens*, *Rubus rosifolius*) to predation where < 15% of the seeds survived (e.g., *Bischofia javanica*, *Casuarina equisetifolia*, *Prosopis pallida*, *Setaria palmifolia*). Rats consumed proportionally more seed mass of the smaller fruits and seeds than the larger ones, but fruit and seed size did not predict seed survival following rat interactions. Although invasive rat control efforts focus on native species protection, non-native plant species, especially those with small seeds that may pass internally through rats, also deserve rat control in order to help limit the spread of such seeds. Black rats may be facilitating the spread of many of the most problematic invasive plants through frugivory and seed dispersal in Hawaii and in other ecosystems where rats and plants have been introduced.

Introduction

Invasive species, defined here as species that are non-native and cause ecological or economic impact (Lockwood et al. 2007), are transforming landscapes worldwide through their effects on biogeochemical cycles and native species distributions (Vitousek and Walker 1989; Rizzo and Garbelotto 2003; Lockwood et al. 2007). How to prevent and arrest such invasions is a topic of much interest (Daehler and Carino 2000; Epanchin-Niell and Hastings 2010). Interactions involving two or more invasive species, such as an invasive plant and an invasive animal, may increase the negative effects on native biota and ecosystems beyond the independent effects of either invasive species (Parker et al. 2006; Oduor et al. 2010). There is great potential for such synergistic impacts involving multiple invasive species (e.g., 'invasional meltdown' scenario; Simberloff and Von Holle 1999) to become more common than in the past because of the increasing number of introductions of invasive species into a given area (Parker et al. 2006; Traveset and Richardson 2006).

Characteristics of successful invasive species may include high reproduction and growth rates, few predators, and high competitive ability (Vermeij 1991; Lockwood et al. 2007). Additional characteristics that are often associated with invasive plants include small seeds and the presence of non-specialized vertebrate seed dispersers (Williams et al. 2000; Traveset and Richardson 2006). Small seeds of fleshy-fruited species are commonly ingested and dispersed by animals via gut passage (Traveset 1998). The sizes of seeds that pass intact through digestive tracts of animals vary by species, and may be influenced by a number of characteristics of the seeds and their fruits such as shape and fruit fleshiness (Traveset 1998; Traveset et al. 2008). The body size of vertebrates may also correlate with the sizes of seeds that pass intact through digestive tracts (Wheelright 1985; Vander Wall 1990). For example, the maximum reported lengths of seeds that passed intact through mammalian digestive tracts were 5-7 mm for white-tailed deer (*Odocoileus virginianus*) and domestic cattle (Gardener et al. 1993; Myers et al. 2004), 3.7 mm for flying foxes (*Pteropus conspicillatus*) (Richards 1990), 2.5 mm for introduced black rats or ship rats (*Rattus rattus*), and 0.11 mm for introduced Pacific rats (*R. exulans*) in New Zealand (Williams et al. 2000). No seeds, including those as small as 0.11 mm, passed intact through the house mouse (*Mus musculus*) in New Zealand (Williams et al. 2000).

A generalized diet may aid invasive animals in colonizing novel environments and maintaining populations (Nogales et al. 2006). For example, introduced slugs are common in forests in Hawaii where they are reported to feed on at least 59 endangered plant species (Joe and Daehler 2008). More than 30 species of plants were identified in stomachs of introduced pigs (*Sus scrofa*) on Santa Catalina Island, USA (Baber and Coblentz 1987), and over 50 species of plants were in stomachs of introduced goats (*Capra hircus*) on Auckland Island, New Zealand (Chimera et al. 1995). Introduced rats (*Rattus* spp.) are among the most ubiquitous invasive mammals introduced to islands worldwide (Drake and Hunt 2009; Towns 2009) and they feed on a variety of fruits, seeds, and vegetative material, as well as invertebrates, eggs, and small birds (Sugihara 1997; Yabe et al. 2010; Chapter 3).

Native biotas on oceanic islands are known to be highly susceptible to displacement and extinction following the introduction of invasive species (Meyer and Florence 1996; Kueffer et al. 2010). The Hawaiian Islands represent an extreme example of an archipelago that suffers from biological invasions because they contain among the largest number of introduced species of all Pacific islands (Denslow et al. 2009). The number of introduced plant species that has naturalized in Hawaii is approximately equal to the number of native plant species (Wagner et al. 1999), and many of these naturalized species are invasive (Daehler and Carino 2000; Denslow et al. 2009). Seed-eating mammals were absent from Hawaii prior to the introduction of the Pacific rat by Polynesian settlers approximately 1000 years ago (Athens et al. 2002), and later arrival of two additional rats (the Norway rat, *R. norvegicus*, and the black rat) and the house mouse with European settlement ca. 230 years ago (Tomich 1986). In contemporary Hawaii, the black rat is the most common rat in natural and semi-natural ecosystems from sea level to nearly 3000 m elevation (Amarasekare 1994; Lindsey et al. 1999; Meyer and Shiels 2009). The black rat is a predator of a wide range of native Hawaiian biota, including arthropods (Cole et al. 2000), birds (VanderWerf 2001), snails (Hadfield et al. 1993), and seeds (Pérez et al. 2008; Shiels and Drake, in press), and this rat has been considered one of the most damaging invasive vertebrates in the world (Towns et al. 2006; Drake and Hunt 2009).

How black rats affect common invasive plant species in Hawaii is largely unknown; however, that these rats are frugivores, seed predators, and seed dispersers of many native and four invasive Hawaiian plants has recently been established (Shiels and Drake, in press). Black rats may disperse seeds either by ingesting them (i.e., gut passage or endozoochory) or by transporting them and then discarding them either whole or partially chewed but with intact embryos (i.e., McConkey et al. 2003; Abe 2007; Shiels and Drake, in press; Chapter 4). The objective of this study was to identify patterns in the ways rats interact positively and negatively with seeds of invasive species. Specifically, I addressed the following questions to determine how black rats affect 25 of the most invasive plant species in Hawaii: 1) To what degree do rats consume the pericarps (fruit tissues) and seeds of these species? 2) Are there seeds that are potentially dispersed as a consequence of rats discarding or partially chewing seeds, or passing them internally? 3) Are there characteristics of fruits and seeds that predict their consumption, predation, and dispersal potential by rats?

Methods

Invasive plant species selection and description

To select the invasive plant species to offer black rats, I surveyed 12 invasive plant experts from the five largest Hawaiian Islands (i.e., Hawaii, Maui, Molokai, Oahu, Kauai) by asking them to list the 25 most problematic invasive plant species in Hawaii. Experts were considered those actively working with invasive plants in the Hawaiian Islands for at least the previous 5 years. I chose 25 plant species based on the highest frequencies listed with the following two constraints: First, to maximize phylogenetic diversity, no more than two species per family and one species per genus was selected. Second, at least three experts had to list a species for it to be used. There were five species that were substituted for slightly higher ranking species because of the availability of ripe fruits and seeds when black rats were in captivity. The 25 species used came from 19 families and had a wide range of fruit and seed sizes (Table 16), and all but seven species have fruit and seed adaptations for animal dispersal (Table 17). The

Table 16. Characteristics of the 25 invasive plant species used in this study. Values are expressed as mean (SE). For fruit and seed measures, a minimum of N = 8 fruit for each species were collected from > 3 individuals. Lengths of fruits and seeds are the longest axial lengths. Mass of fruits, which includes seeds, and mass of the individual seeds are reported on a fresh-mass basis. Species ordering reflects survey results (see Methods) for the most problematic plants in Hawaii; the first species listed were the most problematic based on my informants.

Species[a]	Family	Life form	No. fed to each rat[b]	Fruit				Seed			
				Length (mm)	Width (mm)	Mass (mg)	Fleshiness[c] (%)	Length (mm)	Width (mm)	Mass (mg)	No. per fruit
Psidium cattleianum	Myrtaceae	Tree	1	19.0 (0.3)	17.8 (0.3)	3677 (304)	80.3 (0.8)	3.3 (0.1)	2.4 (0.1)	14.4 (0.7)	16.4 (1.5)
Clidemia hirta	Melastomataceae	Shrub	4	6.9 (0.3)	6.4 (0.2)	214 (21)	79.6 (0.7)	0.5 (0.0)	0.3 (0.0)	< 0.1	360 (57)
Schinus terebinthifolius	Anacardiaceae	Tree	3	4.7 (0.2)	3.9 (0.2)	33 (5)	32.8 (5.4)	3.6 (0.1)	2.4 (0.2)	5.9 (0.0)	1.0 (0.0)
Hedychium gardnerianum	Zingiberaceae	Herb	1	23.5 (1.0)	14.8 (0.3)	2638 (245)	74.1 (0.5)	4.3 (0.1)	3.7 (0.1)	46 (1)	16.3 (1.4)
Miconia calvescens	Melastomataceae	Shrub	8	4.7 (0.2)	4.2 (0.1)	58 (3)	69.7 (1.9)	0.5 (0.0)	0.4 (0.0)	< 0.1	66 (9)
Leucaena leucocephala	Fabaceae	ShrubTree	5	127.8 (6.0)	18.4 (0.6)	923 (54)	13.3 (0.1)	7.2 (0.2)	3.9 (0.1)	44 (1)	13.7 (1.4)
Schefflera actinophylla	Araliaceae	Tree	8	5.9 (0.1)	5.1 (0.1)	98 (3)	84.8 (0.5)	2.1 (0.1)	1.3 (0.1)	0.2 (0.1)	24.3 (1.0)
Ardisia elliptica	Myrsinaceae	Shrub	3	10.2 (0.2)	7.8 (0.4)	420 (10)	77.6 (0.3)	4.9 (0.1)	4.6 (0.1)	74 (2)	1.0 (0.0)
Morella faya	Myricaceae	ShrubTree	2	5.6 (0.4)	4.7 (0.3)	84 (14)	65.0 (3.6)	2.8 (0.2)	1.9 (0.1)	4.7 (1.2)	1.2 (0.1)
Lantana camara	Verbenaceae	Shrub	3	5.0 (0.2)	4.5 (0.2)	78 (8)	64.5 (2.3)	4.5 (0.2)	2.9 (0.2)	20 (1.0)	1.0 (0.0)
Spathodea campanulata	Bignoniaceae	Tree	5	231.7 (10.9)	65.0 (10.4)	34471 (2758)	16.8 (1.5)	8.9 (0.2)	6.7 (0.1)	5.0 (0.3)	1631 (79)
Urochloa maxima	Poaceae	Grass	14	3.1 (0.1)	1.1 (0.1)	1.0 (0.1)	14.0 (9.8)	2.3 (0.1)	0.9 (0.1)	0.9 (0.1)	1.0 (0.0)
Prosopis pallida	Fabaceae	Tree	1	142.9 (6.1)	11.1 (0.4)	4627 (439)	19.7 (1.4)	5.8 (0.3)	3.7 (0.4)	38.5 (3.1)	22.6 (0.8)
Rubus rosifolius	Rosaceae	Shrub	1	15.0 (0.7)	12.6 (0.7)	1138 (153)	83.3 (0.9)	1.5 (0.0)	1.0 (0.0)	0.7 (0.0)	237 (35)
Citharexylum caudatum	Verbenaceae	Tree	4	5.5 (0.2)	5.1 (0.2)	119 (9)	70.2 (0.7)	5.2 (0.2)	3.6 (0.1)	25.9 (2.0)	2.0 (0.0)
Ficus microcarpa	Moraceae	Tree	2	7.3 (0.2)	7.1 (0.2)	162 (19)	64.2 (3.3)	0.9 (0.0)	0.7 (0.0)	< 0.1	12.7 (4.0)
Passiflora suberosa	Passifloraceae	Vine	2	9.3 (0.3)	8.9 (0.3)	354 (41)	86.4 (1.2)	3.3 (0.1)	2.4 (0.1)	9.8 (0.7)	11.0 (1.2)
Buddleia asiatica	Buddleiaceae	Shrub	35	3.3 (0.1)	2.4 (0.1)	2 (0)	13.0 (2.1)	0.6 (0.0)	0.2 (0.0)	< 0.1	177.5 (31.9)
Syzygium cumini	Myrtaceae	Tree	1	17.0 (0.3)	14.2 (0.5)	2466 (216)	77.0 (0.6)	11.5 (0.3)	8.3 (0.2)	584 (33)	1.0 (0.0)
Aleurites moluccana	Euphorbiaceae	Tree	1	46.7 (1.9)	43.5 (0.5)	46855 (2371)	67.1 (1.5)	30.3 (0.5)	29.1 (0.4)	8995 (542)	1.4 (0.1)
Coffea arabica	Rubiaceae	ShrubTree	1	15.0 (0.4)	13.7 (0.3)	1701 (58)	66.5 (0.5)	12.0 (0.2)	8.4 (0.1)	406 (19)	2.0 (0.0)
Cinnamomum burmanii	Lauraceae	Tree	2	9.9 (0.3)	6.9 (0.1)	297 (15)	51.4 (1.3)	8.1 (0.2)	4.9 (0.1)	113.0 (5.1)	1.0 (0.0)
Bischofia javanica	Euphorbiaceae	Tree	2	11.1(0.2)	9.6 (0.2)	730 (33)	68.7 (0.3)	4.1 (0.1)	2.8 (0.1)	19 (1)	2.6 (0.3)
Casuarina equisetifolia	Casuarinaceae	Tree	2	13.4 (0.5)	12.1 (0.4)	650 (58)	22.8 (0.9)	2.9 (0.1)	2.7 (0.1)	0.9 (0.1)	9.9 (3.9)
Setaria palmifolia	Poaceae	Grass	25	3.0 (0.1)	1.4 (0.0)	1.6 (0.1)	21.4 (5.3)	2.8 (0.0)	1.4 (0.0)	1.5 (0.1)	1.0 (0.0)

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[a] Botanical nomenclature for herbs, shrubs, and trees follows Wagner et al. (1999) with recent updates. The red-fruited form of *Psidium cattleianum* was used in this study.

[b] Fruits were offered to each rat for all plant species except *Leucaena* and *Spathodea*, which only had seeds offered.

[c] Fleshiness was calculated as (fresh mass – dry mass)/fresh mass. Dry mass was determined by heating at 105° C for 48 hours.

majority of the selected plant species are native to the Old World (16 species), whereas nine species are native to the Neotropics (Wagner et al. 1999; Table 17). Plant species are hereafter referred to by genus.

Table 17. The origin, approximate number of years in Hawaii, and the likely dispersal vector for 25 invasive plant species used in this study.

Species	Origin[a]	Approx. number of years in Hawaii[a]	Likely dispersal vector
Psidium cattleianum	Tropical America	85	Animal
Clidemia hirta	Tropical America	70	Animal
Schinus terebinthifolius	Tropical America	100	Animal
Hedychium gardnerianum	Temperate, subtropical Asia	70	Animal
Miconia calvescens	Tropical America	50	Animal
Leucaena leucocephala	Tropical America	175	No obvious[b]
Schefflera actinophylla	Tropical Australia and New Guinea	110	Animal
Ardisia elliptica	Tropical Asia	80-90	Animal
Morella faya	Subtropical, temperate Africa	85	Animal
Lantana camara	Tropical America, Caribbean	150	Animal
Spathodea campanulata	Tropical Africa	100	Wind
Urochloa maxima	Tropical Africa	140	No obvious[b]
Prosopis pallida	Tropical America	80	Animal

Species	Origin[a]	Approx. number of years in Hawaii[a]	Likely dispersal vector
Rubus rosifolius	Subtropical, temperate Asia	130	Animal
Citharexylum caudatum	Tropical America	80	Animal
Ficus microcarpa	Tropical, subtropical Asia and Australia	100	Animal
Passiflora suberosa	Tropical, subtropical America	95	Animal
Buddleia asiatica	Tropical, subtropical Asia	100	No obvious
Syzygium cumini	Tropical Asia and Malesia	140	Animal
Aleurites moluccana	Tropical Malesia	1000	Uncertain[c]
Coffea arabica	Tropical Africa	160	Animal
Cinnamomum burmanii	Tropical Indonesia	60	Animal
Bischofia javanica	Tropical, subtropical Asia and Malesia	80	Animal
Casuarina equisetifolia	Tropical, subtropical Australia	230	Wind
Setaria palmifolia	Tropical Asia	110	No obvious

[a] Based on Wagner et al. (1999).

[b] Seeds of *Leucaena leucocephala* and *Urochloa maxima* pass intact through cattle (Gardener et al. 1993), which has been a likely mechanism for their successful invasion in habitats near cattle-grazing.

[c] Seeds of *Aleurites* may be dispersed by water because the fruit are buoyant for 1-2 weeks, or by crows as evidenced by observations in New Caledonia (Guppy 1906).

Rat consumption of pericarp and seed

Adult black rats were captured from five locations on Oahu island, including a dry, lowland coastal scrubland, Ka Iwi Shoreline (1-2 m a.s.l; 21^{o} 17′ N, 157^{o} 39′ W), a dry forest on Lanipo trail in the Koolau Mountains (205 m a.s.l; 21^{o} 18′ N, 157^{o} 47′ W), and three mesic forest sites in the Waianae Mountains (450-625 m a.s.l.; Kahanahaiki Management Unit, 21^{o} 32′ N, 158^{o} 11′ W; Kaluaa Preserve, 21^{o} 28′ N, 158^{o} 5′ W; Makaha Valley, 21^{o} 31′ N, 158^{o} 17′ W). Rats were taken to laboratory facilities at the University of Hawaii in Honolulu, and each rat was held in an individual 38 cm x 22 cm x 18 cm metal-mesh (8 mm) cage. Before beginning feeding trials, rats were allowed to acclimate for at least one week, during which time they were fed a diet of mixed seeds (e.g., corn, sunflower, wheat, barley, oats, sorghum) and occasionally wedges of fruit (tangerine). Rats were checked daily to ensure there was ample food and fresh water, and to clean urine/fecal trays. Feeding trials were performed from October 2007 through March 2010. Approximately each four months, a new set of rats (9-12 individuals, in roughly equal proportions of females and males) were captured from a single or multiple sites and replaced the previous set of rats. A total of 57 rats (111.1 ± 5.0 g; 16.2 ± 0.3 cm body length excluding tail; mean ± SE) were used during this study.

For each feeding trial, 9-12 rats (mean ± SE: 11.0 ± 0.1) were individually offered fruits of a single species (or seeds only for *Leucaena* and *Spathodea*) placed in each cage with no other food for 24 hours. To roughly adjust for differences in fruit volume and mass among species, the number of fruits offered to each rat ranged from one to 35 (Table 16). After 24 hours of exposure to each rat, fruits were visually inspected to estimate the proportion of the pericarp (fruit tissue, and the most outer layers of the fruit for grasses) mass and seed mass remaining. When multiple fruits or seeds were offered to a rat, the proportion of mass remaining was determined by averaging each fruit's or seed's unconsumed mass. For six of the 25 species, trials were continued an additional 24 hour period and inspected, but there was no significant difference in pericarp or seed mass remaining between 24 and 48 hours ($P > 0.05$ for each; Mann-Whitney U tests), so all data presented for each of the 25 species are for the initial 24 hours of rat exposure. The proportion of surviving seeds was determined by inspecting all remaining seeds and seed parts in each cage for damage from chewing and for intact embryos. A seed was considered destroyed if the embryo was not intact or > 50% of the seed was eaten (Pérez et al. 2008; Shiels and Drake, in press). For the smallest seeds (< 3 mm length; Table 16), it was necessary to microscopically inspect rat droppings and extract seeds that had passed through the digestive tracts of rats. To test for viability of such seeds, they were sown on agar, and their germination was compared to conspecific, unconsumed seeds sown on agar. The proportion of seeds that survived following rat exposure was determined from the ratio of surviving seeds relative to the average number of seeds per fruit for each species (see Table 16). Rats were returned to their regular diet for at least 48 hours between feeding trials.

Characteristics that predict rat vulnerability

Eight variables associated with the fruits and seeds were predicted to affect pericarp and seed consumption by black rats: mean fruit and seed length, width, and mass, as well as fruit fleshiness (mass ratio of fresh – dry when heated at 105^{o} C for 48 hours: fresh) and the number of seeds per fruit (Table 16). Because these variables were correlated (e.g., 16 of 28 possible pairwise correlations had R values > 0.50), I used principal components analysis (PCA) to reduce the number of variables to a smaller number of principal components (PCs) that are orthogonal (i.e., not correlated; Quinn and Keough 2002). Aside from fruit fleshiness and the number of seeds in each fruit, each of the variables related to fruit and seed size were log-transformed to meet assumptions of normality. All 25 species were used in the PCA. The PCs were used to calculate factor scores for each species, and I used these factor scores in multiple regressions to test whether the PCs are correlated with the following variables related to fruit and seed attractiveness and vulnerability to black rats: percentage pericarp mass remaining, percentage seed mass remaining, percentage surviving seeds. Percentage of pericarp remaining used 23 species because for two species (*Leucaena* and *Spathodea*) only the seeds were offered to rats. All remaining analyses included all 25 species. All statistical analyses were conducted in SPSS (1998), and significance was based on $P < 0.05$.

Results

Rat consumption of fruit and seed

Black rats ate both the pericarp and the seeds, but the amount of plant material (pericarp and seeds) eaten by black rats (Fig. 22) and the percentage of total seeds that survived (Fig. 23) varied by plant species. Two species were unattractive to rats, including *Aleurites*, which has the largest seeds and had nearly 80% of its pericarp and almost 100% of the seed mass remaining, and the intermediate-sized seeds (3.6 mm longest length) of *Schinus*, which had > 90% of the pericarp and seed mass remaining after 24 hours (Fig. 22). The majority of the species had approximately equal parts of pericarp and seed mass remaining, but at least three species tended to have a greater portion of their seed masses remaining rather than pericarp masses, including *Coffea*, *Syzygium*, and *Lantana*. By contrast, pericarp mass remaining tended to be higher than seed mass remaining for *Casuarina*, *Setaria*, *Urochloa*, and *Ficus* (Fig. 22).

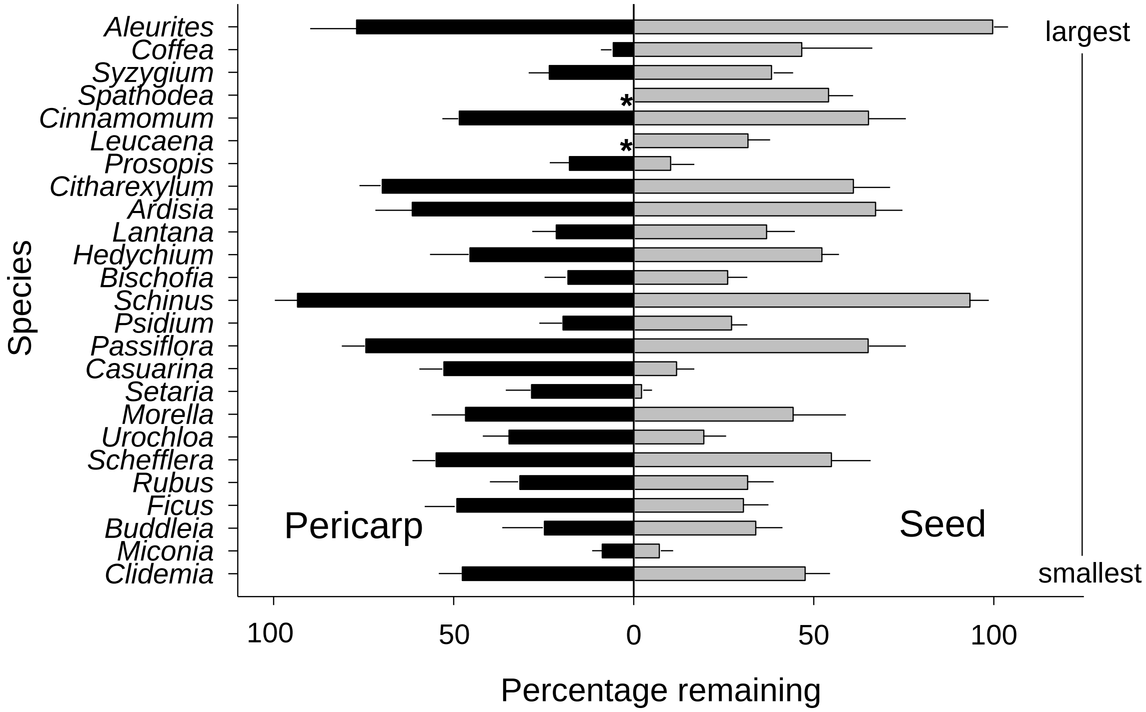

Figure 22. Mean (SE) estimated pericarp mass and seed mass remaining for 25 invasive plant species in Hawaii after offering to black rats (9-12 rats for each trial; mean ± SE: 11.0 ± 0.1). The asterisk (*) signifies the two species (*Leucaena* and *Spathodea*) that were only offered seed. Species ordering on the vertical axis are arranged in ascending seed length.

Following 24 hour exposure to rats, 15 of the 25 species had < 50% average seed mass remaining. Seed mass remaining represents the amount of seed mass that was uneaten and it does not reflect the number of surviving seeds following rat exposure.

Seeds of four of these 15 species, including *Miconia*, *Setaria*, *Casuarina*, and *Prosopis*, appeared most attractive to rats because < 12% of their seed masses remained. Three of these species are relatively small-seeded and were surrounded in either fleshy fruit (*Miconia*) or relatively dry fruit (*Setaria* and *Casuarina*). *Prosopis* have much larger seeds (ca. 2-11 times in length and 25-39 times in mass) than each of these three small seeded species and are surrounded by a sweet, relatively dry, mesocarp (Table 16).

Seed survival varied widely among the 25 species, and can be grouped into three categories (discarded, chewed, and gut passage) based on whether or not surviving seeds were chewed and ingested (Fig. 23). All species had some seeds that were discarded (i.e., not chewed or ingested) by some rats. Fifteen of the species had some seeds that were chewed and not ingested such that their viability was not likely altered (Fig. 23). Several species, including *Aleurites*, *Buddleia*, *Clidemia*, *Ficus*, *Miconia*, and *Rubus*, had no seeds destroyed by rats, and aside from *Aleurites* the 100% seed survival for each of these species resulted from the seeds being small enough to pass intact through the rat's teeth and digestive system (i.e., gut passage). The seeds that survived gut passage were ≤ 1.5 mm in length and ≤ 0.7 mg. Therefore, seeds that are consumed by black rats survive and may be dispersed if their longest axis is ≤ 1.5 mm, whereas seeds ≥ 2.1 mm have a much greater chance of being destroyed. There were no seeds tested between 1.5 mm (*Rubus*) and 2.1 mm (*Schefflera*). Basing such a threshold, which separates endozoochory from predation, on seed mass is less useful than seed length for the tested species because *Schefflera* seeds weigh 0.2 mg but did not survive black rat consumption (Table 17; Fig. 23). Of the nine species with the lowest seed survival (< 35%), *Bischofia*, *Casuarina*, *Setaria*, and *Prosopis* had < 15% survival (Fig. 23), which amounts to an average of ca.

one or three surviving seeds per fruit for *Casuarina* and *Prosopis*, respectively, and generally no surviving seeds per fruit for *Bischofia* and *Setaria* (Table 16; Fig. 23). Aside from the unattractive fruits and seeds of *Aleurites* and *Schinus*, and the seeds with the lowest survival, most species in this study may be occasionally dispersed by black rats if transported seeds in the field were not destroyed.

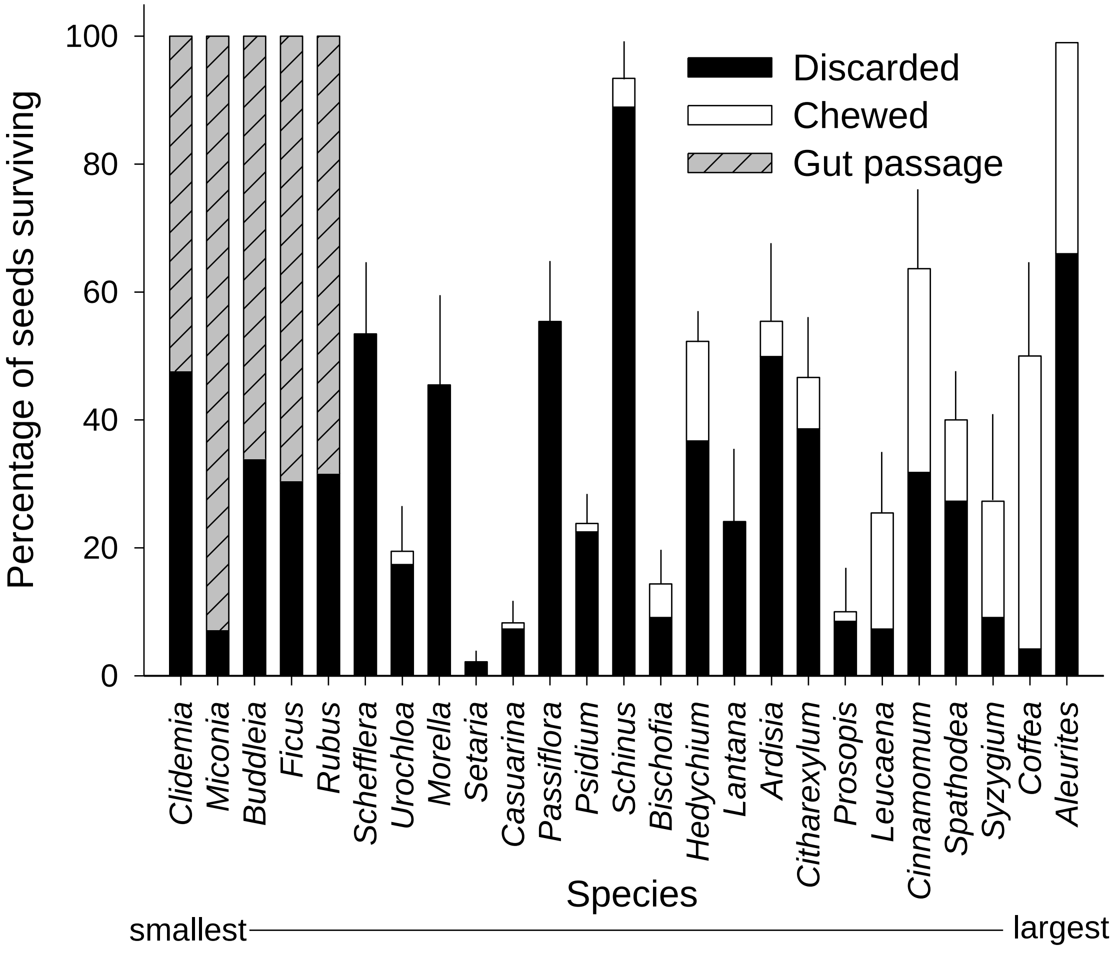

Figure 23. Mean (SE) seed survival of 25 invasive plant species in Hawaii that were offered to captive black rats (9-12 rats for each trial; mean ± SE: 11.0 ± 0.1). The three categories of survival include: discarded (not chewed or ingested), chewed, and gut passage. Error bars reflect total survival (all three categories combined). Species ordering on the horizontal axis are arranged in ascending seed length.

Characteristics that predict rat vulnerability

When the eight fruit and seed characteristics for all 25 species were analyzed by PCA, three PCs with eigenvalues > 1.0 accounted for 96.84% of the measured variation in the dataset (Table 18). Principal component 1, which accounted for 57% of the variation, was dominated by variables related to fruit and seed size (Table 16). The highest factor loadings in PC 1 were for seed width and seed length, and all of the variables relating to fruit and seed length, width, and mass were positively correlated (Table 18). Both PC 2 (25% explained variance) and PC 3 (14% explained variance) had a single variable with a high factor loading, which was the number of seeds per fruit for PC 2 and fruit fleshiness for PC 3 (Table 18).

Table 18. Eigenvalues and factor loadings for the first three principal components of variables relating to the characteristics of fruits and seeds of 25 invasive plant species introduced in Hawaii. Significant factor loadings were based on the recommendations of Comrey (1973) and are shown here with an asterisk (*).

Variable	PC 1	PC 2	PC 3
Eigenvalue	4.58	2.00	1.16
% of total variance explained	57.29	25.06	14.49
Fruit length	0.780*	0.500	-0.304
Fruit width	0.846*	0.489	0.118
Fruit mass	0.877*	0.407	0.213
Fruit fleshiness	0.111	-0.027	0.989*
Seed length	0.900*	-0.371	-0.161
Seed width	0.938*	-0.312	-0.039
Seed mass	0.872*	-0.429	0.022
No. seeds per fruit	-0.164	0.963*	-0.029

Multiple regression revealed that the first three PCs accounted for a significant amount of variation (P = 0.038; $r^2 = 0.282$) in the percentage of seed mass remaining following rat exposure, and that PC 1 accounted for this significant correlation (P = 0.036; d.f. = 3, 21; Fig. 24), and not PC 2 (P = 0.305) or PC 3 (P = 0.162). Therefore, black rats appears to consume proportionally more seed mass of invasive species when the fruit and seed sizes are small than when they are larger (Fig. 24). No PCs were significantly correlated with the percentage of pericarp mass remaining (PC 1 P = 0.871; PC 2 P = 0.349; PC 3 P = 0.537; d.f. = 3, 19) or the percentage of seeds surviving (PC 1 P = 0.205; PC 2 P = 0.125; PC 3 P = 0.055; d.f. = 3, 21).

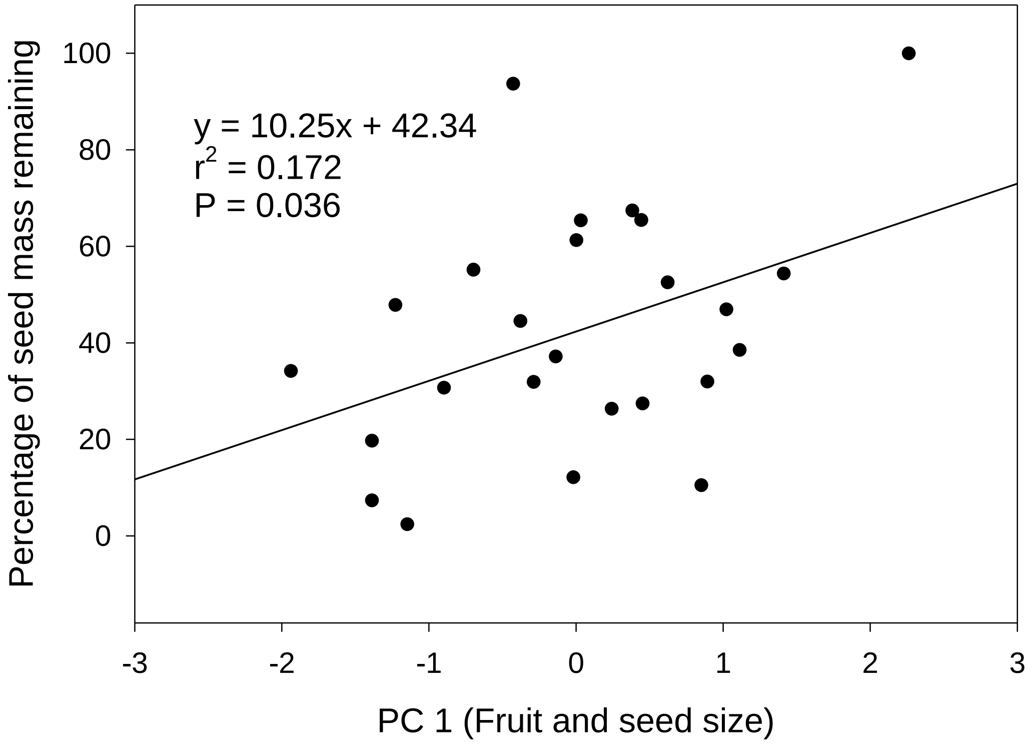

Figure 24. Relationship between seed mass remaining following black rat interaction and PC 1, where PC 1 reflects sizes of the fruits and seeds, including length, width, and mass, of 25 invasive species in Hawaii. Positive values of PC 1 reflect larger fruit and seed sizes.

Discussion

Black rats eat fruits and seeds of a wide range of invasive species including those that are typically dispersed by wind (e.g., *Casuarina*, *Spathodea*). The majority of the seeds of the 25 species studied are potentially dispersed by black rats, particularly those that survived gut passage (i.e., *Clidemia, Miconia, Buddleia, Ficus,* and *Rubus*); controlling rats when these species are fruiting could potentially reduce their spread. Only two species appear to be unattractive to rats, *Aleurites* and *Schinus*, as evidenced by little or no consumption of the pericarp or the seed and > 90% seed survival. Fruit and seed size did not predict seed survival and potential dispersal by black rats, but did predict the proportion of seed consumption. Thus, larger fruits and seeds had proportionally more of their seed mass remaining following interactions with rats than did smaller fruits and seeds. Black rats may benefit from these relatively common, invasive species as a reliable food source, and could be facilitating their seed dispersal within the Hawaiian Islands.

Rat consumption of invasive fruits and seeds can result in seed survival or mortality. Nine of the plant species tested suffered relatively high predation because < 35% of the seeds survived 24 hour exposure to black rats. Several of these species, including *Lantana*, *Leucaena*, *Psidium*, *Syzygium*, and *Urochloa* tended to suffer slightly less predation (15-35% survival) than the most vulnerable (< 15% survival) species, which were *Bischofia*, *Casuarina*, *Setaria*, and *Prosopis*. *Bischofia* is one of the most problematic invasive species on the subtropical Ogasawara Islands in Japan, where it has high growth rates and low mortality rates (Hata et al. 2006). There, the black rat is believed to be the animal responsible for the relatively high post-dispersal seed predation of *Bischofia* (10-50% of the seeds remained after five days), but such seed predation does not appear to be reducing the spread of this plant (Yamashita et al. 2003). No published seed predation studies were found for the wind-dispersed tree *Casuarina* and the grass *Setaria*. Almost every seed of *Setaria* that was offered to black rats was consumed and destroyed, as were > 80% of the seeds of the grass *Urochloa* (formerly *Panicum maximum*), which is an aggressive colonizer in tree plantations and disturbed sites (Ostertag et al. 2008). Introduced grasses suffer relatively high predation in other tropical areas, such as in Costa Rica where seedlings of the dominant non-native *Cynodon dactylon* were reduced 52% by vertebrate seed predators (Wijdeven and Kuzee 2000). Most seeds of *Prosopis* were destroyed by the captive black rats, and the majority of the sugar-rich pericarp was also consumed. A single *Prosopis* tree can produce 19,000-140,000 seeds per year (cited in Gallaher and Merlin 2010), yet introduced rodents and beetles appear to minimize *Prosopis* recruitment through seed predation in many parts of Hawaii (Gallaher and Merlin 2010) and elsewhere (Pasiecznik et al. 2001).

Black rats are not only seed-eaters but are also frugivores for many species (Abe 2007; Meyer and Butaud 2009), including all 23 species that were offered as fruit in my study. For some fleshy-fruited species, such as *Coffea*, *Syzygium*, and *Lantana*, rats tended to consume the pericarp to a greater degree than the seed. In naturalized stands of *Coffea* in Hawaiian forests, I observed freshly fallen *Coffea* seeds without pericarps below parent plants where black rats were foraging the previous night. Many *Coffea* seedlings are found below conspecific trees in rainforests in India where *Coffea* is invading forests adjacent to plantations, but it is unknown if rats play a role in frugivory or seed dispersal in this region (Josi et al. 2009). The omnivorous diet of introduced rats, including consumption of pericarp and seed, has been described in Hawaii (Sugihara 1997; Cole et al. 2000; Beard and Pitt 2006) but the relatively high incidence of frugivory and possible preference of the pericarp over the seed has not been well established for black rats.

Dispersal via gut passage occurred for five of the 25 invasive plants tested (*Clidemia*, *Miconia*, *Buddleia*, *Ficus*, and *Rubus*). Although this type of dispersal has been much more commonly observed in birds than rodents (Herrera and Pellmyr 2002), it has been observed with black rats and two small-seeded (≤ 2.4 mm length) species in New Zealand (Williams et al. 2000) and with *Carpobrotus* spp. seeds (0.3-0.6 mg) on Mediterranean islands (Bourgeois et al. 2005). Additionally, intact *Clidemia* seeds were found in rodent droppings in a wet forest on Maui, Hawaii (Medeiros 2004), and Meyer (1998) suggests that *Miconia* are actively dispersed by introduced rodents in Tahiti. Mature individuals of *Clidemia* and *Miconia* can produce 3-8 million seeds/year (Meyer 1998; Medeiros 2004) and were ranked in the top five most problematic invasive species in Hawaii by my informants. While > 50% of both pericarp and seed masses of *Clidemia* and *Miconia* were consumed by rats in captive-feeding trials, *Miconia* fruit consumption tended to be much greater, with only about 10% of the pericarp and seed remaining after rat interaction. Fruit of *Clidemia*, *Melastoma candidum* (Melastomataceae), and *Rubus* comprised ca. 95% of the food items in stomachs of 19 black rats trapped in lowland forest dominated by invasive plants on Hawaii island (Beard and Pitt 2006). Therefore, where *Clidemia*, *Miconia*, and *Rubus* are locally abundant in Hawaii, their fruit may comprise a large portion of the black rat diet and their seeds are likely dispersed by these rats.

Williams et al. (2000) found that seeds of one invasive species (*Leycesteria formosa*; 0.11 ± 0.01 mm, mean ± SD in length) and one native species (*Solanum aviculare*; 2.4 ± 0.5 mm) survived black rat gut passage in New Zealand. In this Hawaiian study, the seed size threshold that separates survival via gut passage from predation by black rats is ca. 1.5-2.0 mm. Hence, seeds of *Schefflera* (2.1 mm length) and *Urochloa* (2.3 mm) were destroyed when consumed, though they are below the size that Williams et al. (2000) found would safely pass intact through black rats. Size differences between black rats in Hawaii and New Zealand may be one possible explanation for this discrepancy in seed size thresholds because black rats may be slightly smaller in Oahu (111.1 ± 5.0 g in this study; 26 of 92 captured adults were < 120 g; unpublished data) than in New Zealand (120-160 g; Atkinson and Towns 2005), and body size has been shown to positively correlate with sizes of fruit and seed eaten by birds (Wheelwright 1985; Meehan et al. 2002) and moved by rodents (Vander Wall 1990; Muñoz and Bonal 2008).

Very small seeds that pass internally are not the only types of seeds that may be dispersed by black rats. Although less recognized (but see Abe 2007; Shiels and Drake, in press), there is potential for dispersal of seeds that were ≥ 2.1 mm length and were not destroyed following collection because these rats commonly transport fruits and seeds to nearby husking stations for consumption (Campbell et al. 1984; McConkey et al. 2003). Therefore, discarding unchewed seeds after consuming pericarps, and incomplete consumption where seeds are partially chewed but not destroyed, can result in seed dispersal for seeds ≥ 2.1 mm in length, which includes at least 15 species in this study. Adding field trials in Hawaii, as demonstrated by Shiels and Drake (in press) for eight native and four invasive species, would allow further clarification of the likelihood of such seed dispersal by black rats for these 15 species.

Black rats consume a greater proportion of the seed mass in species with small fruits and seeds than they do for large fruits and seeds (Fig. 24). Although the mass of consumed seeds was not determined in several past studies, larger seeds are often preferentially selected by rodents over smaller seeds, probably because of the greater nutritional reserve in larger seeds (Smith and Reichman 1984; Vander Wall 2003). However, Shiels and Drake (in press) found that the intermediate-sized seeds were generally the most attractive species and suffered the highest predation by black rats when 12 species were tested in Oahu montane forest, whereas the three largest seeds, including *Aleurites* and two native species, were among the most unattractive to rats. It is curious that *Aleurites* seeds were not removed by rats in the field (Shiels and Drake, in press) or readily consumed in laboratory trials because gnawed seeds can be found in most forests where *Aleurites* has established both in Hawaii and other Pacific Islands (personal observation); it is possible that consumption of *Aleurites* in the field may be overestimated because the stony seed coats of the chewed seeds persist indefinitely on the forest floor. As in the present study, the smallest seeds in the study by Shiels and Drake (in press) were frequently ingested but not destroyed by black rats. Additionally, relatively small seeds were the most commonly reported seed size that was eaten by introduced rats when numerous New Zealand studies were reviewed (Grant-Hoffman and Barboza 2010). The higher energetic cost involved in moving large fruits and seeds versus small ones, or the energy expenditure needed to overcome defenses such as hard seed coats and secondary compounds, can deter rodents from consuming such food items

(Smith and Reichman 1984; Blate et al. 1998). Reduced time to satiation when large seeds are eaten (Janzen 1971) may also partly explain the difference in black rat consumption of different sized seeds.

Although captive-feeding trials show that black rats have great potential to disperse some invasive seeds via gut passage, introduced birds also disperse some species of invasive seeds in Hawaii (Medeiros 2004; Chimera and Drake 2010) including four of those (*Clidemia*, *Hedychium*, *Psidium*, and *Rubus*) included in my study (Medeiros 2004). The relative importance of bird- versus rat-dispersal cannot be determined without an understanding of the degree of each plant's dispersal limitations and the effectiveness of dispersal attributed to each animal at a given site. Introduced black rats may be the dominant seed dispersing animal on some islands that have relatively few avian frugivores, such as on Palmyra atoll in the Pacific Ocean where black rat densities are 90 indiv./ha (Wegmann 2009). In Hawaii, the relative importance of black rats versus birds or other seed-dispersing animals remains unknown. However, the microsites in the canopy and on the ground where black rats deposit seeds following transport will likely differ from those of birds or other seed-dispersing fauna.

While past motivations for rat control and eradication from islands has resulted from efforts to protect native biota from rat predation (Towns et al. 2006; Howald et al. 2007; Meyer and Butaud 2009), the results from my study show that rat control efforts also need to be applied to areas where invasive plants have established and are fruiting in order to reduce their potential seed dispersal by rats. Although invasive seeds of a wide range of sizes can potentially be dispersed by black rats, the very small seeds (≤ 1.5 mm) are the ones most likely to be dispersed by rats via gut passage. Because of their global colonization of islands that includes a wide range of habitats (e.g., sea level to nearly 3000 m in Hawaii), black rats should not be overlooked as potential dispersers of invasive plants and vectors of their spread.

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CHAPTER SIX:

CONCLUSIONS

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Along with humans, introduced rats (*Rattus rattus*, *R. norvegicus*, and *R. exulans*) and mice (*Mus musculus*) are among the most invasive and widely distributed mammals on the planet; they occur on more than 80% of the world's islands groups (Atkinson 1985; Towns 2009). By incorporating modern technology, such as aerial broadcast of rodenticides, the number of islands where invasive rodents can be successfully removed has recently increased (Howald et al. 2007). However, successful rat and mouse eradication on relatively large (> 5000 ha) or human-inhabited islands such as the main Hawaiian Islands rarely occurs (Howald et al. 2007) despite large sums of money and research efforts annually to combat invasive rodent problems (see Chapter 1 section "Rat history in Hawaii"; Tobin et al. 1990). Therefore, it is highly unlikely that invasive rats and mice will be eradicated from relatively large, human-occupied islands such as Oahu in the near or distant future (Howald et al. 2007); and accepting this may be a first step towards increasing the likelihood of native species conservation in archipelagos like Hawaii where introduced rodents have established.

Determining which invasive rodent species are present at a given site is important because the risks that some rodent species pose to particular (prey) species and/or habitats differ from those posed by other rodent species. Two sympatric species cannot occupy the same niche indefinitely, in a stable environment (Gause 1934), which may partly explain why some rodent species may not occur where others are present (Harper 2006). For example, in New Zealand, mice rarely occur with Pacific rats (Yom-Tov et al. 1999; Ruscoe and Murphy 2005). The behavior and abundance of rodent species may also change when they are sympatric with other rodent species (Grant 1972; Yom-Tov et al. 1999; Russell and Clout 2004). Therefore, determining rodent species composition, relative abundances, diets, and habitat uses are critical for understanding how rodent species may coexist in a given environment and the relative impacts that each rodent species may have upon native and non-native biota. The following questions, hypotheses, and findings from my study relating to rodent species composition, relative abundances, diets, habitat uses, fruit removal, and seed fates, are summarized below.

Question I: How pervasive are rats and mice in Hawaiian mesic forests? What are their distributions, habitat uses, and seasonal fluctuations?

Hypothesis 1: *The abundance of coexisting rodent species is highest for the dominant rodent, the black rat, second highest for mice, and lowest for Pacific rats.*

Findings: This hypothesis was supported. The black rat (7.1 indiv./ha) was the most abundant rodent at all three sites when averaged across all sampling periods, whereas the house mouse (3.7 indiv./ha) was second highest, and the lowest abundance was for the Pacific rat (0.3 indiv./ha; Chapter 2). The period that tended to have the highest black rat abundance was April-May and October-December; there did not appear to be distinct months where Pacific rat and mouse abundances were consistently elevated among sites, but within a site there were fluctuations across sampling months for each species' abundance. Although most studies do not report abundances of more than two introduced rodent species, there are a few studies that have found similar patterns as my study for insular forest habitats (Russell and Clout 2004; Harper 2006; Harper and Cabrera 2010), including those in Hawaii (Tamarin and Malecha 1971; Sugihara 1997; Lindsey et al. 1999). However, some studies in Hawaii have found different patterns of relative abundances for coexisting rodents, such as in high elevation studies where mice are more abundant than black rats (Amarasekare 1994; Banko et al. 2002), or at low elevation wet forest where abundances of Pacific rats are slightly higher or similar to black rats (Beard and Pitt 2006).

Hypothesis 2: *The location of each rodent species' nest/den site, and activity, differs among rodent species: Black rats den and are more active in trees than on the ground, whereas Pacific rats and mice den in, and are more active on, the ground than in trees.* **Findings:** This hypothesis was supported for my studies in the Waianae Mountains. As evidenced by spool-and-line tracking, all of the monitored Pacific rats and all but one of the monitored mice had dens belowground. Additionally from radio-tracking, all five of the radio-collared Pacific rats denned belowground. Black rats commonly denned above- and belowground, as evidenced by radio-tracking and spool-and-line tracking. For the 24 black rats radio-collared and followed at the two sites (KHI and MAK) in my study, ca. 42% had den sites both in the ground and in trees; whereas ca. 43% denned only in trees and ca. 15% denned only in the ground. Using spool-and-line tracking, 25-59% of the monitored black rats had den sites in the trees. In contrast to my findings from Oahu, most studies elsewhere found that black rats den only in trees (Dowding and Murphy 1994; Hooker and Innes 1995; Lindsey et al. 1999). Studies of the locations of den sites for Pacific rats and mice are much less common than those for black rats; however, Lindsey et al. (1999) found that all three Pacific rats in Hawaiian wet forest had belowground den sites. There were no studies found describing the locations of den sites for the house mouse.

The Pacific rat and house mouse used mainly ground surface habitat when monitored by spool-and-line tracking; 70% and 69% of the movements recorded for Pacific rats and mice, respectively, were on the surface. In contrast, 32% of the movements for black rats were on the surface, and the majority (64%) of black rat movement was recorded aboveground at heights of ca. 2.8 m. These findings are similar to those of Hooker and Innes (1995) in New Zealand forest where black rats were primarily arboreal and 73% of the radio-tracking locations were > 2 m aboveground. Lindsey et al. (1999) found that 43 of 44 of the rats they trapped in trees were black rats, and only one Pacific rat was caught in a tree in their 2 year study. Hoare et al. (2007) concluded that Pacific rats on a New Zealand off-shore island were most active on the surface (85% of recorded movements) relative to aboveground (10%). There have been no studies that I know of that track mice to determine their uses of surface, above-, and belowground habitat; however, most studies attempt to trap mice only on the ground surface (Dickman 1992; King et al. 1996; Sugihara et al. 1997; Arthur et al. 2005; Ruscoe and Murphy 2005; Harper 2010).

<u>Question II:</u> What are the diets of rats and mice in Hawaiian mesic forest?

Hypothesis 3: *The diets of introduced rodents differ by species in the following pattern: diets of black rats are dominated by plant material, those of mice by animals, and those of Pacific rats by nearly equal proportions of plant and animal material.*

Findings: This hypothesis was supported for my study at Kahanahaiki (KHI) as evidenced by stomach content analysis. Black rat stomach contents were dominated by plant material (81% relative abundance), and secondarily by arthropods (14%). Mouse stomach contents were dominated by arthropods (57%) rather than plants (36%). The diet of the Pacific rat fell between that of the black rat and the house mouse, as evidenced by Pacific rat stomachs containing 60% plants and 38% arthropods (Chapter 3). These findings are similar to those of Sugihara (1997) from wet forest, where black rats ate more fruits, seeds, and other vegetative material than did Pacific rats. However, several studies in New Zealand have shown that the dominant food type in black rat stomachs is arthropods, particularly weta (Innes 1979; Gales 1982; Miller and Miller 1995). In contrast to these New Zealand studies, Beard and Pitt (2006) from lowland wet forest in Hawaii found that black rat and Pacific rat stomachs contained 99% plant material. Pacific rat diets on 37 Tokelau islands were dominated by plant material (88%; mostly coconut), and contained just 4% arthropods (Mosby et al. 1973). Following a review of studies from Southern Atlantic islands that have been invaded by mice, Angel et al. (2008) concluded that arthropods are the dominant food type in mouse diets. However, the one other Hawaiian study that examined stomach contents of mice occurred in high-elevation shrubland and the mouse diets were plant-dominated (63%; particularly seeds and vegetative material), and contained just 33% arthropods (Cole et al. 2000). It is important to note that the types of food consumed by rodents largely depend upon the types that are available when sampling occurs, as well as a suite of other factors including the richness of rodent species, the chemical and nutritional content of available foods, habitat characteristics, and seasonality (Clark 1982; Harper 2006).

The long-term (lifetime) diets of each of the three introduced rodent species were determined from individuals sampled at KHI through stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$) of bone marrow. Although the stomach content analysis revealed that Pacific rats had an intermediate diet between the more carnivorous house mouse and the more vegetarian black rat, the lifetime diet of the Pacific rat, as revealed by stable isotopes, was nearly indistinguishable from the lifetime diet of the house mouse. There are several possible explanations for the difference between the stomach content and stable isotope findings for Pacific rats, including the similar amounts of caterpillar and/or grass seeds consumed by both mice and Pacific rats, similar foraging microsites for mice and Pacific rats (Chapter 2; Stapp 2002), the small sample size of Pacific rat stomachs analyzed (N = 12), or the assimilation rates of the different types of prey among rodent species (Gannes et al. 1997).

<u>Question III:</u> Which of the dominant species in Hawaiian mesic forest have their diaspores (fruits + seeds) removed from the forest floor by rats and mice? What are the fates of such rodent-handled seeds?

Hypothesis 4: *Vulnerability to diaspore harvest and seed predation by rats is more strongly associated with diaspore size (mass and greatest diameter) than other characteristics.*

Findings: This hypothesis was not supported. Diaspore (fruit + seed) and seed size often influences whether a seed is found by a rodent, removed or consumed in place, and destroyed or discarded intact (Cowan 1992; Izhaki et al. 1995; Williams et al. 2000). For a number of reasons including those associated with optimal foraging (Smith and Reichman 1984), I expected that larger seeds would be harvested, consumed, and destroyed by rodents more commonly than smaller seeds were (Thompson 1987; Crawley 1992; Hulme 1998). Contradicting my expectation, I found that the largest diaspore with the largest seed of all species studied (*Aleurites moluccana*) was not harvested (i.e., 0% removal) from the forest floor, and when offered to black rats in captivity the fruit and seeds were rarely eaten (> 97% of fruit and seed mass was uneaten) and the seeds never destroyed. Similarly, the next two largest seeds examined (*Pouteria sandwicensis* and *Sapindus oahuensis*) were rarely consumed and most (> 85%) survived in captive feeding trials despite 88% of the *P. sandwicensis* diaspores harvested by black rats in the field. Therefore, the likelihood of diaspore harvest from the forest floor, and the likelihood for seed predation, did not appear to be size dependent (Chapter 4). Overall, the largest and smallest seeds tested in the field experiment (Chapter 4) had the highest survival when offered to black rats in captivity, whereas the intermediate sized seeds of both native and non-native species tended to have the lowest survival (Chapters 4 and 5). In a recent review of New Zealand studies, Grant-Hoffman and Barboza (2010) found that relatively small seeds were most commonly reported as eaten by introduced rats. In recent field trials in Hawaiian dry forest (Chimera and Drake, in revision), and in cloud forest on Lord Howe Island (Auld et al. 2010), diaspore and seed size did not appear to influence removal by introduced rodents.

Hypothesis 5: *Seed survival is inversely correlated with seed size, and the upper limit for survival is* ca. *2.5 mm.*

Findings: This hypothesis was not supported. When seeds of 25 of the most problematic invasive plant species were offered to wild black rats in captivity, rats consumed proportionally more seed mass of the smaller fruits and seeds than the larger ones; however fruit and seed size did not predict seed survival (Chapter 5). One possible explanation for the proportionally greater consumption of large fruits and seeds relative to smaller fruits and seeds by black rats may be related to the reduced time to satiation when large seeds are eaten (Janzen 1971). As described in the previous hypothesis, most of the intermediate-sized seeds that I offered to black rats tended to have higher predation (lower survival) relative to the largest and smallest seeds.

There are three ways in which a seed can be dispersed by black rats, and seed size is a critical factor in one of these types of dispersal (gut passage) but less important for the others (discarded seeds or chewed seeds). Because it is a common behavior of black rats to move food items upon collection, they can disperse seeds of a wide range of sizes if they do not destroy the seed or if a fraction of the seeds in a multi-seeded fruit are not destroyed. Similarly, chewed seeds can be dispersed by black rats as long as the chewed seed retains viability. Alternatively, seeds may be dispersed by gut passage if they are small enough to pass intact through the rat's digestive tract without losing viability. I found evidence for all three types of seed dispersal in my studies with black rats (Chapter 4, 5). The possibility of seed dispersal by black rats in Hawaii does not appear to be limited by seed size.

The upper size limit for seed survival following gut passage in black rats was ca. 2.4 mm in New Zealand captive-feeding trials (Williams et al. 2000). However, my findings for black rats in Hawaii revealed that the upper size limit for seed survival is 1.5-2.0 mm (Chapter 5), as evidenced by captive-feeding trials, using 25 invasive species and eight native Hawaiian species, and germination trials with seeds that were passed through the rat's gut (Chapter 4, 5). Additional trials with *Cyanea superba* (unpublished data) reveal that the seed size threshold separating gut passage from seed predation for black rats is ca. 1.5-1.7 mm; therefore, species with seeds that are consumed by black rats with seeds > 1.5 mm are more likely to be destroyed than seeds ≤ 1.5 mm. Basing such a threshold on seed mass is less useful than seed length for the tested species because the 2.1 mm seeds of *Schefflera actinophylla* weigh 0.2 mg and did not survive black rat consumption, whereas *Rubus rosifolius* seeds (1.5 mm length) survived black rat consumption despite the 0.5 mg larger seeds than those of *S. actinophylla*. Additional factors other than seed length and mass may also affect a seed's propensity to survive consumption by rats (e.g., seed coat characteristics), but these have yet to be studied.

Future research involving introduced rodent effects on island flora

Certain aspects of the seed fate of many species that black rats interact with have now been determined using captive feeding trials (ca. 85 species to date from my research), yet the majority of the species in Hawaii alone have not been tested and very few trials exist that measure species vulnerability (either plants or animals) to Pacific rats and the house mouse. Some data exist on the extent to which rodents affect seeds through pre-dispersal seed predation (e.g., *Psidium cattleianum, Diospyros* spp.; unpublished data), but it is largely unknown which of the rodent species is responsible for this; nor is much known about the extent to which species suffer pre-dispersal vs. post-dispersal seed predation. Almost certainly, the effects of introduced rodents are influenced by many features of their habitat, including the plant species with which they interact. Future study on seedling establishment and survival within microhabitats visited by rodents (e.g., husking stations, defecation sites) would help determine the ultimate fate of seeds that were discarded, partially chewed, or defecated by rodents.

The future research needs for improving our understanding and management of rodent impacts on islands could usefully focus on the degree to which seed predation and dispersal by each of the introduced rodents affects plant recruitment. Some of this research has begun at KHI, and we are finding that reducing the abundance of introduced rodents (mainly rats) reduces seed predation on native (*Diospyros* spp.) and endangered (*Cyanea superba*) species (unpublished data; Mosher et al. 2010). Additionally, rodent reduction at KHI appears to have stimulated seedling recruitment of *Diospyros* spp. relative to a nearby forest where rodents were not reduced (unpublished data). Rodent removal experiments where both experimental sites and nearby control sites are monitored simultaneously are necessary to provide resolution to the critical question that many of us commonly ask: To what extent are introduced rodents altering plant recruitment and community structure in Hawaii?

APPENDIX A. Densities (No. indiv./ha) of the 35 woody plant species with stems ≥ 1 cm dbh (measured at 1.3 m above ground) recorded in 10 15 x 15 m plots at Kahanahaiki, Oahu, in August 2008. An asterisk represents a non-native species. *Cyanea superba*, *Cyrtandra dentata*, and *Flueggea neowawraea* are federally endangered species, and *Pteralyxia macrocarpa* is a species of concern. Both the red and yellow varieties of *Psidium cattleianum* are represented at the site. Species ordering based on density.

Species	Family	Life form	Density (No./ha)
*Psidium cattleianum**	Myrtaceae	Tree	1640
Diospyros hillebrandii	Ebenaceae	Tree	631
Psydrax odorata	Rubiaceae	Tree	489
Sapindus oahuensis	Sapindaceae	Tree	324
*Schinus terebinthifolius**	Anacardiaceae	Tree	271
Psychotria mariniana	Rubiaceae	Tree	187
Charpentiera tomentosa	Amaranthaceae	Tree	147
Pouteria sandwicensis	Sapotaceae	Tree	142
Kadua affinis	Rubiaceae	Tree	142
*Aleurites moluccana**	Euphorbiaceae	Tree	129
Hibiscus arnottianus	Malvaceae	Tree	98
Antidesma platyphyllum	Euphorbiaceae	Tree	98
*Cordyline fruticosa**	Agavaceae	Shrub	71
Pisonia umbellifera	Nyctaginaceae	Tree	71
Psychotria hathewayi	Rubiaceae	Tree	49
Freycinetia arborea	Pandanaceae	Liana	44
Nestegis sandwicensis	Oleaceae	Tree	40
Pipturus albidus	Urticaceae	Tree	36
*Psidium guajava**	Myrtaceae	Tree	31
Diospyros sandwicensis	Ebenaceae	Tree	31
Coprosma foliosa	Rubiaceae	Shrub	22

Species	Family	Life form	Density (No./ha)
Pisonia brunoniana	Nyctaginaceae	Tree	22
Bobea sandwicensis	Rubiaceae	Tree	22
Xylosma hawaiiensis	Flacourtiaceae	Tree	22
Myrsine lessertiana	Myrsinaceae	Tree	18
Cyanea superba	Campanulaceae	Tree	18
Flueggea neowawraea	Euphorbiaceae	Tree	18
Morinda trimera	Rubiaceae	Tree	13
Pteralyxia macrocarpa	Apocynaceae	Tree	9
*Buddleia asiatica**	Buddleiaceae	Shrub	4
Rauvolfia sandwicensis	Apocynaceae	Tree	4
Cyrtandra dentata	Gesneriaceae	Shrub	4
*Grevillea robusta**	Proteaceae	Tree	4
Metrosideros polymorpha	Myrtaceae	Tree	4
*Syzygium cumini**	Myrtaceae	Tree	4

APPENDIX B. Mean ± SE seedling (individuals ≤ 50 cm tall) densities of woody species at Kahanahaiki, Oahu. An asterisk represents a non-native species. A total of 80 seedling plots (each 1 x 2 m) were sampled across 10 replicated permanent plots (each 15 x 15 m) in August 2009. Values shown below are N = 10 (where eight seedling plot measures were combined for each permanent plot).

Species	Family	Life form	Seedling density (No./m^2)
*Aleurites moluccana**	Euphorbiaceae	Tree	0.16 ± 0.14
Alyxia stellata	Apocynaceae	Shrub/liana	0.49 ± 0.37
Antidesma platyphyllum	Euphorbiaceae	Tree	0.01 ± 0.01
*Clidemia hirta**	Melastomataceae	Shrub	0.21 ± 0.08
Coprosma foliosa	Rubiaceae	Shrub	0.02 ± 0.02
Diospyros hillebrandii	Ebenaceae	Tree	0.03 ± 0.02
Diospyros sandwicensis	Ebenaceae	Tree	0.01 ± 0.01
Kadua affinis	Rubiaceae	Tree	0.01 ± 0.01
Nestegis sandwicensis	Oleaceae	Tree	0.03 ± 0.03
Pisonia brunoniana	Nyctaginaceae	Tree	0.02 ± 0.01
Pouteria sandwicensis	Sapotaceae	Tree	0.01 ± 0.01
*Psidium cattleianum**	Myrtaceae	Tree	0.46 ± 0.30
Psydrax odorata	Rubiaceae	Tree	0.01 ± 0.01
Sapindus oahuensis	Sapindaceae	Tree	0.01 ± 0.01
*Schinus terebinthifolius**	Anacardiaceae	Tree	0.04 ± 0.03

APPENDIX C. Mean flower, fruit, and seed rain (No./m^2/day) measured at Kahanahaiki, Oahu, from 20 June 2007-6 July 2010. Each value represents the average of 72 sampling periods (separated by ca. 2 weeks) during the three-year monitoring. At each sampling period, flowers, fruits, and seeds were identified in 48 seed buckets that were placed in 12 15 x 15 m plots (four buckets per plot). Several species' reproductive material was too small to identify in the field and therefore was not considered (e.g., most seeds < 1.5 mm unless fruit was present).

Species[a]	Family	Flowers (No./m^2/d)	Fruits (No./m^2/d)	Seeds (No./m^2/d)
*Aleurites moluccana**	Euphorbiaceae	5.08	< 0.01	< 0.01
Alyxia stellata	Apocynaceae	0.01	< 0.01	< 0.01
Antidesma platyphyllum	Euphorbiaceae	0	< 0.01	< 0.01
*Buddleia asiatica**	Buddleiaceae	0.02	0.59	0
Canavalia galeata	Fabaceae	< 0.01	0	0
Carex hawaiiensis	Cyperaceae	0	< 0.01	< 0.01
Charpentiera tomentosa	Amaranthaceae	< 0.01	0	0
*Clidemia hirta**	Melastomataceae	0.01	0.04	0.42
Coprosma foliosa	Rubiaceae	0	0	< 0.01
*Cordyline fruticosa**	Agavaceae	< 0.01	< 0.01	< 0.01
Diospyros spp.	Ebenaceae	0.32	0.03	< 0.01
Dodonaea viscosa	Sapindaceae	0	< 0.01	< 0.01
*Grevillea robusta**	Proteaceae	0.05	< 0.01	0.01
Hibiscus arnottianus	Malvaceae	< 0.01	0	0
Kadua affinis	Rubiaceae	0.02	0	0
Korthalsella degeneri	Viscaceae	0	1.09	1.09
Metrosideros polymorpha	Myrtaceae	0.01	0.05	0
Myrsine lessertiana	Myrsinaceae	< 0.01	0	0
Nestegis sandwicensis	Oleaceae	0	< 0.01	< 0.01
*Oplismenus hirtellus**	Poaceae	0	0.02	0.02

Species[a]	Family	Flowers (No./m^2/d)	Fruits (No./m^2/d)	Seeds (No./m^2/d)
*Paspalum conjugatum**	Poaceae	0	< 0.01	< 0.01
Passiflora spp.*	Passifloraceae	0	0	< 0.01
Pipturus albidus	Urticaceae	0.02	< 0.01	0
Pisonia spp.	Nyctaginaceae	< 0.01	< 0.01	< 0.01
Pouteria sandwicensis	Sapotaceae	0.26	< 0.01	< 0.01
*Psidium cattleianum**	Myrtaceae	2.15	0.43	6.14
*Psidium guajava**	Myrtaceae	0.01	< 0.01	< 0.01
Psychotria spp.	Rubiaceae	< 0.01	< 0.01	< 0.01
Psydrax odorata	Rubiaceae	0.02	0.04	0.05
*Rubus rosifolius**	Rosaceae	< 0.01	0	0.10
Sapindus oahuensis	Sapindaceae	0.22	0.03	0.03
*Schinus terebinthifolius**	Anacardiaceae	5.39	2.58	2.58
Xylosma hawaiiensis	Flacourtiaceae	0.05	0	0
Unknown		0.05	0	< 0.01

[a] Candidate species for the following identified genera include: 1) *Diospyros*: *D. hillebrandii*, *D. sandwicensis*, 2) *Passiflora*: *P. edulis*, *P. suberosa*, 3) *Psychotria*: *P. hathewayi*, *P. mariniana*.

APPENDIX D. Frequency of food types in scat from mongoose (*Herpestes javanicus*; N = 31) and cat (*Felis catus*; N = 13) collected opportunistically by Steve Mosher at Kahanahaiki, Oahu, during 2005-2007. Samples were kept frozen until extraction. Extracted contents were passed through a 0.4 mm mesh sieve, followed by microscopic analysis (10x-20x magnification) using methods described for rodent stomach contents in Chapter 3.

	Rat	Mouse	Reptile	Plant	Arthropod	Mollusk	Bird
Mongoose	26%	77%	87%	84%	97%	10%	26%
Cat	100%	100%	31%	92%	100%	0%	23%

APPENDIX E. Captive feeding trials involving rodent species (N = 11 black rats or N = 2 house mice) offered one of two treatments: 1) a *Deroceras laeva* slug, or 2) a *Deroceras laeva* slug simultaneously with ca. 2 g of rodent chow. Each trial lasted 24 hours. All three rats that were offered rodent chow and a slug ate all the rodent chow and at least part of the slug. Cage dimensions and capture locations of the rodents used in these trials were identical to those described in Chapter 5. All slugs were captured in the Waianae Mountains, Oahu.

Rodent species	Treatment	Killed slug?	Ate slug?	Approx. amount of slug eaten (%)
Black rat	Chow + slug	Yes	Yes	100
Black rat	Chow + slug	Yes	Yes	75
Black rat	Chow + slug	Yes	Yes	75
Black rat	Slug	Yes	Yes	20
Black rat	Slug	Yes	Yes	100
Black rat	Slug	Yes	Yes	100
Black rat	Slug	Yes	Yes	15
Black rat	Slug	Yes	Yes	85
Black rat	Slug	Yes	Yes	100
Black rat	Slug	Yes	Yes	95
Black rat	Slug	Yes	Yes	80
House mouse	Slug	No	No	0
House mouse	Slug	No	No	0

APPENDIX F. Captive feeding trials involving rodent species (N = 11 black rats or N = 2 house mice) offered one *Limax maximus* slug. Each trial lasted 24 hours. Cage dimensions and capture locations of the rodents used in these trials were identical to those described in Chapter 5. All slugs were captured in the Waianae Mountains, Oahu.

Rodent species	Treatment	Killed slug?	Ate slug?	Approx. amount of slug eaten (%)
Black rat	Slug	Yes	Yes	95
Black rat	Slug	Yes	Yes	100
Black rat	Slug	Yes	Yes	85
Black rat	Slug	Yes	No	0
Black rat	Slug	Yes	No	80
Black rat	Slug	Yes	No	0
Black rat	Slug	Yes	No	0
Black rat	Slug	Yes	No	0
Black rat	Slug	Yes	Yes	7
Black rat	Slug	Yes	No	0
Black rat	Slug	Yes	Yes	98
House mouse	Slug	No	No	0
House mouse	Slug	No	No	0

APPENDIX G. Estimated ages of black rats at Kahanahaiki, Oahu. Ages were calculated by adding three months (i.e., ca. time to maturity) to the period from first capture to death by kill-traps. Deaths occurred May 5-15, 2009, during the trap-out. The distance moved, and weight change (+ or – if gained or lost, respectively), were calculated by the difference from trapping locations and mass when first caught and at death. A distance of zero indicates the rat was captured (and killed) in the same location as initially captured.

Ear tag #	Sex	Date of first capture (m-d-y)	Minimum age at death (months)	Distance moved (m)	Weight change (g)
831	Male	02-12-09	6	0	+1
630	Female	08-29-08	11	40	+3
858	Male	04-09-09	4	25	+11
698	Male	10-10-08	10	25	-14
866	Male	04-12-09	4	25	+7
653	Male	08-31-08	11	150	+47
377	Male	01-04-08	19	200	+72
829	Male	02-12-09	6	25	+3
356	Male	01-04-08	19	10	+60
644	Female	08-29-08	11	0	-4
693	Male	10-10-08	10	0	+50
447	Male	02-28-08	18	15	+53
408	Female	01-04-08	19	50	+36
863	Male	04-10-09	4	0	+3
531	Female	04-24-08	16	175	+21
855	Male	04-09-09	4	20	+7
379	Female	01-04-08	19	25	+54
786	Female	12-07-08	6	0	+28

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