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).

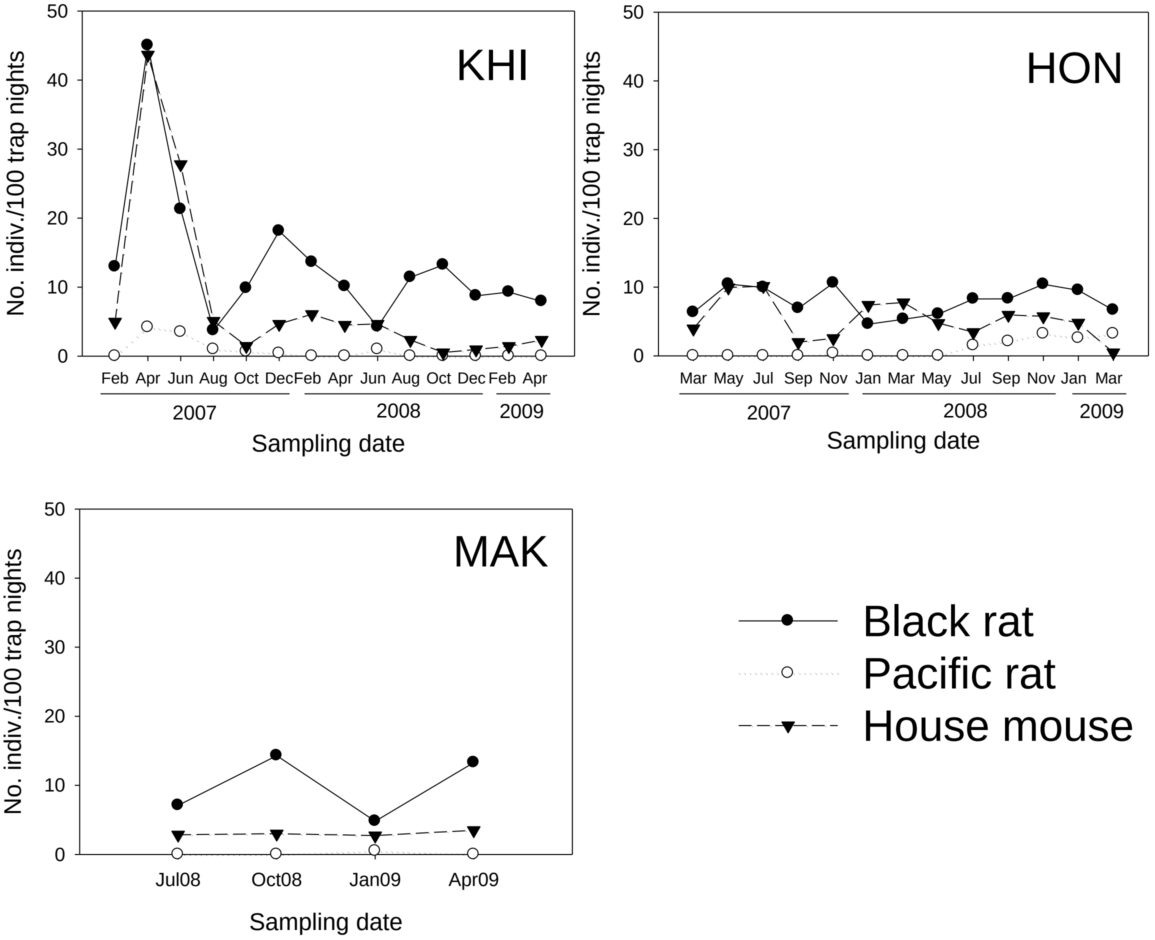

Figure 4. Abundances (No. indiv./100 trap nights) of the three rodent species at the three forest sites (KHI = Kahanahaiki, HON = Honouliuli, MAK = Makaha) in the Waianae Mountains, Oahu. All sampling was by live-trapping.

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.

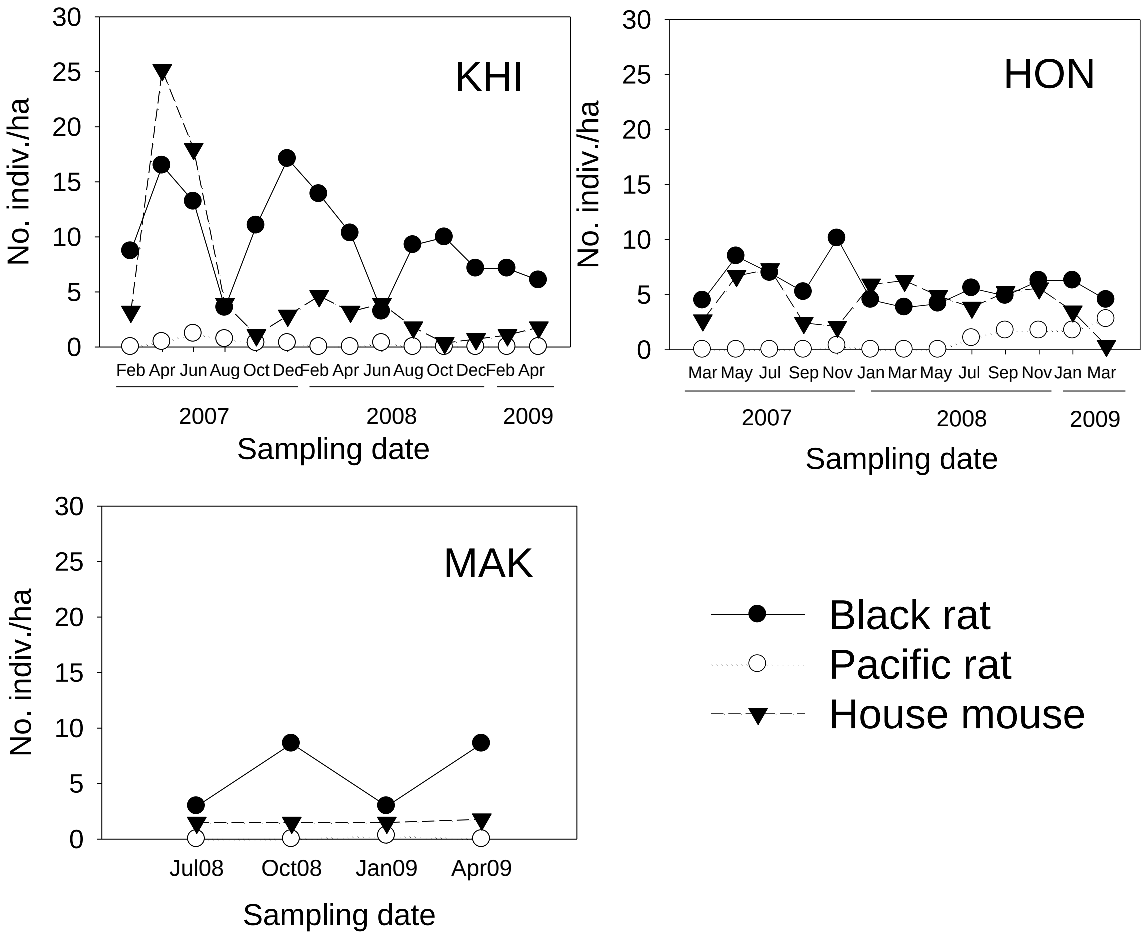

Figure 5. Densities (No. indiv./ha) of the three rodent species at the three forest sites (KHI = Kahanahaiki, HON = Honouliuli, MAK = Makaha) in the Waianae Mountains, Oahu. All sampling was by live-trapping.

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.

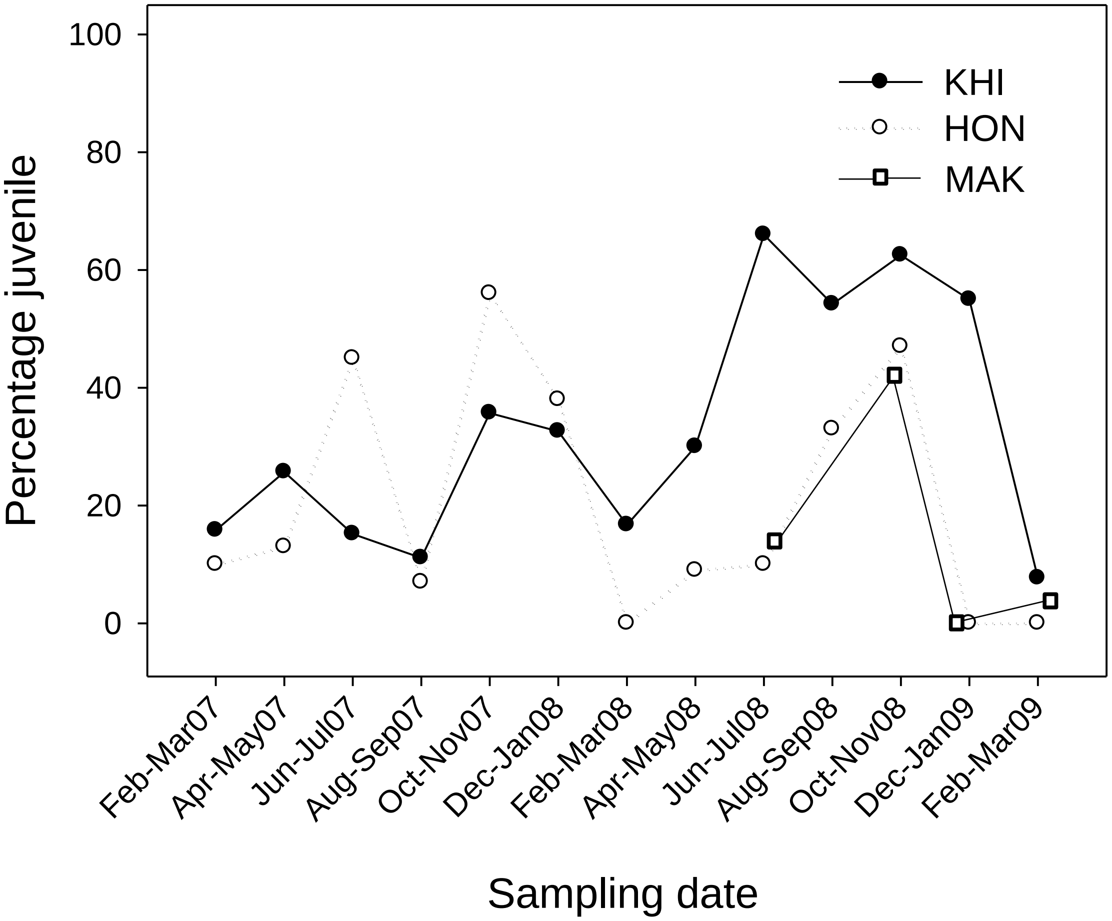

Figure 6. Percentage of captured black rats that were juveniles at the three study sites in the Waianae Mountains, Oahu, Hawaii. The MAK site had four sampling periods during July 2008-April 2009.

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.

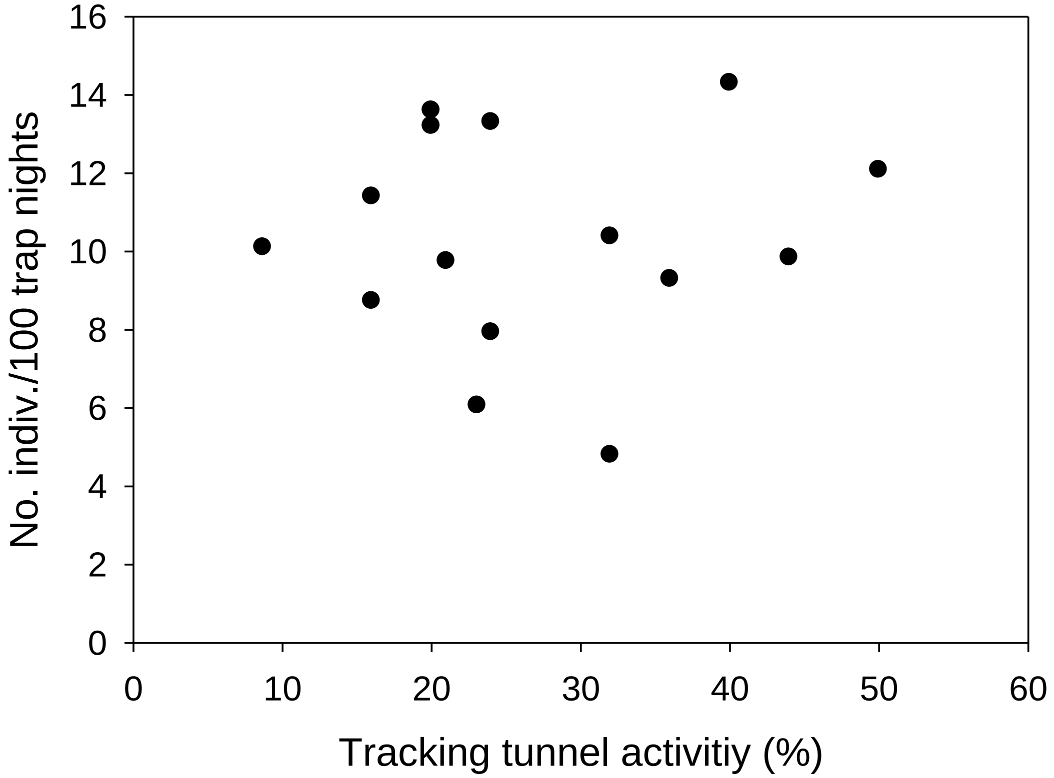

Figure 8. Scatterplot showing the rat (black rat + Pacific rat) observations (activity) in tracking tunnels that were sampled within one week of the rat abundance (No. indiv./100 trap nights) estimates from live-trapping at the three sites (KHI, HON, and MAK). There were no significant relationships 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**

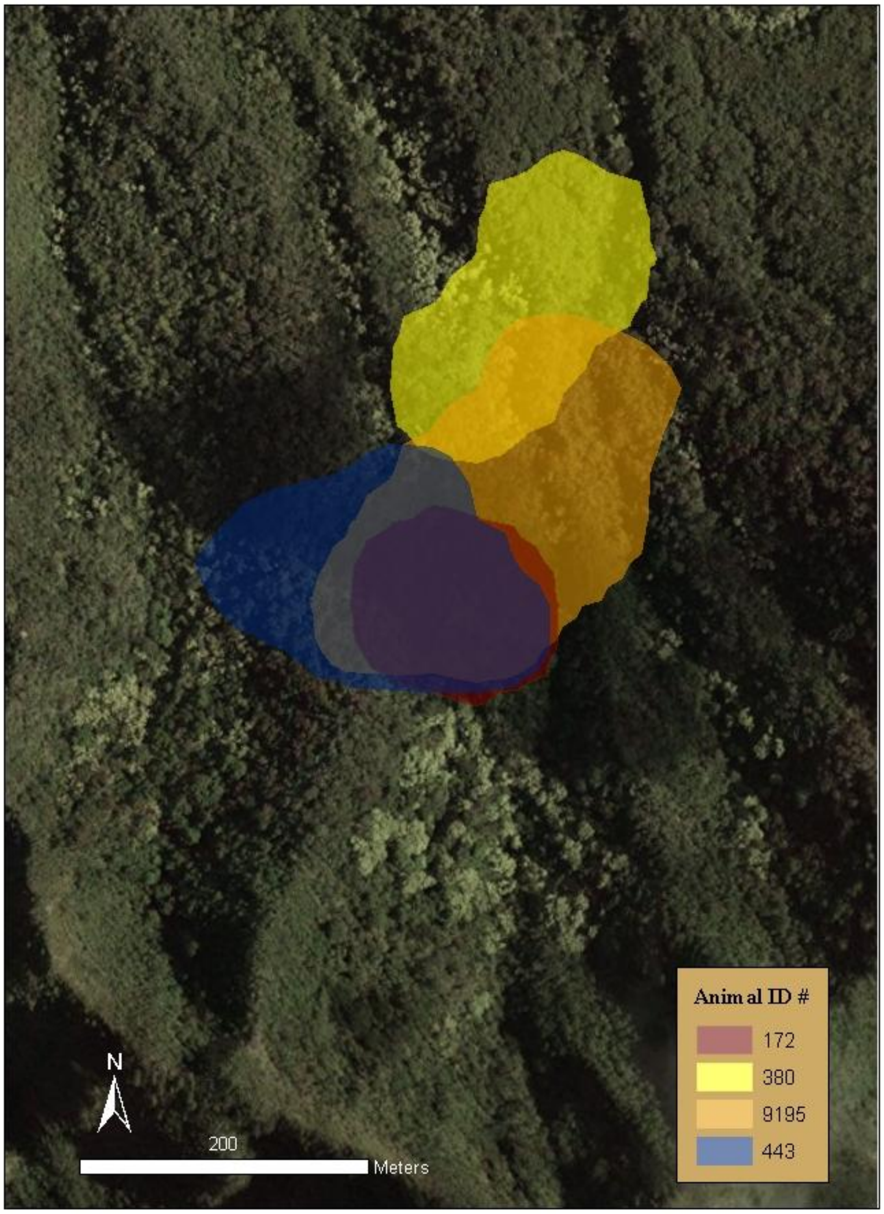

Figure 9. Home-range polygons (95% kernel) for four black rats at MAK, Waianae Mountains, Oahu. Rat 172 and 9195 were male, and 380 and 443 were female.

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 discontinued
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.

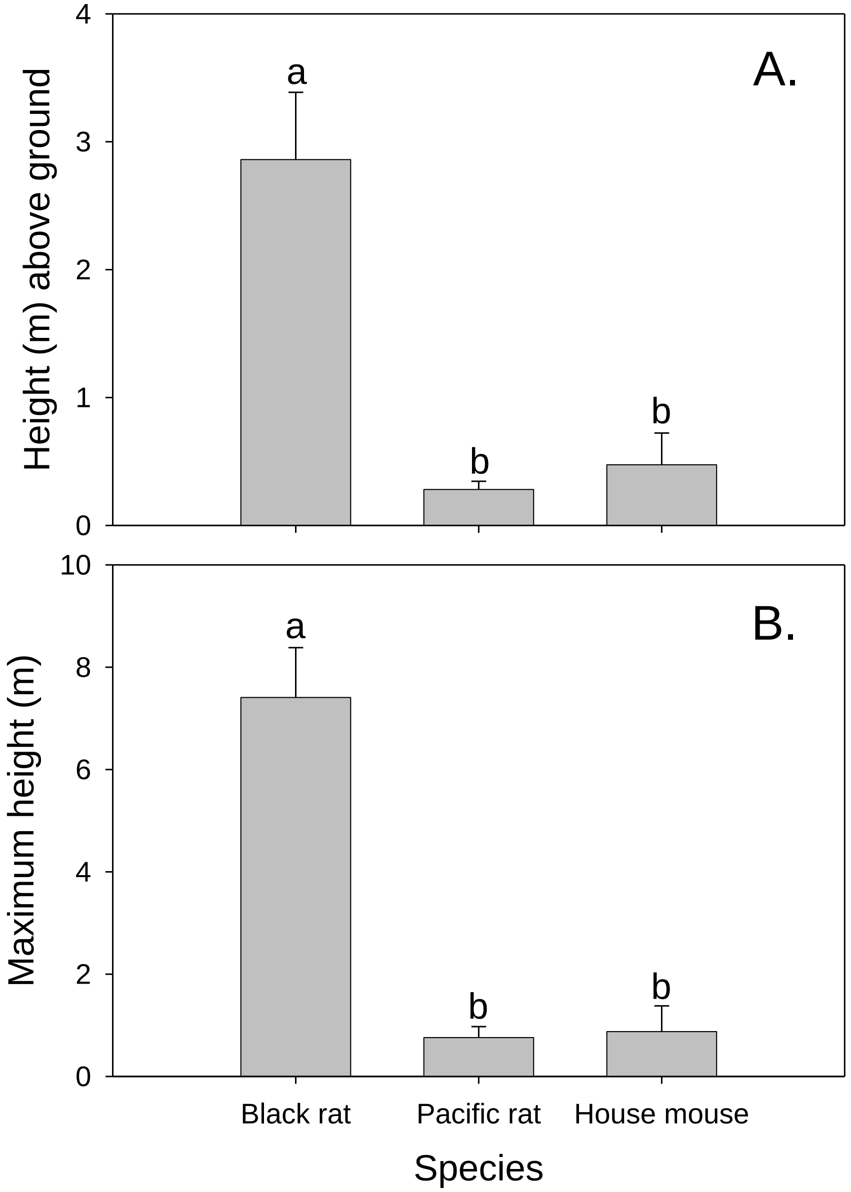

Figure 10. Mean ± SE average (A.) and maximum (B.) height (m) observed above ground after thread bobbins were attached to rodent species at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included because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

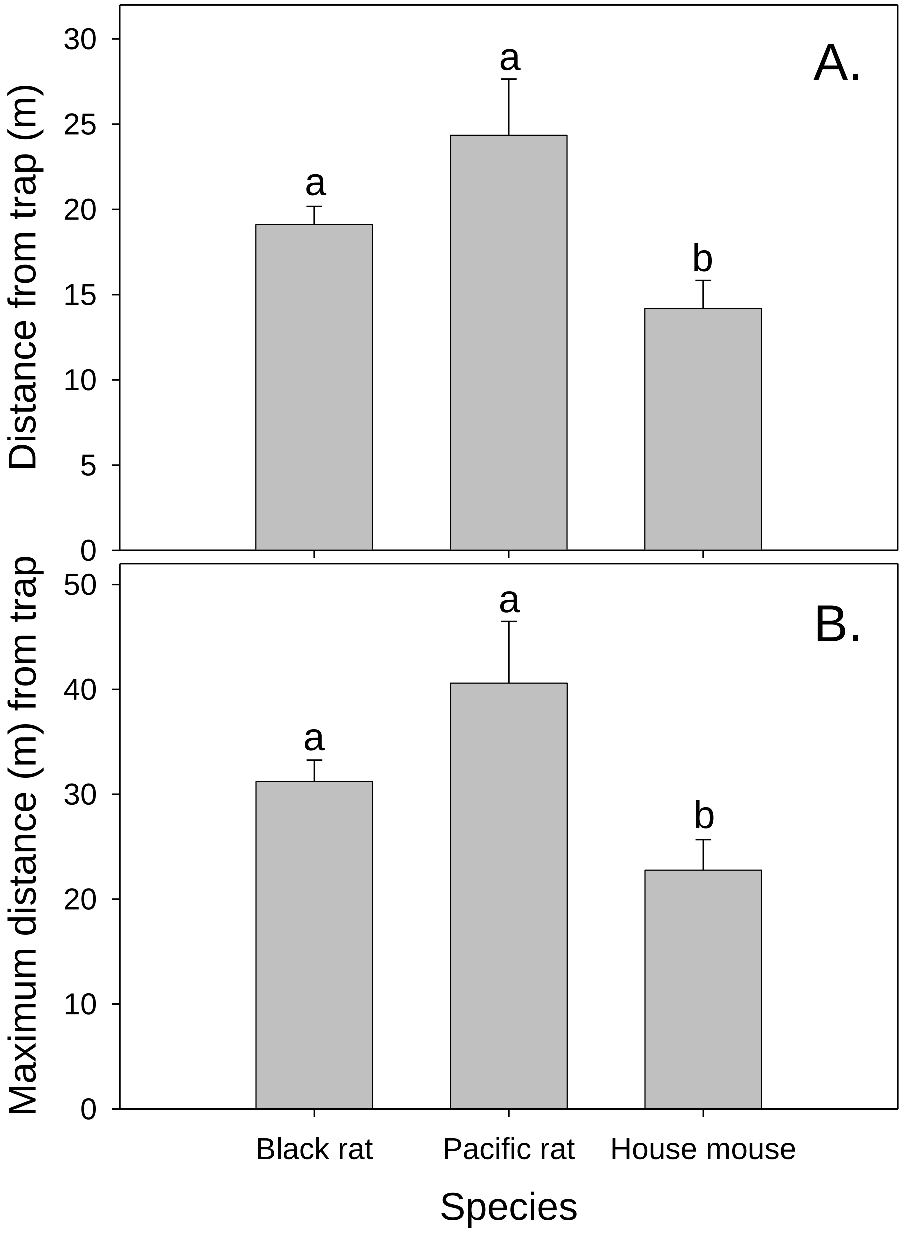

Figure 11. Mean ± SE average (A.) and maximum (B.) distance (m) from trap (point of capture) following bobbin attachment to rodent species at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included 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).

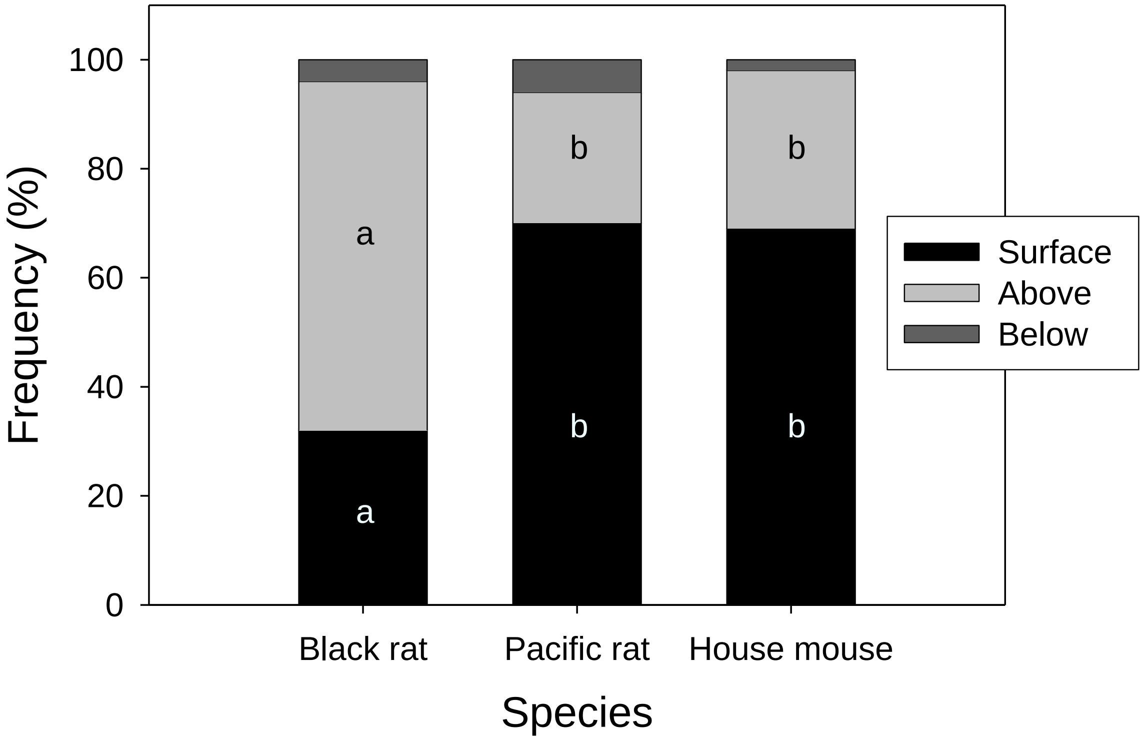

Figure 12. Mean ± SE frequency of each rodent in the three environments (surface-, above-, and belowground) when observed by spool-and-line tracking at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not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

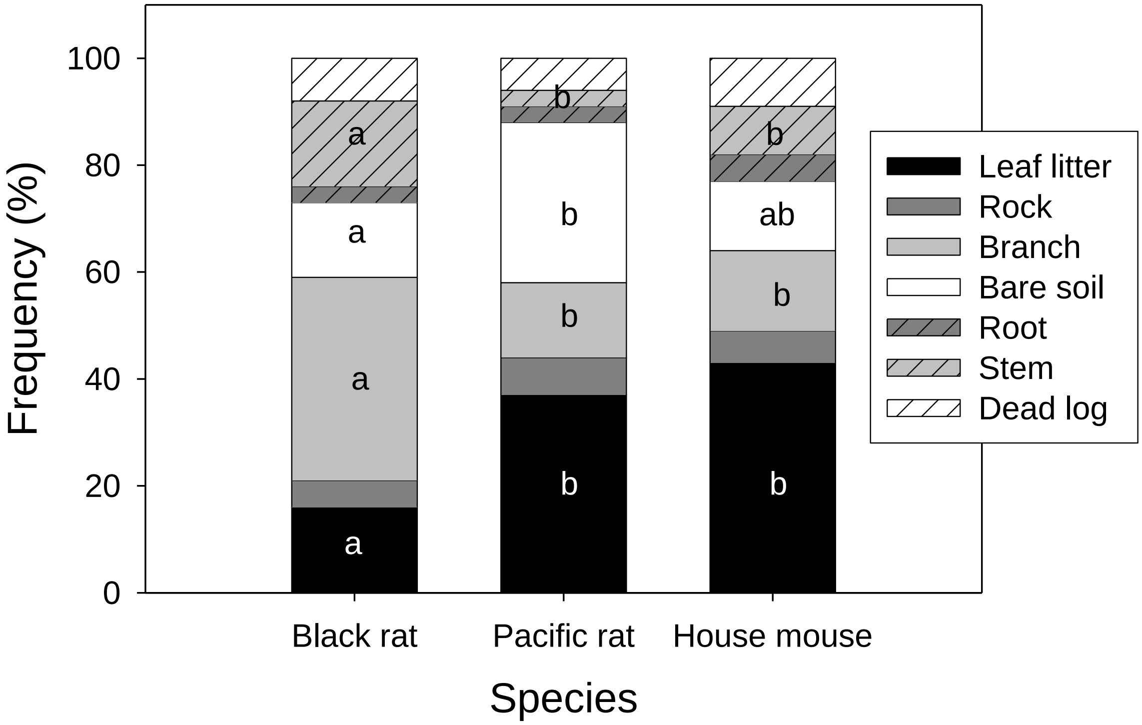

Figure 13. Mean ± SE frequency recorded on substrate types for each rodent at KHI and HON study sites in the Waianae Mountains, Oahu. N = 48 for black rat, N = 10 for Pacific rat, and N = 17 for house mouse. The MAK site was not included because only black rats were measured there. Different letters 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).

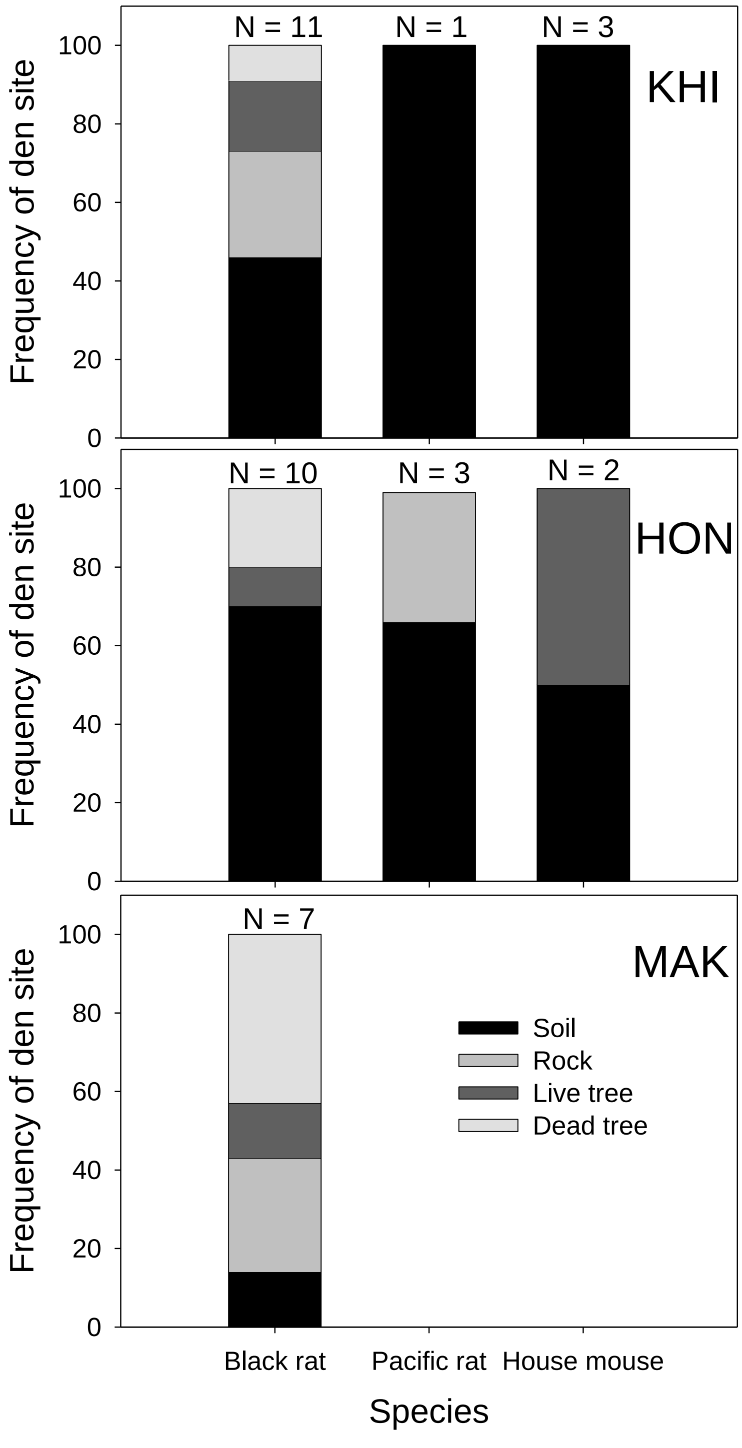

Figure 14. Mean ± SE frequency (%) of den sites occupied by each of the rodent species, as evidenced by the terminus of thread bobbins, at the three study sites in the Waianae Mountains, Oahu. Sample sizes are given above each species. Bobbins were only attached to black rats at MAK.

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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