

Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii?

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

exposure. The combined field and laboratory findings indicate that many interactions between black rats and seeds of native and non-native plants may result in dispersal. Rats are likely to be affecting plant communities through both seed predation and dispersal.

Keywords Black rat · Captive feeding trials · Frugivory · Islands · Rodent · Seed size

Introduction

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

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Meyer and Butaud 2009; Traveset et al. 2009; Towns 2009).

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

The Hawaiian Islands, like many others, lost the majority of their avifauna following human colonization (Steadman 1995) and many of those birds were frugivores and seed dispersers (James and Olson 1991; Olson and James 1991). It is unknown if introduced rats disperse seeds of Hawaiian plants and whether, by doing so, they have replaced some of the functions of the extinct native seed dispersers. The first rats (Pacific rats) in the Hawaiian Islands were introduced by the first human colonists approximately 1,000 years ago, and for the next ca. 800 years Pacific rats were the only rats to consume native biota (Athens et al. 2002). Following European arrival in the late 1700s, three additional rodents were introduced, including the black rat, the Norway rat, and the house mouse (Tomich 1986). In contemporary Hawaii, all four rodents may coexist in a given habitat, though Norway rats rarely occur in forests. The black rat appears to be the most common rat in forests and it is distributed from sea level to nearly 3,000 m (Amarasekare 1994; Lindsey et al. 1999; Meyer and Shiels 2009). Black rats and Pacific rats

are significant predators of numerous native species in Hawaii, including rare and endangered birds (VanderWerf 2001), snails (Hadfield et al. 1993), arthropods (Cole et al. 2000) and plants (Athens et al. 2002; Pérez et al. 2008).

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

Materials and methods

Field site

This research occurred at Kahanahaiki Management Unit (21° 32' N, 158° 11' W), a 36 ha segment of mesic forest in highly dissected terrain (500–660 m a.s.l.; Gagné and Cuddihy 1999) in the northern Waianae Mountains, on the island of Oahu, Hawaii. Kahanahaiki is managed for native species preservation by the US Army, and the forest was fenced in 1996 to exclude feral goats and pigs. Daily air temperature at the site ranges from 16 to 24°C

(A. Shiels, unpublished data) and monthly rainfall varies from 50 to 170 mm (cited in Joe and Daehler 2008). A recent plant inventory at the site documented at least 35 tree species (A. Shiels, unpublished data). We studied 12 of the most common woody plants, including eight native and four non-native species (trees, shrubs, and lianas; Table 1). Botanical nomenclature follows Wagner et al. (1999) with recent updates for two species (Middleton 2002; Terrell et al. 2005). The five most common trees at the study site include the non-native *Psidium cattleianum* and *Schinus terebinthifolius*, and the native *Diospyros hillebrandii*, *Psydrax odorata*, and *Sapindus oahuensis* (Table 1). The two most common shrub species are the non-native *Clidemia hirta* and the native *Alyxia stellata* (Table 1). Plant species are hereafter referred to by genus.

Two species of rat, the black rat (133 ± 3 g; mean \pm SE; $n = 92$ adults) and Pacific rat (47 ± 2 g; $n = 6$ adults), are present at Kahanahaiki (Meyer and Shiels 2009). Our average estimated relative abundance measures using bi-monthly mark-and-recapture sampling over 15 months during 2007–2008 were 17 rats/100 trap nights for black rats and 1 rat/100 trap nights for Pacific rats. No

Norway rats were captured at the study site and the house mouse (10 ± 1 g; $n = 26$) was captured at ca. 6 mice/100 trap nights.

Field trials

Each of the 12 most abundant woody species at Kahanahaiki (Table 1) were tested for their vulnerability to rats by placing fruits in one of four enclosure treatments on the forest floor: (1) no-vertebrate-access, which consisted of a wire metal mesh (1.2 cm aperture) open-bottom cage ($30 \times 30 \times 30$ cm; length \times width \times height) that excluded all potential vertebrate seed predators and dispersers (e.g., rodents, cats, birds, mongoose (*Herpestes javanicus*)) and acted as the control to compare subsequent treatments, (2) small-vertebrate-access, which had the same dimensions as the no-vertebrate-access but had an 8×8 cm opening on each side that allowed small vertebrates such as rodents to access the interior but excluded larger vertebrates (e.g., cats, most birds), (3) open ground, where all vertebrates were able to freely access the station, and (4) open-cage-control, which had three sides of mesh and allowed all vertebrates access; this tested the influence of the caging material on fruit

Table 1 Characteristics of the 12 fleshy-fruited woody plants (values expressed as mean (SE)) used in field trials and captive feeding trials

Species ^a	Family	Life form	Fruit length (mm) ^b	Fruit mass (mg)	Number of seeds per fruit	Seed mass (mg)	Seed length (mm)
Native							
<i>Alyxia stellata</i>	Apocynaceae	Shrub, liana	14.9 (0.4)	983 (38)	1.0 (0.0)	459 (36)	12.9 (0.6)
<i>Coprosma foliosa</i>	Rubiaceae	Shrub	9.3 (0.3)	352 (24)	2.0 (0.0)	42 (3)	6.2 (0.1)
<i>Diospyros hillebrandii</i>	Ebenaceae	Tree	21.3 (0.4)	2,567 (188)	2.7 (0.2)	715 (43)	17.7 (0.7)
<i>Kadua affinis</i>	Rubiaceae	Tree	7.1 (0.3)	164 (25)	9.8 (0.7)	0.7 (0.1)	1.2 (0.1)
<i>Nestegis sandwicensis</i>	Oleaceae	Tree	16.1 (0.4)	1,361 (39)	1.0 (0.0)	604 (33)	15.7 (0.4)
<i>Pouteria sandwicensis</i>	Sapotaceae	Tree	34.2 (0.9)	16,050 (1,910)	2.6 (0.5)	1,787 (955)	17.9 (0.4)
<i>Psydrax odorata</i>	Rubiaceae	Tree	8.3 (0.5)	255 (32)	2.0 (0.0)	93 (20)	6.6 (0.7)
<i>Sapindus oahuensis</i>	Sapindaceae	Tree	29.0 (1.0)	5,420 (440)	1.0 (0.0)	1,509 (90)	18.0 (0.4)
Non-native							
<i>Aleurites moluccana</i>	Euphorbiaceae	Tree	46.7 (1.9)	46,855 (2,371)	1.4 (0.1)	8,995 (542)	30.3 (0.5)
<i>Clidemia hirta</i>	Melastomataceae	Shrub	6.9 (0.3)	214 (21)	360 (57)	<0.1	0.5 (0.0)
<i>Psidium cattleianum</i>	Myrtaceae	Tree	31.3 (0.9)	7,516 (562)	6.9 (0.8)	51 (4)	5.2 (1.6)
<i>Schinus terebinthifolius</i>	Anacardiaceae	Tree	4.7 (0.2)	33 (5)	1.0 (0.0)	5.9 (0.0)	3.6 (0.1)

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

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

removal. Invertebrates were able to access all treatments. Three transects, each 310 m long and at least 30 m distant from the nearest adjacent transect, were established. Along each transect, eight replicates of each of the four treatments were positioned at 10 m intervals. Treatments were assigned randomly with the condition that no more than two of the same treatment could occupy consecutive stations. Each mesh enclosure was pushed into the ground ca. 1 cm and held in place using 8-cm-long turf staples. Each plant species was tested individually, in a single trial run, along one of the three transects, such that each species occupied 32 treatment stations (4 treatments \times 8 replicates). To reduce bias from the influence of previous trials within a transect, each fruit trial was separated by at least 1 month since the previous trial ended. Placing fruits systematically along transects was favored over placement solely beneath adult conspecifics because the limited and clumped distribution of adult plants of some species would likely have restricted trials to areas within a single rat's home-range (A. Shiels, unpublished data).

To determine the animal responsible for fruit removal, motion-sensing cameras (Bushnell Sentry

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

Ripe fruits for each of the 12 species were collected from 3 to 12 individuals or from the ground below conspecific individuals if they had fallen within 24 h. Large fruits (>10 mm along longest axis; seven species; Table 1) were placed within each treatment singly, while small fruits (<10 mm along longest axis; five species; Table 1) were placed as a cluster of up to three. Trials were held from July 2007 to January 2009 and scheduled to coincide with the fruiting season of each species. For each trial, fruits were checked for their presence at each station 24 h after beginning the trial, and then subsequently every 1–7 days. The duration of each trial was species-specific (range = 6–43 days; Table 2) and was limited by natural decomposition (rotting and mold) of the pericarp (Hoch and Adler 1997). For each species

Table 2 Mean (SE) percentage of fruits remaining at the end of each trial for enclosure treatments at Kahanahaiki forest, northwest Oahu, Hawaii

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

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

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

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

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

the percentage of fruit remaining in each treatment was compared using a Kruskal–Wallis test (SPSS 1998) where significance was based on $P < 0.05$. When significant differences among treatments were present for a given species, a second Kruskal–Wallis test identified significant differences among the three vertebrate-accessible treatments.

Captive feeding trials

Adult black rats were captured from wild populations in the Waianae Mountains, Oahu, including forest adjacent to Kahanahaiki, and taken to laboratory facilities at the University of Hawaii in Honolulu. Each rat was held in an individual 38 cm × 22 cm × 18 cm metal-mesh (8 mm) cage. Rats were allowed to acclimate for at least 1 week before beginning feeding trials, during which time the rats were fed a diet of mixed seeds (e.g., corn, sunflower, wheat, barley, oats, sorghum) and occasionally wedges of fruit (tangerine). Rats were checked daily to ensure there was ample food and fresh water, and to clean urine/fecal trays. Approximately every 4 months from August 2007 through January 2009, a new set of rats (7–12 individuals; mean ± SE: 9.7 ± 0.6 , in roughly equal proportions of females and males) was captured from the Waianae Mountains to replace the previous set of rats. A total of 51 rats were used during this study.

Captive feeding trials used the same 12 plant species as those used in the field. For each feeding trial, fruits of a single species, collected fresh from Kahanahaiki, were placed in each cage with a rat for 24 h. The number of fruits offered to each rat matched the quantity used ($n = 1\text{--}3$) for each treatment in the field. Water was always available in each cage. After 24 h of exposure to each rat, fruits were visually inspected to estimate the proportion of pericarp (fruit material) mass and seed mass remaining. When multiple fruits or seeds were offered to a rat, the proportion of mass remaining was determined by averaging visual estimates of each fruit's or seed's unconsumed mass. For seven of the 12 species, trials were continued an additional 24 h period and inspected, but there was no significant difference ($P > 0.05$ for each; Mann–Whitney U tests) in pericarp or seed mass remaining from 24 to 48 h, so all data presented for each of the 12 species are for the initial 24 h of rat exposure. Additionally, for all

but the two smallest species (*Clidemia* and *Kadua*), the proportion of surviving seeds was determined by inspecting all remaining seeds and seed parts for intact embryos. A seed was considered destroyed if the embryo was not intact or $>50\%$ of the seed was eaten (Pérez et al. 2008; Shiels in press). For *Clidemia* and *Kadua*, it was necessary to inspect rat droppings microscopically and extract seeds that had passed through the digestive tracts of rats. To test for viability of such seeds, they were sown on agar, and their germination was compared to conspecific, unconsumed seeds sown on agar. The proportion of seeds surviving rat exposure was determined from the ratio of surviving seeds to the average number of seeds per fruit for each species (see Table 1). Rats were returned to their regular diet for at least 48 h between feeding trials.

Results

Field trials

The percentage of fruit remaining after exposure to animals in the field varied by plant species, and ranged from 0 to 100% (Table 2). Seven of the 12 species had significantly fewer fruits in the three treatments that allowed access to vertebrates (i.e., small-vertebrate-access, open ground, and open-cage-control) relative to the no-vertebrate-access treatments, and there were no significant differences ($P > 0.05$) among the three vertebrate accessible treatments for each of these seven species (Table 2). Both *Nestegis* and *Kadua* had 50–60% of their fruit remaining in the open ground treatment, but substantial variation among vertebrate accessible treatments resulted in a lack of significant differences when all four treatments were compared ($P > 0.05$ for each; Table 2). The largest fruit and seed tested, *Aleurites*, had no fruit removed from any treatment station. Two additional species that appeared relatively unattractive to animals and did not differ significantly among treatments were the common non-native tree *Schinus*, which had 97% of its fruit remaining, and the large-seeded native tree *Sapindus*, which had 83% of its fruit remaining (Table 2).

The dominant non-native tree in the forest, *Psidium*, appeared to be the most attractive species as evidenced by removal of 100% of its fruit within

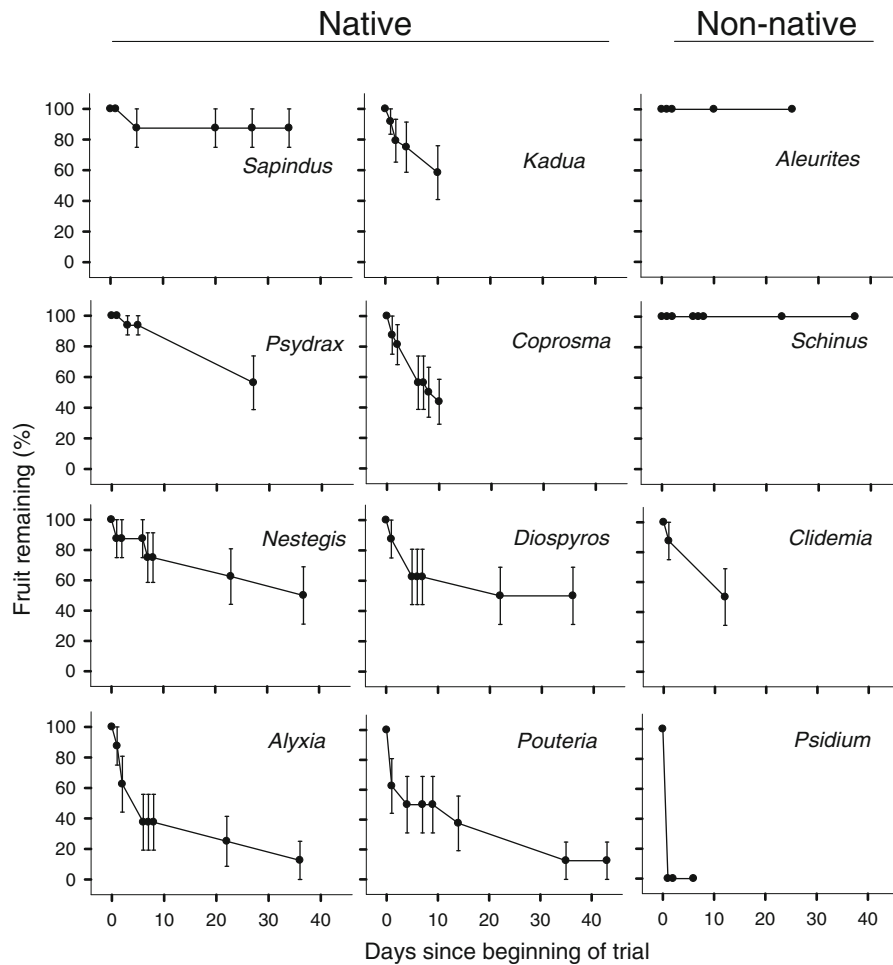


Fig. 1 Mean (SE) percentage of fruit remaining at each sampling period for each species in open ground treatment ($n = 8$ stations per species, except *Psidium* had $n = 6$) at Kahanahaiki forest, northwest Oahu, Hawaii, where the

duration (days) of each trial was restricted to an interval where fruit decomposition was minimal (see Table 2 for trial duration for each species). Species ordering is based roughly on the amount of fruit remaining at the end of the trials

6 days in the vertebrate accessible treatments (Table 2; Fig. 1). Two native species were highly attractive to vertebrates (12.5% fruit remaining in open ground treatment): *Alyxia* and *Pouteria* (Fig. 1). *Pouteria* fruits were removed from three of the eight no-vertebrate-access treatments; in each case a rodent-sized tunnel had been dug under the cage wall. This was the only species that had any of the no-vertebrate-access treatment replicates compromised (Table 2). Six out of 12 species had $\leq 50\%$ of their fruit remaining in open ground treatments, including: *Alyxia*, *Clidemia*, *Coprosma*, *Diospyros*, *Nestegis*, *Pouteria*, and *Psidium* (Table 2; Fig. 1). Besides *Psydrax*, which declined steadily to 56%

remaining by the end of the 27 day trial, the majority of fruit removal for all species in open ground treatments occurred during the first 10–12 days of each trial (Fig. 1).

The motion-sensing cameras photographed black rats during intervals when fruits were removed for seven of nine species (Table 2). A total of 17 photographs of rats were associated with fruit removal (an average 1.9 ± 0.6 rat photographs for each of the nine species). Rarely were animals other than the black rat captured in photographs at the treatment stations, and the few times that they were (including a cat, a mongoose, and three bird species) the fruits at the treatment station where the camera

was triggered were not removed. This gives us confidence that most fruit removal was attributable to black rats.

Captive feeding trials

After determining the degree of fruit removal by rats in the forest, the possible post-removal seed fates of these species were assessed through captive feeding trials. For each of the 12 woody species, rats ate both the pericarp and the seeds, but the amount eaten (Fig. 2) and the number of seeds destroyed (Fig. 3) varied by species. As in the field, *Aleurites*, the species with the largest seeds, appeared to be the least attractive of the 12 species offered; 77% of the pericarp and 99% of the seed mass remained after 24 h. Also matching the field trials, the large-seeded native, *Sapindus*, and the non-native, *Schinus*, seemed relatively unattractive to captive rats, because an average of 83 and 93%, respectively, of both species' pericarp and seed mass remained after rat exposure. *Pouteria* experienced among the highest fruit removal by rats in the field and captive rats ate all but 36% of the pericarp but they left 86% of the seed mass uneaten (Fig. 2).

Eight out of the 12 species had <50% seed mass remaining after 24 h. The most attractive species to captive rats was *Nestegis*, for which the majority of the seed masses were consumed by most (11 of 12) of

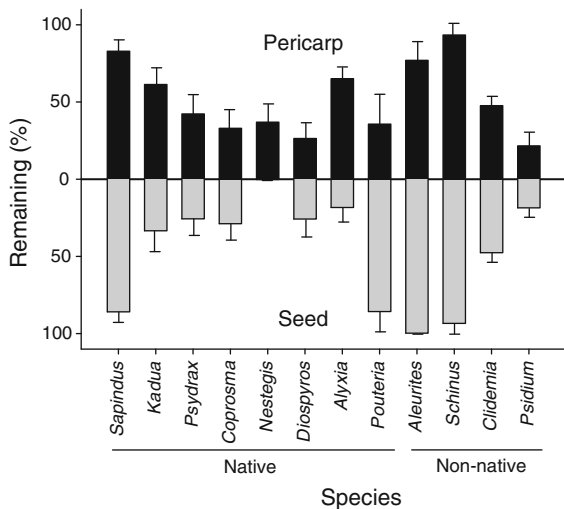


Fig. 2 Mean (SE) estimated percentage of pericarp (fruit tissue) mass and seed mass remaining when fruits were offered to black rats in captivity ($n = 7-12$ rats) for 24 h

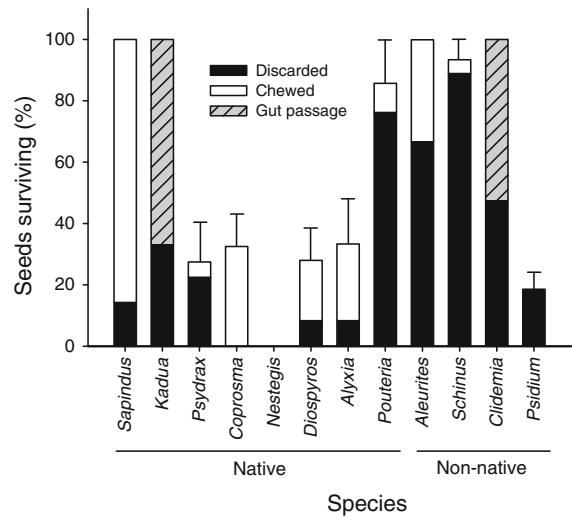


Fig. 3 Mean (SE) percentage of seeds surviving 24 h exposure to captive black rats ($n = 7-12$ rats) where the total number of seeds per fruit for each species was based on mean values described in Table 1. The three categories of seed survival include: discarded (not chewed or ingested), chewed, and gut passage. Error bars reflect total survival (all three categories combined)

the rats and only a few pieces of chewed seed remained in a single cage (Fig. 2). Most of the pericarp of *Nestegis* was also eaten, but the outermost part of the pericarp (the exocarp) was left uneaten in most cages. In addition to the particularly vulnerable seeds of *Nestegis*, both *Alyxia* and *Psidium* each had an average of <20% seed mass remaining (Fig. 2).

Seed survival varied widely, but appeared to group into two levels: high survival (mean $\geq 85\%$; six species) and low survival (0–35%; six species) (Fig. 3). Several species, including *Aleurites*, *Clidemia*, *Kadua* and *Sapindus*, had no seeds destroyed by rats. The three categories of seed survival following rat interaction include: discarded (not chewed or ingested), chewed (but only partially damaged), and gut passage. For both of the very small-seeded species (*Clidemia* and *Kadua*), rats consumed the fruits partially or fully and seeds survived passage through the rat's teeth and digestive system as evidenced by only intact seeds and no seed fragments detected in droppings, and seed germination percentages equal to those of seeds not consumed by rats. While *Aleurites*, *Sapindus*, and *Schinus* had high seed survival resulting from unattractiveness of their fruit (pericarp + seed; Fig. 2), *Pouteria* had high seed survival because its seeds were less attractive than its

pericarp (Figs. 2, 3). Of the five species with low seed survival (<35%), *Psidium* had just 18% survival (Fig. 3), which amounts to an average of ca. one surviving seed per fruit.

Discussion

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

Fruits of native and non-native species were removed by rats in Hawaiian mesic forest, and all but one native species (*Sapindus*) had $\geq 44\%$ fruit removal. In New Zealand, introduced rodents (probably *Rattus* spp.) removed much lower proportions of 11 native seeds (4–24% removal; Moles and Drake 1999) than in our study. For example, removal of *Coprosma* by black rats in our 10 day trial was at least double that for local species of *Coprosma* that were removed by rodents in New Zealand (*C. grandifolia* after 15 days, Moles and Drake 1999; *C. macrocarpa* after 5 days, Grant-Hoffman et al. 2010). Similarly, whereas Hawaiian *Nestegis* had approximately two-

thirds of its fruits remaining after 15 days (or half after 37 days) following exposure to vertebrates, Moles and Drake (1999) found that the New Zealand *Nestegis* (*N. cunninghamii*) had 95% of its seeds remaining after 15 days. Many factors can affect fruit and seed removal by rodents, including rodent densities, food availability, and various characteristics of the fruits and seeds (e.g., size, defenses). In our study, removal of non-native fruits ranged from no removal (*Aleurites*) to 100% within 6 days for *Psidium*, which is one of the most problematic invasive plants in Hawaii (Medeiros 2004; Uowolo and Denslow 2008).

Many factors contribute to the attractiveness and subsequent removal of fruits and seeds (see review by Janzen 1971), and seed removal in field trials is an important first step in determining seed fate (Forget et al. 2005). Larger seeds are often preferentially selected by rodents over smaller seeds (Abramsky 1983; Hulme 1998), perhaps owing to the greater nutritional reserve and the relative ease with which larger seeds are located (Mack 1998). However, our three largest seeds (*Aleurites*, *Pouteria*, *Sapindus*; 17.9–30.3 mm longest axial length) were among the most unattractive to black rats. Intermediate-sized seeds (5.2–17.7 mm) suffered from a high level of predation by rats, whereas the smallest seeds (0.5–1.2 mm) were ingested but not destroyed. In wet forests in both Indonesia (Blate et al. 1998) and Mexico (Mendoza and Dirzo 2007), smaller-seeded species were more attractive and more heavily depredated by rodents than were larger-seeded species. Palm fruit of *Lepidorrhachis mooreana* had high fruit removal by black rats on Lord Howe Island, but a sympatric palm (*Hedyscepe canterburyana*) that has fruits 18 times larger suffered little removal by black rats (Auld et al. 2010). Additionally, relatively small seeds were the most commonly reported seed size consumed by introduced rats when a suite of New Zealand studies were reviewed (Grant-Hoffman and Barboza 2010). The physical and chemical defenses in seeds and fruits complicate generalizations of seed-size preference to mammals (Steele et al. 1993; Mendoza and Dirzo 2009). The possible chemical defenses in *Aleurites*, *Sapindus* and *Schinus* (Wagner et al. 1999) and the physical defenses of a hard and thick seed coat in *Aleurites* (Wagner et al. 1999) may have influenced the very low attraction and predation of these common species. In contrast, *Nestegis* and *Psidium* suffered the highest predation levels in the

captive feeding trials, suggesting limited defenses against black rats for seeds of these two species. Despite the high levels of predation for *Nestegis* in the laboratory and 50% fruit removal from the open ground treatment in the field, the accessible fruit in the field were not removed in greater proportions than in the no-vertebrate-access treatment. Seed fragments and rodent-chewed seeds from unripe and ripe fruits were common below parent plants of *Nestegis*, perhaps indicating seed predation prior to natural fruit fall (A. Shiels, personal observation) and providing one possible explanation for the discrepancy between field and laboratory trials for *Nestegis*. Seed size preference and seed defensive traits are just two of the many possible characteristics that may influence seed removal and predation by rats.

There were at least two types of seed dispersal observed in black rat interactions with the woody species in this study and these can be distinguished by the degree of pericarp consumption and seed damage (Fig. 4). The first type (occasional dispersal in Fig. 4) occurs when a rat transports fruits or seeds, presumably with the intention to eat them (Herrera and Pellmyr 2002), but some of the chewed seeds are not destroyed. At least six of our species showed evidence of this pattern, where entire seeds were not damaged or were partially damaged, but with the embryos left intact such that the seeds potentially remained viable (e.g., *Alyxia*, *Coprosma*, *Diospyros*, *Psidium*, *Psyrax*). There are many examples of rodents in continental ecosystems that scatterhoard seeds, thereby dispersing those that they transport and then neglect to eat (Vander Wall 1990; Forget 1993; Wang and Chen 2009), but there is no evidence of such seed caching for the black rat (Vander Wall 1990). Additionally, partial seed damage is tolerated by several tropical species (Dalling et al. 1997; Mack 1998) and even accelerates germination in others (Vallejo-Marín et al. 2006) including two endemic Hawaiian palm species that were experimentally damaged to simulate black rat gnawing (Pérez et al. 2008). Another pattern of behavior could involve removing and discarding the unwanted pericarp prior to chewing seeds (rare dispersal in Fig. 4), but no species followed this pattern in our study.

A second type of seed dispersal (via gut passage or endozoochory; Herrera and Pellmyr 2002) was observed for *Clidemia* and *Kadua*, and resulted from rats consuming the pericarp but not chewing the

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

Fig. 4 The four scenarios by which black rats may interact with fruits and disperse seeds

small seeds prior to gut passage (frequent dispersal in Fig. 4). Although this type of dispersal is much more common with birds than rodents (Herrera and Pellmyr 2002; Forget et al. 2005), it has been demonstrated with captive black rats for two small-seeded species (<2.5 mm length) from New Zealand (Williams et al. 2000). Elsewhere, intact *Clidemia* seeds were found in rodent droppings in a wet forest on Maui, Hawaii (Medeiros 2004), and intact *Carpobrotus* spp. seeds were found in black rat droppings on Mediterranean islands (Bourgeois et al. 2005). Finally, the interaction of black rats with *Pouteria* fits none of the dispersal categories described by Herrera and Pellmyr (2002) because rats consumed only the fleshy pericarp and discarded the large seeds (frequent dispersal, Fig. 4). Other vertebrates are known to harvest and transport fruits prior to eating pericarps and discarding seeds, including native flying foxes (*Pteropus tonganus*) in the South Pacific with *Pouteria grayana* (McConkey and Drake 2006), and native jays (*Cyanocorax cyanomelas*) in Bolivia with *Guetarda viburnoides*; the latter interaction increases plant population growth more than in nearby populations where seeds were dispersed by gut passage through other birds (Loayza and Knight 2010). Our results indicate that rats interact with fruits differently depending on the species, and that a range of seed sizes (varying 36-fold in length and >1,500-fold in mass if *Clidemia* is compared to *Pouteria* or *Sapindus*) can be dispersed by black rats.

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

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

Combining field trials with captive feeding trials using wild black rats represents a discontinuity between fruit removal and seed fate that may not be as realistic as if each fruit that a rat interacted with in the field was followed to its ultimate fate. However, it is notoriously difficult to elucidate all steps of a seed’s fate (Forget et al. 2005). A common shortcoming of seed fate trials conducted in the field is the uncertain identity of the animal responsible for seed damage (Abramsky 1983; Forget 1993; Mendoza and Dirzo 2007). Additionally, even if photographs capture the species responsible for seed or fruit removal, it is often uncertain whether the animal that removed the fruit or seed is responsible for all or part of the condition in which it is later recovered (Forget et al. 2005; Vander Wall et al. 2005). Although we were able to identify the animal removing fruits from the forest floor, we combined field trials with captive feeding trials to determine seed fate because it is very difficult to unobtrusively mark small seeds (like those

that passed intact through the rat’s digestive system) so they can be recovered in the field. Because the sites where rats defecate or deliver seeds (Abe 2007; e.g., husking stations, McConkey et al. 2003) may not always be suitable for germination or establishment, the conclusions using the methodology in this study are limited to seed survival after interaction with the black rat and prior to the germination and establishment stage of recruitment.

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

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