

Frugivory by introduced black rats (*Rattus rattus*) promotes dispersal of invasive plant seeds

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

through rats, also deserve rat control in order to help limit the spread of such seeds. Black rats may be facilitating the spread of many of the most problematic invasive plants through frugivory and seed dispersal in Hawaii and in other ecosystems where rats and plants have been introduced.

Keywords Captive-feeding trials · Hawaiian Islands · Non-native · Seed predation · Seed size · Weeds

Introduction

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

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to become more common than in the past because of the increasing number of introductions of invasive species into a given area (Parker et al. 2006; Traveset and Richardson 2006).

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

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

invertebrates, eggs, and small birds (Sugihara 1997; Yabe et al. 2010).

Native biotas on oceanic islands are known to be highly susceptible to displacement and extinction following the introduction of invasive species (Meyer and Florence 1996; Kueffer et al. 2010). The Hawaiian Islands represent an extreme example of an archipelago that suffers from biological invasions because they contain among the largest number of introduced species of all Pacific islands (Denslow et al. 2009). The number of introduced plant species that has naturalized in Hawaii is approximately equal to the number of native plant species (Wagner et al. 1999), and many of these naturalized species are invasive (Daehler and Carino 2000; Denslow et al. 2009). Seed-eating mammals were absent from Hawaii prior to the introduction of the Pacific rat by Polynesian settlers approximately 1,000 years ago (Athens et al. 2002), and later arrival of two additional rats (the Norway rat, *R. norvegicus*, and the black rat) and the house mouse with European settlement ca. 230 years ago (Tomich 1986). In contemporary Hawaii, the black rat is the most common rat in natural and semi-natural ecosystems from sea level to nearly 3,000 m elevation (Amarasekare 1994; Lindsey et al. 1999; Meyer and Shiels 2009). The black rat is a predator of a wide range of native Hawaiian biota, including arthropods (Cole et al. 2000), birds (VanderWerf 2001), snails (Hadfield et al. 1993), and seeds (Pérez et al. 2008; Shiels and Drake 2010), and this rat has been considered one of the most damaging invasive vertebrates in the world (Towns et al. 2006; Drake and Hunt 2009).

How black rats affect common invasive plant species in Hawaii is largely unknown; however, that these rats are frugivores, seed predators, and seed dispersers of many native and four invasive Hawaiian plants has recently been established (Shiels and Drake 2010). Black rats may disperse seeds either by ingesting them (i.e., gut passage or endozoochory) or by transporting them and then discarding them either whole or partially chewed but with intact embryos (i.e., McConkey et al. 2003; Abe 2007; Shiels and Drake 2010). The objective of this study was to identify patterns in the ways rats interact positively and negatively with seeds of invasive species. Specifically, I addressed the following questions to determine how black rats affect 25 of the most invasive plant species in Hawaii: (1) To what

degree do rats consume the pericarps (fruit tissues) and seeds of these species? (2) Are there seeds that are potentially dispersed as a consequence of rats discarding or partially chewing seeds, or passing them internally? (3) Are there characteristics of fruits and seeds that predict their consumption, predation, and dispersal potential by rats?

Methods

Invasive plant species selection and description

To select the invasive plant species to offer black rats, I surveyed 12 invasive plant experts from the five largest Hawaiian Islands (i.e., Hawaii, Maui, Molokai, Oahu, Kauai) by asking them to list the 25 most problematic invasive plant species in Hawaii. Experts were considered those actively working with invasive plants in the Hawaiian Islands for at least the previous 5 years. I chose 25 plant species based on the highest frequencies listed with the following two constraints: First, to maximize phylogenetic diversity, no more than two species per family and one species per genus was selected. Second, at least three experts had to list a species for it to be used. There were five species that were substituted for slightly higher ranking species because of the availability of ripe fruits and seeds when black rats were in captivity. The 25 species used came from 19 families and had a wide range of fruit and seed sizes (Table 1), and all but seven species have fruit and seed adaptations for animal dispersal (Appendix). The majority of the selected plant species are native to the Old World (16 species), whereas nine species are native to the Neotropics (Wagner et al. 1999; Appendix). Plant species are hereafter referred to by genus.

Rat consumption of pericarp and seed

Adult black rats were captured from five locations on Oahu island, including a dry, lowland coastal scrubland, Ka Iwi Shoreline (1–2 m a.s.l.; 21°17'N, 157°39'W), a dry forest on Lanipo trail in the Koolau Mountains (205 m a.s.l.; 21°18'N, 157°47'W), and three mesic forest sites in the Waianae Mountains (450–625 m a.s.l.; Kahanahaiki Management Unit, 21°32'N, 158°11'W; Kaluaa Preserve, 21°28'N, 158°5'W; Makaha Valley, 21°31'N, 158°17'W). Rats

were taken to laboratory facilities at the University of Hawaii in Honolulu, and each rat was held in an individual 38 cm × 22 cm × 18 cm metal-mesh (8 mm) cage. Before beginning feeding trials, rats were allowed to acclimate for at least 1 week, during which time they were fed a diet of mixed seeds (e.g., corn, sunflower, wheat, barley, oats, sorghum) and occasionally wedges of fruit (tangerine). Rats were checked daily to ensure there was ample food and fresh water, and to clean urine/fecal trays. Feeding trials were performed from October 2007 through March 2010. Approximately every 4 months, a new set of rats (9–12 individuals, in roughly equal proportions of females and males) were captured from a single or multiple sites and replaced the previous set of rats. A total of 57 rats (111.1 ± 5.0 g; 16.2 ± 0.3 cm body length excluding tail; mean \pm SE) were used during this study.

For each feeding trial, 9–12 rats (mean \pm SE: 11.0 ± 0.1) were individually offered fruits of a single species (or seeds only for *Leucaena* and *Spathodea*) placed in each cage with no other food for 24 h. To roughly adjust for differences in fruit volume and mass among species, the number of fruits offered to each rat ranged from one to 35 (Table 1). After 24 h of exposure to each rat, fruits were visually inspected to estimate the proportion of the pericarp (fruit tissue, and the most outer layers of the fruit for grasses) mass and seed mass remaining. When multiple fruits or seeds were offered to a rat, the proportion of mass remaining was determined by averaging each fruit's or seed's unconsumed mass. For six of the 25 species, trials were continued an additional 24 h period and inspected, but there was no significant difference in pericarp or seed mass remaining between 24 and 48 h ($P > 0.05$ for each; Mann–Whitney U tests), so all data presented for each of the 25 species are for the initial 24 h of rat exposure. The proportion of surviving seeds was determined by inspecting all remaining seeds and seed parts in each cage for damage from chewing and for intact embryos. A seed was considered destroyed if the embryo was not intact or >50% of the seed was eaten (Pérez et al. 2008; Shiels and Drake 2010). For the smallest seeds (<3 mm length; Table 1), it was necessary to microscopically inspect rat droppings and extract seeds that had passed through the digestive tracts of rats. To test for viability of such seeds, they were sown on agar, and their germination

Table 1 Characteristics of the 25 invasive plant species used in this study

Species ^a	Family	Life form	No. fed to each rat ^b	Fruit				Seed			
				Length (mm)	Width (mm)	Mass (mg)	Fleshiness ^c (%)	Length (mm)	Width (mm)	Mass (mg)	No. per fruit
<i>Psidium cattleianum</i>	Myrtaceae	Tree	1	19.0 (0.3)	17.8 (0.3)	3,677 (304)	80.3 (0.8)	3.3 (0.1)	2.4 (0.1)	14.4 (0.7)	16.4 (1.5)
<i>Clidemia hirta</i>	Melastomataceae	Shrub	4	6.9 (0.3)	6.4 (0.2)	214 (21)	79.6 (0.7)	0.5 (0.0)	0.3 (0.0)	<0.1	360 (57)
<i>Schinus terebinthifolius</i>	Anacardiaceae	Tree	3	4.7 (0.2)	3.9 (0.2)	33 (5)	32.8 (5.4)	3.6 (0.1)	2.4 (0.2)	5.9 (0.0)	1.0 (0.0)
<i>Hedychium gardnerianum</i>	Zingiberaceae	Herb	1	23.5 (1.0)	14.8 (0.3)	2,638 (245)	74.1 (0.5)	4.3 (0.1)	3.7 (0.1)	46 (1)	16.3 (1.4)
<i>Miconia calvescens</i>	Melastomataceae	Shrub, tree	8	4.7 (0.2)	4.2 (0.1)	58 (3)	69.7 (1.9)	0.5 (0.0)	0.4 (0.0)	<0.1	66 (9)
<i>Leucaena leucocephala</i>	Fabaceae	Shrub, tree	5	127.8 (6.0)	18.4 (0.6)	923 (54)	13.3 (0.1)	7.2 (0.2)	3.9 (0.1)	44 (1)	13.7 (1.4)
<i>Schefflera actinophylla</i>	Araliaceae	Tree	8	5.9 (0.1)	5.1 (0.1)	98 (3)	84.8 (0.5)	2.1 (0.1)	1.3 (0.1)	0.2 (0.1)	24.3 (1.0)
<i>Adesmia elliptica</i>	Myrsinaceae	Shrub	3	10.2 (0.2)	7.8 (0.4)	420 (10)	77.6 (0.3)	4.9 (0.1)	4.6 (0.1)	74 (2)	1.0 (0.0)
<i>Morella faya</i>	Myricaceae	Shrub, tree	2	5.6 (0.4)	4.7 (0.3)	84 (14)	65.0 (3.6)	2.8 (0.2)	1.9 (0.1)	4.7 (1.2)	1.2 (0.1)
<i>Lantana camara</i>	Verbenaceae	Shrub	3	5.0 (0.2)	4.5 (0.2)	78 (8)	64.5 (2.3)	4.5 (0.2)	2.9 (0.2)	20 (1.0)	1.0 (0.0)
<i>Spathodea campanulata</i>	Bignoniaceae	Tree	5	231.7 (10.9)	65.0 (10.4)	34,471 (2,758)	16.8 (1.5)	8.9 (0.2)	6.7 (0.1)	5.0 (0.3)	1,631 (79)
<i>Urochloa maxima</i>	Poaceae	Grass	14	3.1 (0.1)	1.1 (0.1)	1.0 (0.1)	14.0 (9.8)	2.3 (0.1)	0.9 (0.1)	0.9 (0.1)	1.0 (0.0)
<i>Prosopis pallida</i>	Fabaceae	Tree	1	142.9 (6.1)	11.1 (0.4)	4,627 (439)	19.7 (1.4)	5.8 (0.3)	3.7 (0.4)	38.5 (3.1)	22.6 (0.8)
<i>Rubus rosifolius</i>	Rosaceae	Shrub	1	15.0 (0.7)	12.6 (0.7)	1,138 (153)	83.3 (0.9)	1.5 (0.0)	1.0 (0.0)	0.7 (0.0)	237 (35)
<i>Citharexylum caudatum</i>	Verbenaceae	Tree	4	5.5 (0.2)	5.1 (0.2)	119 (9)	70.2 (0.7)	5.2 (0.2)	3.6 (0.1)	25.9 (2.0)	2.0 (0.0)
<i>Ficus microcarpa</i>	Moraceae	Tree	2	7.3 (0.2)	7.1 (0.2)	162 (19)	64.2 (3.3)	0.9 (0.0)	0.7 (0.0)	<0.1	12.7 (4.0)
<i>Passiflora suberosa</i>	Passifloraceae	Vine	2	9.3 (0.3)	8.9 (0.3)	354 (41)	86.4 (1.2)	3.3 (0.1)	2.4 (0.1)	9.8 (0.7)	11.0 (1.2)
<i>Buddleia asiatica</i>	Buddleiaceae	Shrub, tree	35	3.3 (0.1)	2.4 (0.1)	2 (0)	13.0 (2.1)	0.6 (0.0)	0.2 (0.0)	<0.1	177.5 (31.9)
<i>Syzygium cumini</i>	Myrtaceae	Tree	1	17.0 (0.3)	14.2 (0.5)	2,466 (216)	77.0 (0.6)	11.5 (0.3)	8.3 (0.2)	584 (33)	1.0 (0.0)
<i>Aleurites moluccana</i>	Euphorbiaceae	Tree	1	46.7 (1.9)	43.5 (0.5)	46,855 (2,371)	67.1 (1.5)	30.3 (0.5)	29.1 (0.4)	8,995 (542)	1.4 (0.1)
<i>Coffea arabica</i>	Rubiaceae	Shrub, tree	1	15.0 (0.4)	13.7 (0.3)	1,701 (58)	66.5 (0.5)	12.0 (0.2)	8.4 (0.1)	406 (19)	2.0 (0.0)
<i>Cinnamomum burmannii</i>	Lauraceae	Tree	2	9.9 (0.3)	6.9 (0.1)	297 (15)	51.4 (1.3)	8.1 (0.2)	4.9 (0.1)	113.0 (5.1)	1.0 (0.0)
<i>Bischofia javanica</i>	Euphorbiaceae	Tree	2	11.1(0.2)	9.6 (0.2)	730 (33)	68.7 (0.3)	4.1 (0.1)	2.8 (0.1)	19 (1)	2.6 (0.3)
<i>Casuarina equisetifolia</i>	Casuarinaceae	Tree	2	13.4 (0.5)	12.1 (0.4)	650 (58)	22.8 (0.9)	2.9 (0.1)	2.7 (0.1)	0.9 (0.1)	9.9 (3.9)
<i>Setaria palmifolia</i>	Poaceae	Grass	25	3.0 (0.1)	1.4 (0.0)	1.6 (0.1)	21.4 (5.3)	2.8 (0.0)	1.4 (0.0)	1.5 (0.1)	1.0 (0.0)

Values are expressed as mean (SE). For fruit and seed measures, a minimum of $n = 8$ fruit for each species were collected from >3 individuals. Lengths of fruits and seeds are the longest axial lengths. Mass of fruits, which includes seeds, and mass of the individual seeds are reported on a fresh-mass basis. Species ordering reflects survey results (see section “[Invasive plant species selection and description](#)”) for the most problematic plants in Hawaii; the first species listed were the most problematic based on my informants

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

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

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

was compared to conspecific, unconsumed seeds sown on agar. The proportion of seeds that survived following rat exposure was determined from the ratio of surviving seeds relative to the average number of seeds per fruit for each species (see Table 1). Rats were returned to their regular diet for at least 48 h between feeding trials.

Characteristics that predict rat vulnerability

Eight variables associated with the fruits and seeds were predicted to affect pericarp and seed consumption by black rats: mean fruit and seed length, width, and mass, as well as fruit fleshiness (mass ratio of fresh – dry when heated at 105°C for 48 h: fresh) and the number of seeds per fruit (Table 1). Because these variables were correlated (e.g., 16 of 28 possible pairwise correlations had *R* values >0.50), I used principal components analysis (PCA) to reduce the number of variables to a smaller number of principal components (PCs) that are orthogonal (i.e., not correlated; Quinn and Keough 2002). Aside from fruit fleshiness and the number of seeds in each fruit, each of the variables related to fruit and seed size were log-transformed to meet assumptions of normality. All 25 species were used in the PCA. The PCs were used to calculate factor scores for each species, and I used these factor scores in multiple regressions to test whether the PCs are correlated with the following variables related to fruit and seed attractiveness and vulnerability to black rats: percentage pericarp

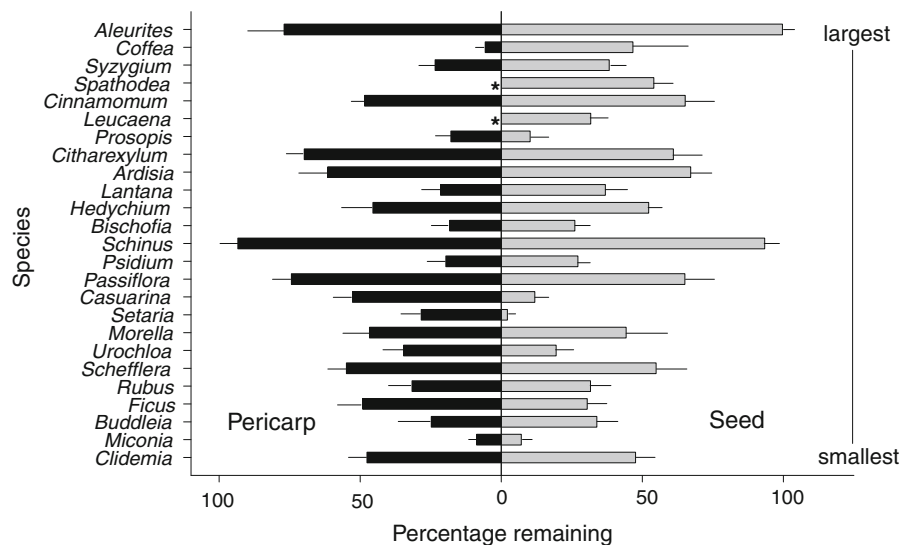
mass remaining, percentage seed mass remaining, percentage surviving seeds. Percentage of pericarp remaining used 23 species because for two species (*Leucaena* and *Spathodea*) only the seeds were offered to rats. All remaining analyses included all 25 species. All statistical analyses were conducted in SPSS (1998), and significance was based on *P* < 0.05.

Results

Rat consumption of fruit and seed

Black rats ate both the pericarp and the seeds, but the amount of plant material (pericarp and seeds) eaten by black rats (Fig. 1) and the percentage of total seeds that survived (Fig. 2) varied by plant species. Two species were unattractive to rats, including *Aleurites*, which has the largest seeds and had nearly 80% of its pericarp and almost 100% of the seed mass remaining, and the intermediate-sized seeds (3.6 mm longest length) of *Schinus*, which had >90% of the pericarp and seed mass remaining after 24 h (Fig. 1). The majority of the species had approximately equal parts of pericarp and seed mass remaining, but at least three species tended to have a greater portion of their seed masses remaining rather than pericarp masses, including *Coffea*, *Syzygium*, and *Lantana*. By contrast, pericarp mass remaining tended to be higher than seed mass remaining for *Casuarina*, *Setaria*, *Urochloa*, and *Ficus* (Fig. 1).

Fig. 1 Mean (SE) estimated pericarp mass and seed mass remaining for 25 invasive plant species in Hawaii after offering to black rats (9–12 rats for each trial; mean ± SE: 11.0 ± 0.1). The asterisk (*) signifies the two species (*Leucaena* and *Spathodea*) that were only offered seed. Species ordering on the vertical axis are arranged in ascending seed length



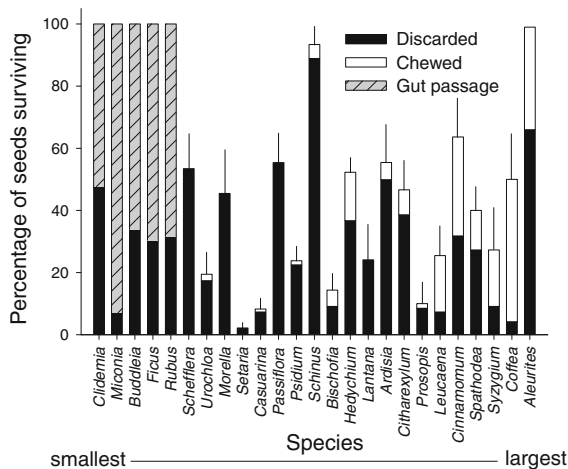


Fig. 2 Mean (SE) offered survival of 25 invasive plant species in Hawaii that were offered to captive *black rats* (9–12 rats for each trial; mean \pm SE: 11.0 ± 0.1). The three categories of survival include: discarded (not chewed or ingested), chewed, and gut passage. *Error bars* reflect total survival (all three categories combined). Species ordering on the *horizontal axis* are arranged in ascending seed length

Following 24 h exposure to rats, 15 of the 25 species had <50% average seed mass remaining. Seed mass remaining represents the amount of seed mass that was uneaten and it does not reflect the number of surviving seeds following rat exposure. Seeds of four of these 15 species, including *Miconia*, *Setaria*, *Casuarina*, and *Prosopis*, appeared most attractive to rats because <12% of their seed masses remained (Fig. 1). Three of these species are relatively small-seeded and were surrounded in either fleshy fruit (*Miconia*) or relatively dry fruit (*Setaria* and *Casuarina*). *Prosopis* have much larger seeds (ca. 2–11 times in length and 25–39 times in mass) than each of these three small seeded species and are surrounded by a sweet, relatively dry, mesocarp (Table 1).

Seed survival varied widely among the 25 species, and can be grouped into three categories (discarded, chewed, and gut passage) based on whether or not surviving seeds were chewed and ingested (Fig. 2). All species had some seeds that were discarded (i.e., not chewed or ingested) by some rats. Fifteen of the species had some seeds that were chewed and not ingested such that their viability was not likely altered (Fig. 2). Several species, including *Aleurites*, *Buddleia*, *Clidemia*, *Ficus*, *Miconia*, and *Rubus*, had no seeds destroyed by rats, and aside from *Aleurites* the 100% seed survival for each of these species resulted from the seeds being small enough to pass intact through the rat's teeth and digestive system (i.e., gut passage). The

seeds that survived gut passage were ≤ 1.5 mm in length and ≤ 0.7 mg. Therefore, seeds that are consumed by black rats survive and may be dispersed if their longest axis is ≤ 1.5 mm, whereas seeds ≥ 2.1 mm have a much greater chance of being destroyed. There were no seeds tested between 1.5 mm (*Rubus*) and 2.1 mm (*Schefflera*). Basing such a threshold, which separates endozoochory from predation, on seed mass is less useful than seed length for the tested species because *Schefflera* seeds weigh 0.2 mg ($0.5 \text{ mg} < \text{Rubus}$ seeds) but did not survive black rat consumption (Table 1; Fig. 2). Of the nine species with the lowest seed survival (<35%), *Bischofia*, *Casuarina*, *Setaria*, and *Prosopis* had <15% survival (Fig. 2), which amounts to an average of ca. one or three surviving seeds per fruit for *Casuarina* and *Prosopis*, respectively, and generally no surviving seeds per fruit for *Bischofia* and *Setaria* (Table 1; Fig. 2). Aside from the unattractive fruits and seeds of *Aleurites* and *Schinus*, and the seeds with the lowest survival, most species in this study may be occasionally dispersed by black rats if transported seeds in the field were not destroyed.

Characteristics that predict rat vulnerability

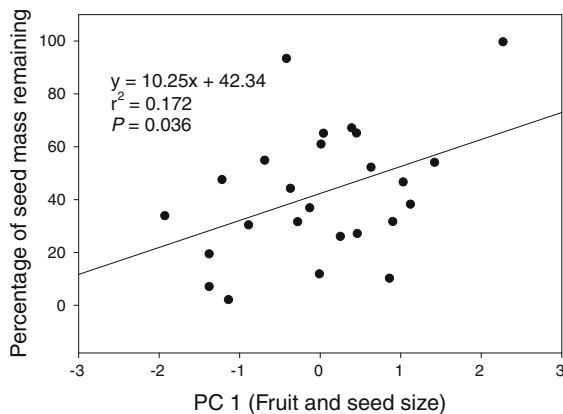
When the eight fruit and seed characteristics for all 25 species were analyzed by PCA, three PCs with eigenvalues >1.0 accounted for 96.84% of the measured variation in the dataset (Table 2). Principal component 1, which accounted for 57% of the variation, was dominated by variables related to fruit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

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

Table 2 Eigenvalues and factor loadings for the first three principal components of variables relating to the characteristics of fruits and seeds of 25 invasive plant species introduced in Hawaii

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

^a Significant factor loadings were based on the recommendations of Comrey (1973) and are shown here with an asterisk (*)

**Fig. 3** Relationship between seed mass remaining following *black rat* interaction and PC 1, where PC 1 reflects sizes of the fruits and seeds, including length, width, and mass, of 25 invasive species in Hawaii. *Positive* values of PC 1 reflect larger fruit and seed sizes

with the percentage of pericarp mass remaining (PC 1 $P = 0.871$; PC 2 $P = 0.349$; PC 3 $P = 0.537$; $df = 3, 19$) or the percentage of seeds surviving (PC 1 $P = 0.205$; PC 2 $P = 0.125$; PC 3 $P = 0.055$; $df = 3, 21$).

Discussion

Black rats eat fruits and seeds of a wide range of invasive species including those that are typically

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

Rat consumption of invasive fruits and seeds can result in seed survival or mortality. Nine of the plant species tested suffered relatively high predation because <35% of the seeds survived 24 h exposure to black rats. Several of these species, including *Lantana*, *Leucaena*, *Psidium*, *Syzygium*, and *Urochloa* tended to suffer slightly less predation (15–35% survival) than the most vulnerable (<15% survival) species, which were *Bischofia*, *Casuarina*, *Setaria*, and *Prosopis*. *Bischofia* is one of the most problematic invasive species on the subtropical Ogasawara Islands in Japan, where it has high growth rates and low mortality rates (Hata et al. 2006). There, the black rat is believed to be the animal responsible for the relatively high post-dispersal seed predation of *Bischofia* (10–50% of the seeds remained after 5 days), but such seed predation does not appear to be reducing the spread of this plant (Yamashita et al. 2003). Also in the Ogasawara Islands, seeds of *Casuarina stricta*, which is similar to the common *Casuarina* in Hawaii, is frequently found with predation scars from black rats (Chiba 2010). Almost every seed of *Setaria* that was offered to black rats was consumed and destroyed, as were >80% of the seeds of the grass *Urochloa* (formerly *Panicum maximum*), which is an aggressive colonizer in tree plantations and disturbed sites (Ostertag et al. 2008). Both *Setaria* and *Urochloa* seed fragments and vegetative stalks were found in stomachs of black rats captured near agricultural fields in Hawaii (Kami 1966). Introduced grasses suffer relatively high predation in other tropical areas, such as in Costa Rica where seedlings of the dominant

non-native *Cynodon dactylon* were reduced 52% by vertebrate seed predators (Wijdeven and Kuzee 2000). Most seeds of *Prosopis* were destroyed by the captive black rats, and the majority of the sugar-rich pericarp was also consumed. A single *Prosopis* tree can produce 19,000–140,000 seeds per year (cited in Gallaher and Merlin 2010), yet introduced rodents and beetles appear to minimize *Prosopis* recruitment through seed predation in many parts of Hawaii (Gallaher and Merlin 2010) and elsewhere (Pasicznik et al. 2001).

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

Dispersal via gut passage occurred for five of the 25 invasive plants tested (*Clidemia*, *Miconia*, *Buddleia*, *Ficus*, and *Rubus*). Although this type of dispersal has been much more commonly observed in birds than rodents (Herrera and Pellmyr 2002), it has been observed with black rats and two small-seeded (≤ 2.4 mm length) species in New Zealand (Williams et al. 2000) and with *Carpobrotus* spp. seeds (0.3–0.6 mg) on Mediterranean islands (Bourgeois et al. 2005). Additionally, intact *Clidemia* seeds were found in rodent droppings in a wet forest on Maui, Hawaii (Medeiros 2004), and Meyer (1998) suggests that *Miconia* are actively dispersed by introduced rodents in Tahiti. Mature individuals of *Clidemia* and *Miconia* can produce 3–8 million seeds/year (Meyer 1998; Medeiros 2004) and were ranked in the top five most problematic invasive species in Hawaii by my informants. While $>50\%$ of both pericarp and seed masses of *Clidemia* and *Miconia* were consumed by

rats in captive-feeding trials, *Miconia* fruit consumption tended to be much greater, with only about 10% of the pericarp and seed remaining after rat interaction. Fruit of *Clidemia*, *Melastoma candidum* (Melastomataceae), and *Rubus* comprised ca. 95% of the food items in stomachs of 19 black rats trapped in lowland forest dominated by invasive plants on Hawaii island (Beard and Pitt 2006). Therefore, where *Clidemia*, *Miconia*, and *Rubus* are locally abundant in Hawaii, their fruit may comprise a large portion of the black rat diet and their seeds are likely dispersed by these rats.

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

Very small seeds that pass internally are not the only types of seeds that may be dispersed by black rats. Although less recognized (but see Abe 2007; Shiels and Drake 2010), there is potential for dispersal of seeds that were ≥ 2.1 mm length and were not destroyed following collection because these rats commonly transport fruits and seeds to nearby husking stations for consumption (Campbell et al. 1984; McConkey et al. 2003). Therefore, discarding unchewed seeds after consuming pericarps, and incomplete consumption where seeds are partially chewed but not destroyed, can result in seed dispersal for seeds ≥ 2.1 mm in length, which includes at least 15 species in this study. Adding field trials in Hawaii, as demonstrated by Shiels and Drake (2010) for eight

native and four invasive species, would allow further clarification of the likelihood of such seed dispersal by black rats for these 15 species.

Black rats consume a greater proportion of the seed mass in species with small fruits and seeds than they do for large fruits and seeds (Fig. 3). Although the mass of consumed seeds was not determined in several past studies, larger seeds are often preferentially selected by rodents over smaller seeds, probably because of the greater nutritional reserve in larger seeds (Smith and Reichman 1984; Vander Wall 2003). However, Shiels and Drake (2010) found that the intermediate-sized seeds were generally the most attractive species and suffered the highest predation by black rats when 12 species were tested in Oahu montane forest, whereas the three largest seeds, including *Aleurites* and two native species, were among the most unattractive to rats. It is curious that *Aleurites* seeds were not removed by rats in the field (Shiels and Drake 2010) or readily consumed in laboratory trials because gnawed seeds can be found in most forests where *Aleurites* has established both in Hawaii and other Pacific Islands (personal observation); it is possible that consumption of *Aleurites* in the field may be overestimated because the stony seed coats of the chewed seeds persist indefinitely on the forest floor. As in the present study, the smallest seeds in the study by Shiels and Drake (2010) were frequently ingested but not destroyed by black rats. Additionally, relatively small seeds were the most commonly reported seed size that was eaten by introduced rats when numerous New Zealand studies were reviewed (Grant-Hoffman and Barboza 2010). The higher energetic cost involved in moving large fruits and seeds versus small ones, or the energy expenditure needed to overcome defenses such as hard seed coats and secondary compounds, can deter rodents from consuming such food items (Smith and Reichman 1984; Blate et al. 1998). Reduced time to satiation when large seeds are eaten (Janzen 1971) may also partly explain the difference in black rat consumption of different sized seeds.

Although captive-feeding trials show that black rats have great potential to disperse some invasive seeds via gut passage, introduced birds also disperse some species of invasive seeds in Hawaii (Medeiros 2004; Chimera and Drake 2010) including four of those (*Clidemia*, *Hedychium*, *Psidium*, and *Rubus*)

included in my study (Medeiros 2004). The relative importance of bird- versus rat-dispersal cannot be determined without an understanding of the degree of each plant's dispersal limitations and the effectiveness of dispersal attributed to each animal at a given site. Introduced black rats may be the dominant seed dispersing animal on some islands that have relatively few avian frugivores, such as on Palmyra atoll in the Pacific Ocean where black rat densities are 90 indiv./ha (Wegmann 2009). In Hawaii, the relative importance of black rats versus birds or other seed-dispersing animals remains unknown. However, the microsites in the canopy and on the ground where black rats deposit seeds following transport will likely differ from those of birds or other seed-dispersing fauna.

While past motivations for rat control and eradication from islands has resulted from efforts to protect native biota from rat predation (Townsend et al. 2006; Howald et al. 2007; Meyer and Butaud 2009), the results from my study show that rat control efforts also need to be applied to areas where invasive plants have established and are fruiting in order to reduce their potential seed dispersal by rats. Although invasive seeds of a wide range of sizes can potentially be dispersed by black rats, the very small seeds (≤ 1.5 mm) are the ones most likely to be dispersed by rats via gut passage. Because of their global colonization of islands that includes a wide range of habitats (e.g., sea level to nearly 3,000 m in Hawaii), black rats should not be overlooked as potential dispersers of invasive plants and vectors of their spread.

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Appendix

See Table 3.

Table 3 The origin, approximate number of years in Hawaii, and the likely dispersal vector for 25 invasive plant species used in this study

Species	Origin ^a	Approx. number of years in Hawaii ^a	Likely dispersal vector
<i>Psidium cattleianum</i>	Tropical America	85	Animal
<i>Clidemia hirta</i>	Tropical America	70	Animal
<i>Schinus terebinthifolius</i>	Tropical America	100	Animal
<i>Hedychium gardnerianum</i>	Temperate, subtropical Asia	70	Animal
<i>Miconia calvescens</i>	Tropical America	50	Animal
<i>Leucaena leucocephala</i>	Tropical America	175	No obvious ^b
<i>Schefflera actinophylla</i>	Tropical Australia and New Guinea	110	Animal
<i>Ardisia elliptica</i>	Tropical Asia	80–90	Animal
<i>Morella faya</i>	Subtropical, temperate Africa	85	Animal
<i>Lantana camara</i>	Tropical America, Caribbean	150	Animal
<i>Spathodea campanulata</i>	Tropical Africa	100	Wind
<i>Urochloa maxima</i>	Tropical Africa	140	No obvious ^b
<i>Prosopis pallida</i>	Tropical America	80	Animal
<i>Rubus rosifolius</i>	Subtropical, temperate Asia	130	Animal
<i>Citharexylum caudatum</i>	Tropical America	80	Animal
<i>Ficus microcarpa</i>	Tropical, subtropical Asia and Australia	100	Animal
<i>Passiflora suberosa</i>	Tropical, subtropical America	95	Animal
<i>Buddleia asiatica</i>	Tropical, subtropical Asia	100	No obvious
<i>Syzygium cumini</i>	Tropical Asia and Malesia	140	Animal
<i>Aleurites moluccana</i>	Tropical Malesia	1,000	Uncertain ^c
<i>Coffea arabica</i>	Tropical Africa	160	Animal
<i>Cinnamomum burmanii</i>	Tropical Indonesia	60	Animal
<i>Bischofia javanica</i>	Tropical, subtropical Asia and Malesia	80	Animal
<i>Casuarina equisetifolia</i>	Tropical, subtropical Australia	230	Wind
<i>Setaria palmifolia</i>	Tropical Asia	110	No obvious

^a Based on Wagner et al. (1999)

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

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

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