

Large-scale rodent control reduces pre- and post-dispersal seed predation of the endangered Hawaiian lobeliad, *Cyanea superba* subsp. *superba* (Campanulaceae)

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Abstract Large-scale rodent control can help to manage endangered species that are vulnerable to invasive rodent consumption. A 26 ha rodent snap-trap grid was installed in montane forest on Oahu Island, Hawaii, in order to protect endangered snails and plants. To assess the effectiveness of this trapping operation in reducing fruit consumption and seed predation of the endangered Hawaiian lobeliad, *Cyanea superba* subsp. *superba*, pre- and post-dispersal *C. superba* fruit

consumption were monitored for 36 plants at the site with rodent control (Kahanahaiki) and 42 plants at an adjacent site without rodent control (Pahole). Over 47 % of all monitored fruit were eaten on the plants at Pahole compared to 4 % at Kahanahaiki. Images captured using motion-sensing cameras suggest that black rats (*Rattus rattus*) were the only pre-dispersal fruit consumers. To quantify post-dispersal fruit consumption, and to identify the culprit frugivore(s), mature fruit were placed in tracking tunnels positioned on the forest floor and checked daily. At Pahole, all of the fruit were consumed by rats compared to 29 % at Kahanahaiki. Lastly, to determine if rodents from the sites were predators or dispersers of *C. superba* seed, fruit were fed to captive black rats and house mice (*Mus musculus*). Black rats consumed entire fruit, killing all the seed, while mice did little damage to the fruit and seed. Therefore, large-scale rat trapping can directly benefit the reproduction of *C. superba* subsp. *superba*. Controlling black rats at restoration sites appears integral to the successful restoration of this endangered plant species.

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Introduction

Four rodents (black rats, *Rattus rattus*; Norway rats, *Rattus norvegicus*; Pacific rats, *Rattus exulans*, and

house mice, *Mus musculus*) are widespread invasive species that have been shown to negatively impact insular floras (Cuddihy and Stone 1990; Campbell and Atkinson 1999; Campbell and Atkinson 2002; Towns et al. 2006; Angel et al. 2009; Meyer and Butaud 2009; Auld et al. 2010). These rodents may have indirect impacts upon plants by modifying plant habitat and ecosystem functioning. For example, they may reduce native seed dispersal and pollination (Atkinson 1977; Atkinson 1985), or alter nutrient cycling and disturbance regimes associated with seabird nesting (Fukami et al. 2006; Mulder et al. 2009; Grant-Hoffman et al. 2010a, b). Rodents may also directly influence plants through the consumption of vegetative and reproductive parts (Sugihara 1997; McConkey et al. 2003; Salvande et al. 2006; Grant-Hoffman and Barboza 2010; Shiels 2011). As seed predators (see Grant-Hoffman and Barboza 2010 for a review), invasive rodents have been implicated in the breakdown of reproductive cycles of numerous island plant species (Campbell and Atkinson 2002; Meyer and Butaud 2009; Auld et al. 2010; Chimera and Drake 2011; Shiels and Drake 2011).

In Hawaii, the majority of studies concerning the effects of introduced rodents on the native flora have only recently been conducted (Athens et al. 2002; Pérez et al. 2008; Shiels 2010; Chimera and Drake 2011; Shiels and Drake 2011). Rodents were absent from Hawaii prior to the introduction of the Pacific rat by Polynesian settlers approximately 800 years ago (Wilmshurst et al. 2011). Athens et al. (2002) has suggested that Pacific rats were largely responsible for the decline of the native palms (*Pritchardia* spp.) that once dominated lowland forests on west Oahu. Three additional rodent species (Norway rat, black rat, and house mouse) were introduced by Europeans approximately 200 years ago (Atkinson 1977). Based on the results of contemporary studies, all four rodent species, and particularly black rats, probably have either directly or indirectly impacted the native Hawaiian flora (Cole et al. 2000; Shiels and Drake 2011). Today, Norway rats are most abundant in urban and agricultural lands on the main Hawaiian Islands and appear to be uncommon in native forest (Lindsey et al. 1999; Shiels 2010). Pacific rats are typically most common in lowland environments, although they have been recorded in montane rainforests up to 2,000 m (Sugihara 1997). House mice and black rats occupy most habitats from sea level to the alpine zones up to

3,000 m and are the most widespread of all introduced rodents in Hawaii (Tomich 1969; Shiels 2010).

In light of the nearly ubiquitous invasion of rodents on islands globally, rodent eradication has become a widely adopted strategy for the restoration of isolated islands (Towns and Broome 2003; Howald et al. 2007). However, when islands are either too large, or where rodent eradication is physically, socially or politically impractical, a targeted “Mainland Island” approach, first adopted in New Zealand (Saunders and Norton 2001), may limit rodent populations within areas surrounded by a matrix of habitat without rodent control. Such an approach may employ either the use of rodenticides and/or traps that must be regularly monitored (Saunders and Norton 2001).

In one of the first attempts to adopt a Mainland Island approach to rodent control in Hawaii, a 26 ha rodent trapping grid was established by the Oahu Army Natural Resources Program (OANRP) in montane forest on the island of Oahu, in May 2009. This ongoing trapping operation uses methods established by the New Zealand Department of Conservation (NZ DOC 2007; King et al. 2011). The trapping aims to reduce rodent (mainly rat) populations for the benefit of an endangered tree snail (*Achatinella mustelina*) and ten species of endangered plants.

One of these plant species is *Cyanea superba* subsp. *C. superba* (hereafter *C. superba*), a Hawaiian lobeliad historically recorded from mesic forest in the northern Waianae Mountains on Oahu (Wagner et al. 1999). The last wild plants of *C. superba* died in 2002. Seed previously collected from these remaining plants were germinated in nurseries and by mid-2011 over 800 *C. superba* had been outplanted across five restoration plantings in the Waianae Mountains. The decline of *C. superba* was attributed to habitat destruction, competition with invasive weeds, herbivory by introduced ungulates and slugs, and seed predation by introduced rodents (USFWS 1998; USFWS 2007; Joe and Daehler 2008). Casual observations indicated that introduced rodents (presumably rats) consumed significant quantities of *C. superba* fruit on the mature plants (USFWS 1998). However, whether these introduced rodents are predators or dispersers of the relatively small *C. superba* seed (<2 mm) remains unknown.

Our study had three aims: (1) to estimate the proportion of pre- and post-dispersal consumption of *C. superba* fruit by introduced rodents, (2) to

determine if the rodent species that consume fruit are seed predators or dispersers, and (3) to investigate the effectiveness of large-scale rodent trapping in reducing pre- and post-dispersal fruit and seed consumption of *C. superba*.

Methods and materials

Study site

The study was undertaken at two montane forest reserves located immediately adjacent to one another in the northern Waianae Mountain Range, Island of Oahu (21° 32'N, 158° 11'W). Kahanahaiki Management Unit (36 ha) (hereafter Kahanahaiki) is managed by OANRP, while Pahole Natural Area Reserve (266 ha) (hereafter Pahole) is managed by the State of Hawaii Department of Land and Natural Resources. The two populations of *C. superba* monitored in this study were ca. 400 m apart over highly dissected terrain. Given their proximity, both sites likely share a similar altitude (500–660 m a.s.l.), monthly rainfall (50–170 mm; cited in Joe and Daehler 2008), and daily temperature range (16–24 °C; Shiels and Drake 2011). At both sites, vegetation communities were a mixture of native and introduced mesic forest species. The native canopy species included *Metrosideros polymorpha* and *Acacia koa*; however, introduced trees were the canopy dominants and included *Psidium cattleianum*, *Psidium guajava*, *Aleurites moluccana*, *Schinus terebinthifolius* and *Grevillea robusta*. The subcanopy was also a mix of native (e.g., *Diospyros hillebrandii*, *Planchonella sandwicensis*, *Pipturus albidus*, *Psydrax odorata*, *Hibiscus arnottianus*, *Pisonia umbellifera* and *Pisonia brunoniana*) and introduced species (*P. guajava*, *P. cattleianum*, *S. terebinthifolius*; Shiels 2010). Year-round fruit production occurs at the sites; the greatest numbers of fruit are produced between November and March, which overlaps with *C. superba* fruit production (A. Shiels, unpublished data). Through the use of fencing and subsequent trapping within the reserves, both sites have been free of introduced ungulates for the past 12 years.

Invasive rodents are common at Kahanahaiki and Pahole. A 26-month trap and release study of rodent densities and habitat use at Kahanahaiki, beginning in February 2007, revealed the presence of black and Pacific rats and house mice, but the absence of Norway rats (Shiels 2010). Black rats were the most common

rodent (9.8 individuals/ha), followed by mice (5.1 individuals/ha) and Pacific rats were rare (0.2 individuals/ha; Shiels 2010). Given the proximity of Pahole and Kahanahaiki, the density of these rodents is likely to be similar at both sites.

Study species

Cyanea superba is a single stemmed tree typically reaching 4–6 m (Wagner et al. 1999). The 0.5–1.0 m leaves are held in a rosette at the stem apex. Flowering is from September to mid-October (OANRP 2009) on racemes that hang up to 350 mm below the canopy of leaves (Wagner et al. 1999). The corolla is curved, white to cream in color, and 5.5–8.8 cm long (Wagner et al. 1999). The fruit are oval berries 25 mm long (± 0.63 (SE), $n = 31$) and 21 mm wide (± 0.54 , $n = 31$) with a green-white exocarp and orange-red mesocarp containing ca. 130 seeds (± 16.9 , $n = 31$) (R. Pender, unpublished data). Each seed averages 1.86 mm long (± 0.02 , $n = 20$). Fruit mature between late November and early February (R. Pender, unpublished data).

Rodent trapping at Kahanahaiki

Rodent trapping at Kahanahaiki commenced in May 2009 using 440 snap traps (Victor® model M326, Woodstream Corporation, Pennsylvania, USA) placed in individual 40 × 14 × 19 cm (l × w × h) wooden boxes with a single 4.5 × 4.5 cm entry hole nearest to the baited end of the snap trap (King et al. 2011). All trap-boxes were located along transects that collectively covered the 26 ha area. Trap spacing along the perimeter was 12.5 m (234 traps), and all interior transects had 25 m between each trap (206 traps). Each transect was approximately 50 m distant from the next closest transect. The traps were baited with either peanut butter or FeraFeed (a non-toxic feed paste containing a mixture of peanut butter and grains; Connovation Limited, Auckland, New Zealand), and half of a macadamia nut was also usually added to the bait. Traps were initially checked daily for 2 weeks, then every 2 weeks thereafter. Figure 1 summarizes the quantities of rats trapped each month between May 2009 and February 2010 (the period prior to and including the *C. superba* fruiting season monitored in the current study). A total of 576 rats and 274 mice were trapped at Kahanahaiki during this period.

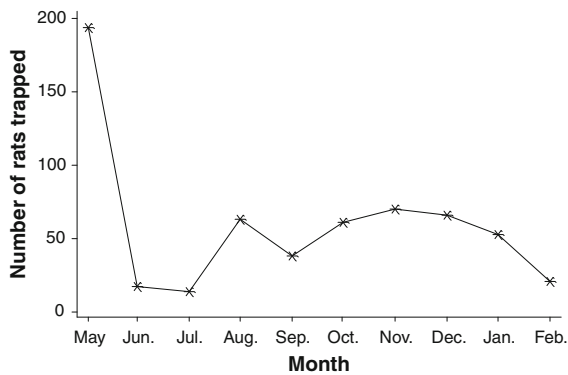


Fig. 1 Number of monthly rat (*Rattus* spp.) captures from 440 snap-traps arranged in a 26 ha trapping grid at Kahanahaiki, Oahu, between May 2009 (start of trapping) and February 2010. The current study was undertaken during December 2009 and January 2010, which was the fruiting season for *C. superba*

Rodent activity at each site

To assess and compare rodent activity between Kahanahaiki and Pahole, seven plastic tracking tunnels (50 cm × 10 cm × 10 cm; Connovation Limited, Auckland, New Zealand) containing tracking cards that were not baited (The Black Trakka Gotcha Traps LTD, Warkworth, New Zealand) were placed at both sites for five consecutive nights, beginning on 15 December 2009. Each tunnel was placed within 2 m of the base of a fruiting *C. superba* tree. The minimum distance between any two stations was ca. 10 m. All tracking tunnels were checked every 24 h, and when footprints were present, the tracking card was removed and replaced with a new (untracked) card. The footprints on tracked cards were used to identify each animal species.

Pre-dispersal fruit consumption

To determine the level of pre-dispersal consumption of *C. superba* fruit, both sites were monitored every 2–3 days from the time fruit began to mature until the fruiting season ended (1 December 2009–28 January 2010). A total of 36 plants were monitored at the Kahanahaiki rodent control site and 42 plants were monitored at the Pahole non-treatment site. On the first monitoring visit, fruit in each infructescence were counted and the infructescence numbered using a tag attached to the peduncle. During each subsequent visit, the number of fruit on a given infructescence that

had been partially or wholly consumed was recorded. The identities of the fruit-consuming animals were determined from the indentations in the fruit or pericarp (e.g., rodent chewing results in incisor marks distinct from bird or invertebrate indentations), as well as by photographs from the motion-sensing cameras (see below). Fruit that had been consumed were marked on their calyx with an ink pen to avoid mistakenly rerecording the consumption during later visits. In cases where infructescences aborted (i.e., no mature fruit formed) and fell, they were no longer monitored and were not included in the analysis. At the end of the fruiting season, total fruit consumption by rodents on each plant was determined by calculating the percentage of consumed fruit compared with those left undamaged from all infructescences on individual plants. Mean fruit consumption was then calculated for all plants at each site.

Motion-sensing cameras

Three infrared day/night still image cameras (Moultrie Game Spy D40, Moultrie Products, LLC, Alabama, USA) were used at each of the two sites to record animal visitation to ripe infructescences on *C. superba* plants during 16–28 December. The cameras were placed at an equal height to, and 1–2 m from, fruiting infructescences by securing them to introduced trees or 2.5 m long stakes. The cameras were moved every 3–4 days to randomly selected plants at each site. Color, still frame photos, were stored on solid disk (SD) cards and later copied onto a computer for viewing. The SD cards were removed and replaced each time the camera was moved. Each photo was viewed and all animals in the photos were identified; the activity (e.g., on the vegetative portion, on the infructescence, or eating fruit) of each animal was also noted. To avoid overestimating visits by individual vertebrate species, a 15 min interval (indicated by time stamps on photos) was required if consecutive visits were to be recorded as discrete visitation events.

Post-dispersal fruit consumption

To assess whether rats and mice consume *C. superba* fruit that fall to the ground (i.e., post-dispersal consumption) seven tracking tunnels were placed under fruiting *C. superba* trees at both sites (using the same methods, timing, and spacing, described for the

rodent activity assessment, above). Tracking cards were baited with ripe *C. superba* fruit. All tracking tunnels were checked every 24 h, and when footprints were present, the tracking card was removed and replaced with a new (untracked) card. The footprints on tracked cards were used to identify each animal species. The number of fruit that were consumed was recorded. A consumed fruit included those partially or wholly consumed or otherwise missing from the tracking tunnel; therefore, the amount of the exocarp, mesocarp, or seed consumed from each individual fruit was not quantified. Fruit were replaced if moldy or if any portion was consumed; otherwise fruit were not replaced during the 5-night study.

Captive-feeding trials

Three male and three female adult black rats were captured from forest adjacent to Kahanahaiki and Pahole in December 2007 and taken to the University of Hawaii Lyon Arboretum Rodent Housing Facility. 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 2 weeks before beginning the feeding trial, during which time the rats were fed mixed seed (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.

On 13 January 2008, a single ripe fruit of *C. superba*, was placed in each rat's cage. After 48 h of exposure, fruit were visually inspected to estimate the proportion of the pericarp (fruit material) and seed mass remaining. Because seed of *C. superba* are small (ca. 1.86 mm length at longest axis), it was necessary to collect the droppings from each rat and microscopically inspect them for intact seed. Seed with at least half of their original mass remaining were extracted from droppings and sown onto agar Petri dishes to compare germination success with unconsumed (intact) *C. superba* seed ($n = 3$ agar Petri dishes with five unconsumed seeds sown on each; Shiels 2011). All fruit and seed for the captive-feeding trials were collected from unmonitored plants at Kahanahaiki. All Petri dishes were placed on a laboratory bench-top (23 °C ambient temperature) at the University of Hawaii where germination of sown seed was assessed weekly for a 10 week period.

In December 2009, two house mice were caught at Ka Iwi Shoreline in southeastern Oahu and held in captivity in a similar fashion as the rats. Each mouse was offered a fresh *C. superba* fruit, and after 24 h the fruit and mouse droppings were inspected using the same methodology as used for black rats. The shorter (24 h) time period for the trials with mice relative to black rats was used for two reasons: (1) minimal food was consumed during the first 24 h, and (2) house mice have higher metabolic rates when compared to rats (MacAvoy et al. 2006).

Data analysis

Percentages of pre-dispersal fruit consumption at both sites were arcsin square-root transformed and tested for equal variances using a Levene's test. Upon verification of parametric assumptions, a two sample *t* test was used to compare fruit consumption between sites ($n = 36$ for Kahanahaiki, $n = 42$ for Pahole). For both the unbaited tracking tunnels that were used to assess rodent activity, and those used for assessing post-dispersal fruit consumption, we used Fisher's exact tests to compare 1) rat, and 2) mice activity in tunnels ($n = 7$ tunnels per site in both cases) between Kahanahaiki and Pahole. Although fruit and tracking cards were checked daily, statistical analyses were based on whether or not the tracking tunnel had been visited (for unbaited tunnels), or whether or not the fruit was consumed (for post-dispersal fruit consumption), at any point during the 5 day period. All analyses were completed in R (version 2.12.0, R Development Core Team 2010), and all means are presented ± 1 SE.

Results

Fruit production

The 36 plants monitored at Kahanahaiki collectively produced 192 infructescences, with a mean of five per plant (± 0.42). The mean number of fruit produced per plant was 85 (± 9.74), with 16 fruit (± 0.43) produced per infructescence. In total, 3,062 fruit were monitored at Kahanahaiki across all plants. At Pahole, the 42 plants collectively produced 194 infructescences, with a mean of four per plant (± 0.38). The mean number of fruit produced per plant at Pahole was 60 (± 6.77) with

13 fruit (± 0.39) produced per infructescence. In total, 2,426 fruit were monitored across all plants at Pahole.

Rodent activity at the study sites

The incidence of rat activity around the *C. superba* trees (measured using unbaited tracking tunnels; $n = 7$ per site) was significantly less at Kahanahaiki than at Pahole ($df = 1$, $P = 0.005$). By contrast, mouse activity was similar between the two sites ($df = 1$, $P = 0.286$).

Pre-dispersal fruit consumption

At Pahole, without rodent control, 41 of the 42 plants had some fruit consumed by rodents. By contrast, at Kahanahaiki where rodents were controlled, 14 of the 36 plants had some fruit consumed by rodents. Almost half of the fruit on all monitored Pahole plants were consumed whereas at Kahanahaiki mean consumption of fruit by rodents was $< 5\%$ ($t = 10.68$, $df = 76$, $P < 0.0001$; Fig. 2). At both sites, consumption rates of *C. superba* fruit were highest around the middle of the fruiting season (Fig. 3).

Motion-sensing cameras and evidence of fruit consumption by animals

Nine plants were monitored with motion sensing cameras for a total of 28 camera nights at Pahole and 12 plants for a total of 39 camera nights at Kahanahaiki. Only one avian frugivore, a single Japanese white-eye (*Zosterops japonicus*), was photographed

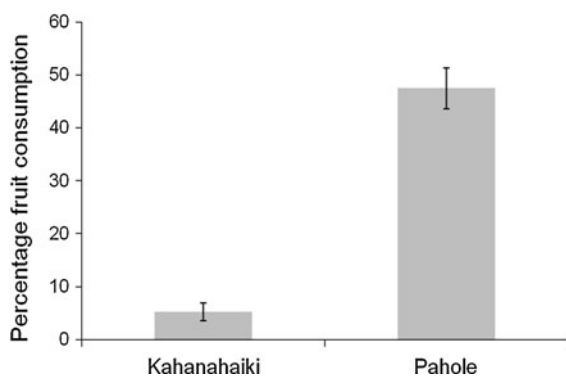


Fig. 2 Mean (\pm SE) percentage pre-dispersal consumption of *C. superba* fruit at Kahanahaiki ($n = 36$ plants) (rodent control) compared to Pahole ($n = 42$ plants) (no rodent control) recorded throughout the fruiting season

during daylight hours perching on a *C. superba* stem, but not interacting with the fruit. Black rats were the only animals photographed interacting with *C. superba* fruit (Fig. 4) and these were the likely culprits of all fruit consumption. All black rat visitations were at night. Eighteen photographs of individual visits by black rats to three plants were obtained at Pahole compared to seven photographed visits by black rats to three plants at Kahanahaiki. There was no evidence (e.g., absence of bird bill marks) that any other vertebrates interacted with the fruit.

Post-dispersal fruit consumption

Based on footprints, rats and mice visited *C. superba* fruit in the tracking tunnels on the forest floor at both sites. In several cases, rats and mice visited the same tunnel as evidenced by rat and mouse tracks on the same tracking card (71 and 14 % of cards at Pahole and Kahanahaiki, respectively). Rat consumption of *C. superba* fruit from the tracking tunnels was significantly higher at Pahole (100 % of fruit) compared to Kahanahaiki (29 % of fruit) after 5 days ($df = 1$, $P = 0.021$; Fig. 5). When rat tracks were observed on tracking cards (100 % at Pahole; 14 % at Kahanahaiki), the fruit was typically consumed entirely or otherwise missing. Where only mouse prints were recorded on tracking cards (43 % at Pahole; 71 % at Kahanahaiki), the fruit always remained in the tunnel and had little ($< 10\%$) fruit consumption, which was largely limited to nibbling on the exocarp. There was no significant difference in mouse consumption of *C. superba* fruit between Pahole and Kahanahaiki ($df = 1$, $P = 0.559$; Fig. 5).

Captive feeding trials

After 48 h of exposure of *C. superba* fruit to black rats in captivity, all six rats had eaten all of the seed and mesocarp. Five of the six rats consumed the entire fruit, and the single rat that did not consume all of the fruit had just 15 % of the fruit exocarp remaining in its cage. Seed coats and very small (< 1 mm) fragments of seed were recovered from each rat's droppings. None of the seed fragments that were extracted from rat droppings germinated when sowed, yet control seed (those sowed without passing through rats) readily ($86.7 \pm 6.7\%$) germinated. Therefore, black rats destroyed all of the seed that they consumed in the captive feeding trials.

Fig. 3 Total pre-dispersal consumption of individual *C. superba* fruit recorded during each field visit to Pahole (gray bars) and Kahanahaiki (black bars) during the study period (December 2009–January 2010)

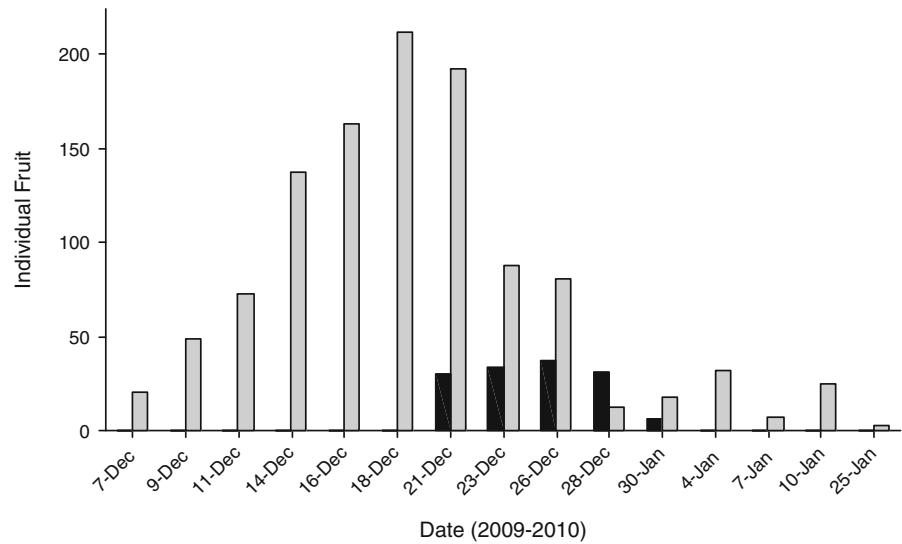


Fig. 4 Black rat interaction with *C. superba* fruit. *Photograph A*: A black rat feeding on the fruit of *C. superba* on a plant at Pahole. The image was captured using a motion-sensing camera. *Photograph B*: Black rat damage to a *C. superba* fruit placed in a

tracking tunnel at Pahole. Note the tooth marks on the exocarp and total removal of the mesocarp of the fruit. Part of the exocarp and the calyx (held by fingers) remain

When captive mice were offered *C. superba* fruit and assessed after 24 h, there was very little consumption of the pericarp (97.5 % \pm 0.5 fruit remained in each cage) and seed (98.0 % \pm 1.0 seed remained

in each cage). There were no obvious fragments or intact seed in the mice droppings, indicating that the few seed that may have been consumed by mice were likely killed upon consumption.

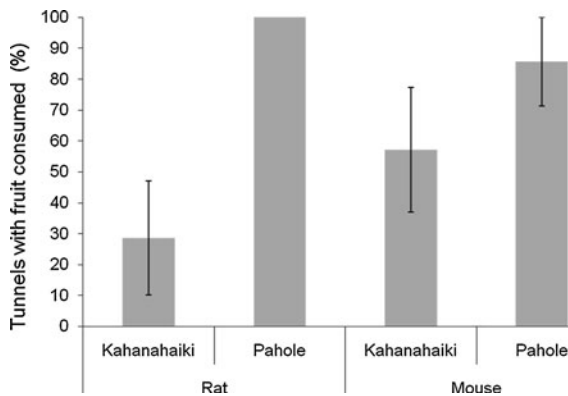


Fig. 5 Mean (\pm SE) percentage of tracking tunnels containing *C. superba* fruit that were consumed by rats or mice at Kahanahaiki and Pahole

Discussion

Results from pre- and post-dispersal fruit consumption combined with evidence from photographs and captive feeding trials suggest that invasive black rats are significant frugivores and seed predators of *C. superba*. First, black rats ate the fruit and destroyed all of the *C. superba* seed offered to them in captivity, suggesting that they destroy the seed that they consume in the field. Second, the considerable difference in both pre- and post-dispersal fruit consumption between Pahole and Kahanahaiki suggests that: (1) black rats are the major frugivores and seed predators where they freely interact with *C. superba*, and (2) large-scale rodent trapping significantly reduces pre- and post-dispersal fruit consumption and seed predation by rats at Kahanahaiki.

Black rats consumed almost half of all ripe *C. superba* fruit on the plants at Pahole. By contrast, trapping of rats at Kahanahaiki significantly reduced the pre-dispersal fruit consumption at Kahanahaiki (4%). Black rats are arboreal and feed in trees and on the ground (Delgado Garcia 2002; Auld et al. 2010; Shiels and Drake 2011). Shiels (2010) found that black rats spend 64% of their time above ground at Kahanahaiki. This allows them to freely access ripe fruit before they are dispersed. However, owing to the difficulty of quantifying fruit removal in plant canopies, few comparative studies have assessed levels of pre-dispersal fruit consumption by invasive rats. Meyer and Butaud (2009) found that rats (presumably

black rats) consumed and destroyed the seed in 99% of the fruit crop in trees of the Polynesian sandalwood (*Santalum insulare*) in Tahiti. Similarly, Delgado Garcia (2002) found that invasive black rats consumed 58% of the fruit of *Viburnum tinus* in the Canary Islands. These findings, and those of the current study, suggest that invasive black rats may be significant, yet underappreciated, pre-dispersal seed predators in the habitats that they have invaded.

The post-dispersal consumption of *C. superba* fruit showed a similar trend to that of pre-dispersal consumption, with all fruit consumed at Pahole compared with 29% at Kahanahaiki. The amount of post-dispersal fruit consumption recorded for *C. superba* was more pronounced than most other studies of native plants on Pacific islands. For example, Auld et al. (2010) found that up to 54 and 94% of fruits of the palm species, *Hedyscepe canterburyana* and *Lepidorrhachis mooreana*, respectively, were removed by black rats in a study conducted on Lord Howe Island. Rodent baiting significantly lowered fruit removal for both palm species. In a 2.5-year-study conducted at Kahanahaiki, Shiels and Drake (2011) placed fruit of 12 woody plant species on the ground in a series of vertebrate exclusion treatments. Six of the 12 species had the majority (>50%) of their fruit removed in treatments that were accessible to rats, and motion-sensing cameras also recorded only black rats removing fruit. Additional recent studies demonstrating post-dispersal fruit removal by invasive rodents have been conducted elsewhere in Hawaii (Chimera and Drake 2011) and in New Zealand (Moles and Drake 1999; Grant-Hoffman et al. 2010a).

The high rate of post-dispersal fruit consumption recorded in our study may partly owe to experimental design. First, due to the limited availability of undamaged fruit at Pahole, our study used a relatively small sample size ($n = 7$ tracking tunnels at each site), with tunnel nights undertaken during the peak period of pre-dispersal fruit consumption (Fig. 3). Second, tracking tunnels were placed in close proximity to one another at each site, which potentially allowed for a small number of rats to circulate among the tunnels. Further, we placed ripe fruit in the tracking tunnels; however, the majority of fruit that fall after natural abscission from the parent plant are already in an advanced stage of decomposition (R. Pender, per. obs.). Our study did not assess whether black rats

consume decomposing fruit. For these reasons, we may have slightly overestimated the rate of fruit consumption by rats under the parent plants.

Because of the difficulties in determining seed fate (e.g., if a seed consumed by an animal survives consumption), there have been few studies that have been able to determine if seeds removed by invasive rats are depredated (but see Williams et al. 2000; Pérez et al. 2008; Shiels and Drake 2011). The results from our laboratory feeding trials imply that black rats destroy all the seed in the *C. superba* fruit that they consume. Similarly, >80 % of the seeds from two native Hawaiian palms (*Pritchardia* spp.), which are ca. 6–10 times larger in seed length (>1,000 times larger in seed mass) than *C. superba*, were consumed and destroyed by captive black rats (Pérez et al. 2008). Williams et al. (2000) found that black rats in New Zealand destroyed seed larger than ca. 2.4 mm. However, a recent study by Shiels (2011) using captive black rats from Oahu that were fed the fruit of 25 different plant species, found that seed ≤ 1.5 mm survived gut passage but those seed ≥ 2.1 mm were destroyed. The seed of *C. superba* average 1.86 mm and were destroyed when ingested by black rats. The slightly smaller seed sizes that are destroyed by black rats in Hawaii (i.e., 1.86 mm and larger; Shiels 2011; this study) compared to New Zealand (>2.4 mm; Williams et al. 2000) may be explained by the larger average body sizes of black rats in New Zealand relative to those on Oahu (Shiels 2011).

Based on the results from tracking tunnels containing *C. superba* fruit, and the fruit offered in laboratory feeding trials, mice do not appear to be important seed predators of *C. superba*. Seed of a variety of species are commonly consumed by the house mouse, yet fleshy fruit is a small part (ca. 10 %) of mice diets in Hawaii (Cole et al. 2000; Shiels 2010) and other islands that they have invaded (Ruscoe and Murphy 2005; Angel et al. 2009). Additionally, it is unlikely that Pacific rats substantially affect *C. superba* fruit and seed destruction at our study sites because their densities were low (i.e., <1 indiv./ha; Shiels 2010) and there was no evidence that they visited *C. superba* fruit in trees or in the tracking tunnels.

Our photographic evidence revealed that only black rats consumed fruit on the *C. superba* plants. Despite the presence of introduced avian frugivores at both sites, we found no evidence that birds visited ripe fruit on the plants. Several introduced passerines, including

white-rumped shama (*Copsychus malabaricus*), Japanese white eye, red-billed leiothrix (*Leiothrix lutea*), red-whiskered bulbul (*Pycnonotus jocosus*), and red-vented bulbul (*Pycnonotus cafer*) are common at both study sites and are known to eat fruit of other native plant species (Foster and Robinson 2007; Chimera and Drake 2010; R. Pender, pers. obs.). Given the small populations of *C. superba*, resident bird species may favor more common fruit sources. Although our post-dispersal experiment excluded birds from interacting with *C. superba* fruit, it is possible that frugivorous passerines or the introduced galliform, Erckel's francolin (*Francolinus erckelii*), may consume fruit on the ground after they have fallen from the plant. Based on a past diet study of Erckel's francolin at Kahanahaiki (A. Shiels, unpublished data), and additional passerines in Hawaiian forests (Foster and Robinson 2007), it is highly likely that *C. superba* seed would be passed intact (i.e., dispersed) by birds if they ate the fruit.

Because we demonstrate that black rats destroy seed and potentially influence the recruitment of *C. superba* seedlings, we strongly support continued rat control at *C. superba* restoration sites during the fruiting season. To further our understanding of this rat-plant interaction, as well as increase the efficiency of rat control in *C. superba* restoration plantings, we recommend surveys at each of the current restoration sites to quantify animal fruit consumption, seed predation, and seedling recruitment. This information could also be used to compare large-scale rodent control sites, such as Kahanahaiki, to small-scale localized rodent control sites to help identify the minimum amount of rodent control effort required during the fruiting season to prevent rats from negatively affecting the regeneration of this species.

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