

Could poor seed dispersal contribute to predation by introduced rodents in a Hawaiian dry forest?

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Abstract Dry forests are among the most diverse, yet threatened, communities in Hawai'i. Dry forests throughout the archipelago suffer from a lack of natural regeneration of trees. Two factors that may limit tree recruitment include poor seed dispersal and seed predation by rodents. Poor or limited dispersal of fleshy-fruited species results in seeds and fruits falling directly under parents. Dispersed and non-dispersed seeds may differ in their vulnerability to predation. We tested effects of seed location (under/away from parent trees) and pulp (presence/absence) on predation of four native species that suffer from limited dispersal and one readily-dispersed alien species in Kanaio Natural Area Reserve, Maui. Three natives (*Diospyros sandwicensis*, *Pleomele auwahiensis*, *Santalum ellipticum*), had significantly more seeds removed under parent trees than in exposed sites away from trees. For the one alien (*Bocconia frutescens*) and two native trees (*D. sandwicensis*, *P. auwahiensis*) that were evaluated, significantly more intact fruits were removed than were cleaned seeds. Presence of teeth marks and gnawed seed husk

fragments indicate introduced rodents are destroying many of the seeds they remove. These results suggest that seed predation is disproportionately concentrated among poorly-dispersed seeds and may contribute to recruitment failure.

Keywords Dispersal failure · Fruit pulp · Hawaiian Islands · *Rattus rattus* · Seed predation

Introduction

Most oceanic island ecosystems, including the Hawaiian Islands, lack native rodents (Drake and Hunt 2009). Through primarily inadvertent human transport, the Polynesian rat (*Rattus exulans* (Peale)), the black or ship rat (*R. rattus* L.), the Norway or roof rat (*R. norvegicus* (Berkenhout)) and the house mouse (*Mus musculus* L.) have been introduced to many islands throughout the world, with devastating impacts on the insular biota (Townsend et al. 2006; Drake and Hunt 2009; Meyer and Butaud 2009; Traveset et al. 2009). In the Hawaiian Islands, these rodents have negatively impacted native birds (Atkinson 1977; Scott et al. 1986), snails and arthropods (Hadfield et al. 1993; Cole et al. 2000; Hadfield and Saufield 2009), and plants, including many rare and endangered species (Stone 1985; Sugihara 1997; Cole et al. 2000). Although introduced rodents are notorious

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plant and seed predators in other insular ecosystems (Clark 1982; Campbell et al. 1984; Allen et al. 1994; Moles and Drake 1999; Campbell and Atkinson 2002; Delgado Garcia 2002; McConkey et al. 2003; Meyer and Butaud 2009), and have been anecdotally implicated in seed destruction in Hawaiian dry forests, (Medeiros et al. 1986; Cabin et al. 2000; Athens et al. 2002; Athens 2009), no studies have empirically documented their impacts on seeds of dry forest taxa. Because many dry forest species produce fruits with one to few large seeds (Wagner et al. 1999; Pau et al. 2009), and because rodents in general are significant predators of large seeds (Stiles 2001), introduced rodents could be limiting seedling recruitment through their effects on seed mortality (Crawley 2001).

Biologically diverse dry forests once covered a significant portion of the leeward sides of the Hawaiian Islands (Cuddihy and Stone 1990; Athens et al. 2002). Impacts from land clearing, fire, and invasive species have reduced them to approximately 10 percent of their former area (Loope 1998; Mehrhoff 1998). A troubling phenomenon affecting the persistence and potential restoration of Hawaiian dry forest communities is a problem characteristic of tropical dry forests worldwide (Janzen 1988)—the almost complete lack of natural regeneration of native tree species (Loope 1998; Cabin et al. 2000). Several factors may contribute to seedling recruitment failure. These include natural fluxes in flowering and fruiting cycles associated with climatically episodic environments, browsing and trampling by ungulates, competition with weeds, loss of pollinators, impacts of non-native invertebrates and pathogens on seed and seedling survival, modifications in microclimate and microhabitats suitable for seed germination and seedling survival, loss of native animals that scarified and dispersed seeds, and seed predation by introduced animals such as rodents (Janzen 1988; Bullock 1995; Aide et al. 2000; Cabin et al. 2000; Holl et al. 2000; Zimmerman et al. 2000; Traveset and Richardson 2006; Chimera and Drake 2010). Prior to human contact, Hawaii's lowland dry forests supported a diverse assemblage of native birds, including large flightless geese and ducks (family Anatidae) and frugivores such as crows (family Corvidae) and thrushes (family Turdidae) among others (Ziegler 2002). The native avifauna has since been replaced almost exclusively by non-native gamebirds and smaller generalists such as the

Japanese white-eye (*Zosterops japonicus*) (Pratt et al. 1987; Pratt et al. 2009). Lack of fruit processing or pulp removal by absent or extinct native frugivores may facilitate detection of seeds and contribute to increased predation levels by introduced rodents (Nystrand and Granstrom 1997; Moles and Drake 1999). Consequently, seed predation by rodents could be influencing community composition and structure of Hawaiian dry forests.

In many remnant Hawaiian dry forests, isolated trees are surrounded by a lower-statured matrix of shrublands, non-native grasslands and largely barren lava flows (Cuddihy and Stone 1990; Mueller-Dombois and Fosberg 1998). Loss of native dispersers and subsequent dispersal failure can result in higher seed densities under parent trees than in the more open matrix, and non-native birds may disproportionately disperse the smaller seeds of non-native plants (Chimera and Drake 2010). The scattered spatial distribution of dry forest trees can also result in concentrated seed rain under trees due to the preferential movements of birds to these foraging and perching sites, which consequently may serve as recruitment foci for bird-disseminated species (McDonnell and Stiles 1983; Ferguson and Drake 1999; Jordano and Schupp 2000; Shiels and Walker 2003; Clark et al. 2004). Sites beneath trees can therefore provide microsites for seedling establishment and may play a role in the succession and regeneration of degraded areas (Uhl 1998; Wijdeven and Kuzee 2000).

Despite the potential benefits, however, non-random deposition under trees, combined with high seed rain under parent trees, could also influence seed predation levels (Hulme 1998). Several studies report higher predation levels under trees and vegetation than in open areas (Howe et al. 1985; Chapman and Chapman 1996; Hulme 1997; Wenny 2000; Holl 2002). Others have found no difference (DeSteven and Putz 1984; Terborgh et al. 1993), or higher predation levels in exposed areas or grasslands (Hay and Fuller 1981; Uhl 1998; Wijdeven and Kuzee 2000). Holl and Lulow (1997) reported lower predation levels under isolated pasture trees as opposed to either open pastures or intact forests. Seed predators may avoid exposed sites to minimize risks from aerial predators such as owls (Murúa and González 1982; Sánchez-Cordeiro and Martínez-Gallardo 1998), a factor that could influence seed removal in Hawaiian

dry forests. Lower seed densities in exposed sites may also contribute to reduced predation levels, as seed predators may concentrate foraging activity in areas with higher seed densities closer to the seed source (Janzen 1971; Hulme 1998).

To better understand interactions between tree distribution and seed predation in different microhabitats of a Hawaiian dry forest, we addressed the following questions:

- (1) Are rodents removing seeds of dry forest species from the forest floor?
- (2) Is there a difference in removal levels of seeds under parent trees and in exposed sites away from parent trees?
- (3) Does the presence of fruit pulp or fleshy arils affect seed removal?

Methods

Study site

This study was conducted in the Kanaio Natural Area Reserve (KNAR), on leeward East Maui, Hawai'i, at 750–850 m elevation (20°36'N, 156°20'W). Mean monthly temperatures range between 20–30°C with mean annual rainfall of approximately 750 mm, mostly falling from October to April (Giambelluca et al. 1986). The 354-hectare reserve was established in 1990 to protect exemplary representatives of Hawaiian dry forest taxa and communities, including twenty-two native tree species. Anecdotal observations by the authors suggest that only eight of these species may be regenerating. Certain non-native trees and shrubs, however, including the widespread *Bocconia frutescens*, *Schinus terebinthifolius*, and *Lantana camara*, among others, regenerate without the difficulties experienced by native species (Chimera, personal observation). At least two non-native rodent species, the black rat (*Rattus rattus*), and the house mouse (*Mus musculus*) currently occur in KNAR (Medeiros et al. 1986).

Measuring seed removal levels

To examine seed removal levels of common dry forest trees, seeds from four native (endemic) and one non-native tree species were used. We selected native

species that were common enough to provide ample trees for the experimental design, and that represented a range of seed sizes (Table 1). Native fleshy-fruited taxa include *Reynoldsia sandwicensis* Gray, *Diospyros sandwicensis* (A. DC.) Fosberg, *Santalum ellipticum* Gaud., and *Pleomele auwahiensis* St. John (Chimera 2004). Each native tree suffers from limited dispersal, with almost all fruits falling directly under the parent canopy (Chimera and Drake 2010). An invasive, non-native neotropical tree with arillate seeds, *Bocconia frutescens* L., was also used. This tree is abundant at the site and produces large numbers of seeds that are readily dispersed by non-native birds, but also fall in large numbers under parent trees (Chimera and Drake 2010). Hereafter, all study species are referred to by genus name only. Mean tree heights ranged between 3 to 6 m. All reproductively mature study trees were first recorded along 12 parallel transects (10-m widths) of 100–675 m length and spaced 50 m apart. Study trees were randomly selected from this subset of individuals such that no selected trees were within 25 m of each other. Fifteen trees of each species were selected for the placement of sets of treatments.

Treatments

Four treatments were used, based on designs of Moles and Drake (1999): “open ground”, a depression (11 cm × 11 cm × 1 cm deep) in the ground; “open pot”, square black plastic flower pots (110 mm × 110 mm wide; 150 mm tall) with one side cut away and filled with soil such that inside and outside soil levels were equal; pot with “rodent access”, open pots covered with 12-mm steel mesh with an opening (35 mm × 35 mm) large enough to allow rodent access but small enough to deter feeding by game birds; pot with “rodent-proof” mesh, open pots with 12-mm mesh designed to prevent rodent but not invertebrate access. Open ground treatments were used as a control to determine if rodents were attracted or deterred by pots. Pots with rodent access, but excluding game birds, separated potential differences in removal levels between rodents and ground-foraging birds. Rodent-proof pots were used to determine the level of seed removal or damage caused by invertebrates.

To investigate whether removal was affected by location, sets of four treatments were placed under

Table 1 Dry forest tree species used in predation trials including means (± 1 SE) of seed length (L) and width (W) without pulp and number of seeds per fruit

Species	Family	Fruit type	L (mm)	W (mm)	Seeds/fruit
<i>Bocconia frutescens</i>	Papaveraceae	Arillate ^a	4.08 (0.03)	2.71 (0.02)	1
<i>Diospyros sandwicensis</i>	Ebenaceae	Berry	12.44 (0.15)	4.98 (0.09)	1.54 (0.11)
<i>Pleomele auwahiensis</i>	Agavaceae	Berry	7.62 (0.06)	6.15 (0.06)	1.3 (0.09)
<i>Reynoldsia sandwicensis</i>	Araliaceae	Drupe	5.34 (0.05)	2.92 (0.03)	9.08 (0.23)
<i>Santalum ellipticum</i>	Santalaceae	Drupe	7.88 (0.05)	6.96 (0.04)	1

$n = 100$ for seed measurements, $n = 50$ for seeds/fruit

^a Single-seeded, arillate capsule

each tree crown (with a minimum distance of one meter separating each treatment), and equivalent sets were placed in adjacent, exposed sites, on a random compass direction, five meters from the edge of the tree crown. Exposed sites consisted of barren rock, low-stature grasses, shrubs and herbaceous species less than 50 cm tall (Chimera 2004). Experiments were arranged in a 2×4 factorial block design for three species and a 2×5 factorial block design for two species (*Bocconia* and *Diospyros*) with one additional treatment (see below). For purposes of statistical analysis, each tree vicinity constituted an individual block with four or five treatments (factor 1) and two locations (under trees and in exposed sites, factor 2), per block (Zar 1999). Sets of tree and exposed site treatments in the vicinity of a particular tree were treated as a block because the distance separating them (five meters) was closer than the distance between individual study trees (25 meters minimum), and is assumed to be within the home range of an individual rodent (Tomich 1986).

For each species, a set of five seeds was placed in each of the four treatments under each of 15 conspecific fruiting trees (e.g. sets of *Santalum* seeds under fruiting *Santalum* trees, sets of *Pleomele* seeds under fruiting *Pleomele* trees, etc.) and in each of 15 exposed sites, for a total of 600 seeds per species (300 under trees, 300 in exposed sites). Only trees estimated to have at least 25 percent of branches with mature fruit were used. Seeds within ripe fruit were collected from five haphazardly-selected trees of each species as they became available. Fruit pulp was removed from seeds unless otherwise stated. Pulp was removed using water and paper towels, and seeds were allowed to dry before use. During the cleaning process, seeds which sank in water were

considered viable and used in experimental trials. Any floating seeds were discarded.

To test the effects of pulp on seed removal levels for two species, *Diospyros* and *Bocconia*, additional sets of five intact *Diospyros* berries (1.54 ± 0.11 seeds/berry; Table 1), and five *Bocconia* seeds with arils attached (“arillate seeds”) were also placed in open ground treatments under trees and in exposed areas (thereby constituting a fifth treatment for these two species only). For these species, removal rates were compared between seeds and whole fruits to evaluate the effect of fruit pulp presence or absence on predation. It is unlikely that *Bocconia* seeds would be naturally dispersed to exposed sites with arils still present, so their inclusion in exposed site treatments is a control for purposes of statistical analysis only. To test the effects of pulp on seed removal for *Pleomele*, a separate trial was conducted in which sets of five fresh berries (1.3 ± 0.09 seeds/berry; Table 1) with pulp intact were placed in each of the four treatments under a different set of 15 trees and exposed sites, for a total of 600 fruits from this species (300 under trees, 300 in exposed sites).

Seed and fruit removal were recorded over five 15-day periods between April and June 2003. In all trials, fresh seeds were used 1 day after collection, and placement under trees coincided with peak fruiting of each study species (Chimera and Drake 2010). Because rodent population densities are often correlated with biotic factors such as fruiting phenology (Choquenot and Ruscoe 2000; Efford et al. 2006), we expected at least some rodents to be present in the area at the time of the study. Seeds were categorized as removed if taken from the treatment area or if destroyed at the treatment site. Seed removal does not always equal predation, as

some seeds may have been secondarily dispersed or partially consumed, rather than destroyed, by rodents or game birds (Vander Wall et al. 2005; Perez et al. 2008; Shiels and Drake 2010). Measures of seed removal may therefore overestimate predation levels, although the rodents likely responsible for removal are primarily seed eaters (Tomich 1986). Because no trapping was conducted for this study, it was unknown which rodents would remove seeds, but trapping around rare trees (independent of this study) caught both black rats (*Rattus rattus*) and house mice (*Mus musculus*) throughout the year. Because both rodents are generalist seed predators (Sugihara 1997), no attempt was made to distinguish between the impacts of the two rodent species at the site.

Analysis

Numbers of seeds remaining under trees were compared with those in exposed sites. Removal levels were not compared between species. Differences between combinations of treatment and location (tree or exposed) were compared using a general linear model, with mean number of seeds remaining as the dependent variable, individual tree (including surrounding area within a 5 m radius) as the blocking factor, and treatment and location as explanatory variables with one interaction term: treatment \times location. Because some observation values equaled zero, data were square root transformed ($X + 0.5$) to meet assumptions of normality (Zar 1999). Tukey tests were used to determine significantly different treatments (Zar 1999; Ryan and Joiner 2001). Because removal trials for *Pleomele* seeds and fruits were conducted simultaneously, mean numbers of seeds and fruits (square root $\{X + 0.5\}$) remaining in open ground treatments were further compared between locations using a two-way ANOVA, with a Tukey test identifying differences among treatments. Statistical analyses were performed using Minitab 15.1.30.0 (Minitab Inc. 2007).

Results

For four of five species investigated, rodents did remove seeds and/or fruits over the 15-day trial periods (Fig. 1). There were little or no differences in

removal of seeds from open ground, open pot, or rodent accessible treatments (Fig. 2). Although these results do not discount the possibility that game birds may have removed seeds from some treatments, the data confirm that rodents were at least partially responsible. Because no seeds or fruits of any species were removed from rodent-proof pots at any point during the study, and no signs of invertebrate damage were noted during the 15-day trial durations, it is assumed that rodents were the main culprits in documented removal levels, and the focus of analysis is on the rodent-accessible treatments. Tooth marks, droppings and seed husks further suggest that rodents were primarily responsible for seed removal. *Bocconia* and *Pleomele* seed husks remained in many of the treatments. Rodent bite marks and partially consumed seeds were present in several *Diospyros* treatments. Seed husks and fragments were also present in about half of the rodent-accessible *Santalum* treatments.

Removal levels after 15 days differed among species and by location, ranging from 100% of *Santalum* seeds under trees to 0% of *Reynoldsia* seeds under trees or in exposed sites (Fig. 1; Table 2). In most instances, the majority of seeds and/or fruits were gone within the first few days (Fig. 1).

Location of seeds (under trees versus exposed sites) was important for three species. Significantly more *Diospyros*, *Pleomele* and *Santalum* seeds were removed under trees than from exposed sites, but removal levels did not differ for *Bocconia* or *Reynoldsia* (Table 2; Fig. 2).

Presence of pulp or arils on seeds also influenced removal levels for the three species evaluated. For *Bocconia*, significantly more arillate seeds were removed than cleaned seeds (Table 2; Fig. 2). Some of the remaining arillate seeds had arils removed with no apparent damage to seeds. For *Diospyros*, significantly more berries than seeds were removed from trees and exposed sites (Table 2; Fig. 2). For *Pleomele*, significantly more berries were removed than seeds, but location was not significant (Table 3; Fig. 3).

Discussion

Higher removal levels under trees than in exposed sites for seeds of three native species (*Diospyros*,

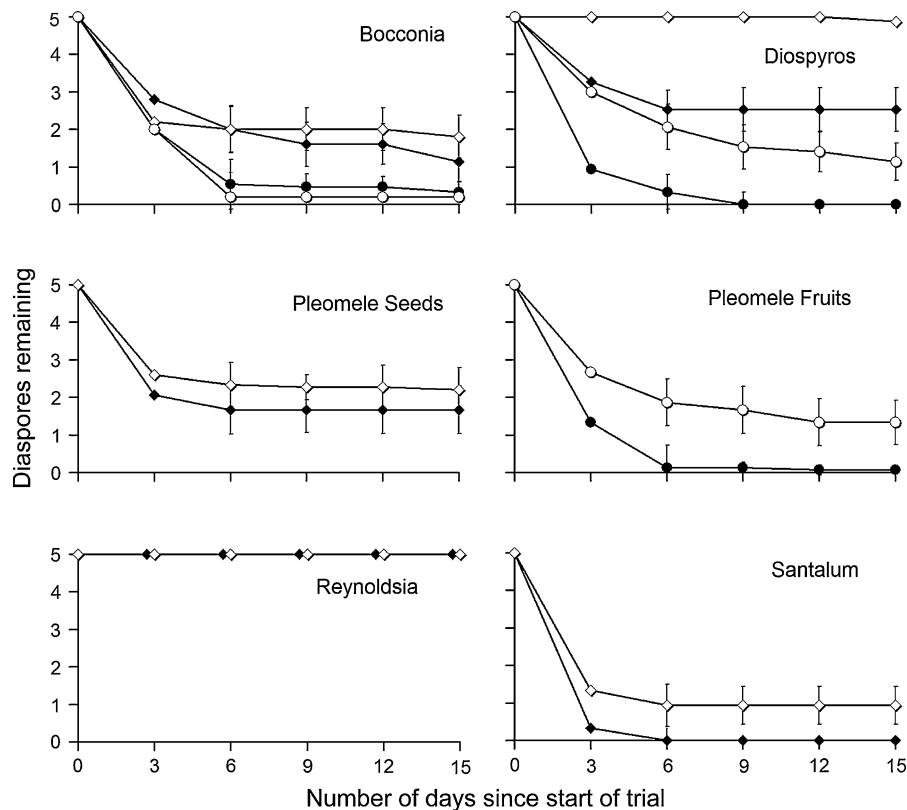


Fig. 1 Removal rates of seeds and fruits from the Kanaio Natural Area Reserve. Mean number of seeds or fruits remaining ± 1 SE for open ground treatments under trees and in exposed sites ($n = 15$ trees \times 5 seeds per treatment). *Filled diamond* cleaned seeds under trees; *open diamond* cleaned seeds in exposed sites; *filled circle* seeds (with pulp) under trees; *open circle* seeds (with pulp) in exposed sites. Cleaned

seed and intact fruit treatments were placed together under trees and in exposed sites for *Bocconia* and *Diospyros*. Graphs for *Pleomele* seeds and fruits are presented separately, as cleaned seed treatments and intact fruit treatments were placed under separate sets of trees and exposed sites. Only cleaned seed treatments were used in *Reynoldsia* and *Santalum* trials

Pleomele, *Santalum*) suggest that poor dispersal can contribute to increased seed predation levels by introduced rodents. Higher removal levels for fruits versus cleaned seeds of the one introduced (*Bocconia*) and two native species (*Diospyros*, *Pleomele*) that were evaluated suggest that lack of pulp removal by frugivores may further contribute to a greater predation risk. Dispersal failure may be attributable to the extinction of native birds and replacement with an introduced avifauna that disproportionately disperse seeds of non-native trees and shrubs (Chimera and Drake 2010). The potential benefits of pulp removal, dispersal, and escape from predation afforded to at least one invasive tree (*Bocconia*), combined with dispersal failure and increased predation levels for native species, is likely contributing to the

continued decline of already degraded Hawaiian dry forest ecosystems (Cuddihy and Stone 1990; Mehrhoff 1998).

The variable seed removal levels for tree species in this study are consistent with inter-specific differences common in the literature (Chapman and Chapman 1996; Hulme 1998; Figueroa et al. 2002; Jones et al. 2003). Average predation levels on cleaned seeds for all species combined, whether under trees (59%) or in exposed sites (41%), are comparable to levels reported from forests throughout the world. Levels of rodent seed predation typically exceed 50% for many species in a number of different ecosystems (Hulme 1998). In a forest site in Spain, approximately 70% of *Ilex aquifolium* seeds were removed after two 2-week periods (Ramón

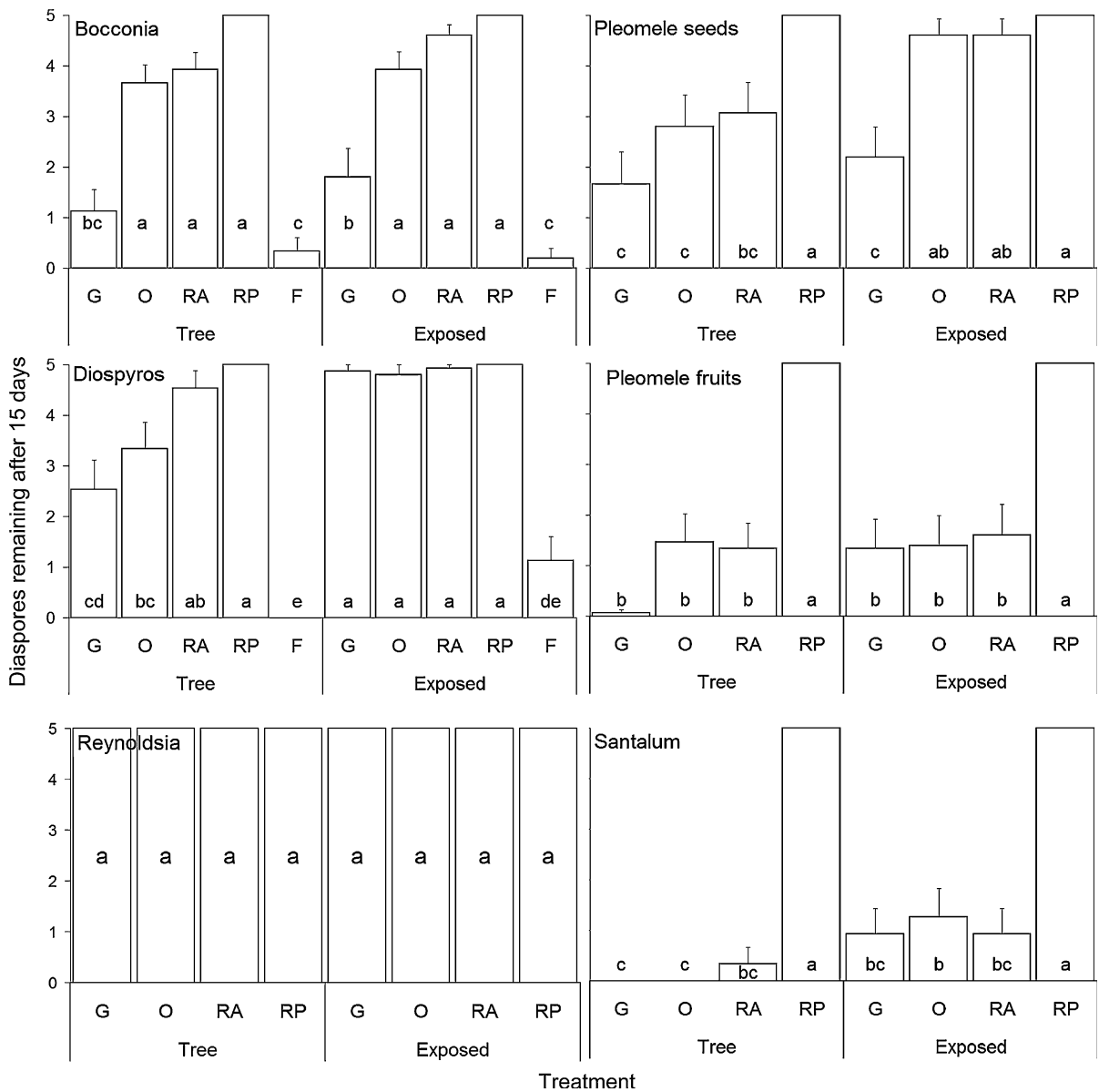


Fig. 2 Removal of seeds and/or fruits under trees and in exposed sites after 15 days. Treatments include *G* open ground, *O* open pots, *RA* pots with rodent access, *RP* rodent-proof pots, *F* fruits on open ground ($n = 15$ trees * 5 seeds/fruits per treatment). *Bocconia* and *Diospyros* trials include all treatments. Graphs for *Pleomele* seeds and fruits are presented separately, as cleaned seed and intact fruit treatments were

placed under separate sets of trees and exposed sites. *Reynoldsia* and *Santalum* trials did not include fruit (*F*) treatments. Bars represent the mean +1 SE. Letters at the base of bars show the results of the Tukey test. Within a species, treatments sharing the same letter are not significantly different ($P > 0.05$)

Obeso and Fernández-Calvo 2002). In the northern territories of Hong Kong, between 73 and 86% of seeds were removed for four shrubland species, and between 33 and 83% were removed for six grassland species after 60 days (Hau 1997). For a tropical dry

forest shrub in Mexico, 64% of seeds were removed (Gryj and Dominguez 1996). Excluding *Reynoldsia*, with no seeds removed during the 15-day study duration, average seed removal levels were 73% under trees and 51% in exposed sites.

Table 2 General linear models for mean number of seeds and/or fruits (square root $\{X + 0.5\}$) remaining versus block, treatment, location (under tree or exposed), and the interaction of treatment (Trt) and location (Loc) after 15 days for four dry forest trees in Kanaio Natural Area Reserve

Species	Source of variation	df	SS (model III)	MS	F	P
<i>Bocconia frutescens</i>	Block	14	4.89	0.35	2.51	0.003
	Treatment	4	52.49	13.12	94.35	0.000
	Location	1	0.23	0.23	1.66	0.200
	Trt \times Loc	4	0.34	0.08	0.60	0.662
	Error	126	17.52	0.14		
	Total	149	75.47			
<i>Diospyros sandwicensis</i>	Block	14	2.26	0.16	1.02	0.442
	Treatment	4	40.15	10.04	63.17	0.000
	Location	1	4.33	4.33	27.26	0.000
	Trt \times Loc	4	2.43	0.61	3.83	0.006
	Error	126	20.02	0.16		
	Total	149	69.19			
<i>Pleomele auwahiensis</i> Seeds	Block	14	12.25	0.88	3.16	0.000
	Treatment	3	14.88	4.96	17.91	0.000
	Location	1	3.06	3.06	11.06	0.001
	Trt \times Loc	3	1.55	0.52	1.87	0.140
	Error	98	27.15	0.28		
	Total	119	58.89			
<i>Pleomele auwahiensis</i> Fruits	Block	14	12.10	0.86	3.31	0.000
	Treatment	3	35.23	11.74	45.03	0.000
	Location	1	0.31	0.31	1.19	0.278
	Trt \times Loc	3	0.93	0.31	1.19	0.316
	Error	98	25.56	0.26		
	Total	119	74.13			
<i>Santalum ellipticum</i>	Block	14	8.35	0.60	4.38	0.000
	Treatment	3	47.06	15.69	115.26	0.000
	Location	1	1.65	1.65	12.12	0.001
	Trt \times Loc	3	0.73	0.24	1.79	0.155
	Error	98	13.34	0.14		
	Total	119	71.13			

Tests were not performed on *Reynoldsia*, as no seeds were removed from any treatments

Table 3 Two-way ANOVA results for the effects of treatment (seed or fruit) and location (under tree or exposed) on removal levels for *Pleomele auwahiensis*

Source of variation	df	SS	MS	F	P
Treatment (seed/fruit)	1	2.62	2.62	5.82	0.019
Location (tree/exposed)	1	1.43	1.43	3.17	0.080
Interaction	1	0.13	0.13	0.29	0.591
Error	56	25.23	0.45		
Total	59	29.41			

A recent evolutionary history without seed-eating rodents might be one factor that contributes to relatively high removal levels for some Hawaiian species (Ziegler 2002). Other native Hawaiian dry forest species, including *Nestegis sandwicensis* (Oleaceae), *Alectryon macrococcus* (Sapindaceae), *Nesoluma polynesianum* (Sapotaceae) and *Pouteria sandwicensis* (Sapotaceae) also suffer from conspicuous predation, as evidenced by the large piles of their seed husks under most trees (Chimera pers.

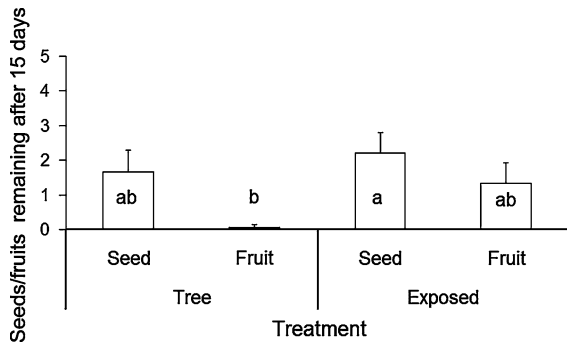


Fig. 3 Removal of *Pleomele auwahiensis* seeds and fruits on the open ground under trees and in exposed sites after 15 days. ($n = 15$ trees * 5 seeds/fruits per treatment). Bars represent the mean + 1 SE. Letters at the base of bars show the results of the Tukey test. Treatments sharing the same letter are not significantly different ($P > 0.05$)

obs.). Removal levels for this study are much higher than the 10% reported for 11 species in New Zealand, with an island biota similarly lacking native rodents (Moles and Drake 1999). An evolutionary history of exposure to rodents may not be a key factor for one species, however, as the non-native neotropical tree *Bocconia* had the second highest percentage of seeds removed both from under trees and in exposed sites. Comparisons between a larger sample of island and mainland congeners would therefore be required to identify particularly vulnerable species for which evolutionary history and predator naivety may be important.

Removal levels of seeds and fruits also differed between locations. In three trials, more seeds were removed under trees than exposed sites, but location was not significant for *Bocconia* seeds and fruits or *Pleomele* fruits (Table 2; Fig. 2). In no instance were more seeds removed from exposed sites. Microhabitat can be an important factor influencing seed predation levels. Many studies document lower predation levels by small mammals in open versus forested areas (Aide and Cavellier 1994; Bustamante and Simonetti 2000; Holl 2002). Others report that higher levels occur in open sites versus under trees (Uhl 1998; Wijdeven and Kuzee 2000). Because seed densities can influence predation (Hulme 1998), greater removal levels were expected under trees than in exposed sites due to much higher seed densities found under trees at KNAR (Chimera and Drake 2010). This study lends support to that hypothesis, but interspecific differences may also contribute to disparities in removal levels.

Avian predators such as owls may also deter rodent foraging in exposed areas, thereby reducing seed predation in open sites (Murúa and González 1982; Sánchez-Cordeiro and Martínez-Gallardo 1998). Two owl species occur in KNAR, the native Hawaiian short-eared owl (*Asio flammeus*), and the common barn-owl (*Tyto alba*), a North American species introduced in 1958 for rodent control in sugar cane fields (Tomich 1962). If seed densities or avian predators do influence removal levels in exposed locations, these effects were negligible in two of the trials (Table 2). It is possible that owls occur at numbers too low to noticeably affect seed predation in exposed sites, and those differences that were significant may be attributed to other factors.

For the trials that did not differ, location of exposed site treatments, within five meters of tree crowns, may be too close to account for truly separate microhabitats, although differences in vegetative cover, exposure, leaf litter, understory humidity and seed densities suggest otherwise. Placing five seeds in each treatment results in much higher seed densities in exposed sites than would naturally occur away from tree crowns. This increased density, intended to simulate a hypothetical dispersal event by a frugivore, or a direct-seeding technique for restoration purposes (Brooks et al. 2009), could contribute to unnaturally high predation levels, as rodents have demonstrated the ability to more easily locate larger versus smaller seed piles (Hammond 1995). None of the preceding explanations satisfactorily address why removal levels differed in locations for three trials, but not for the other two, so yet another factor may be responsible for the variability. It may be that the study duration accounted for differences detected by location, and keeping seeds out longer might have resulted in equivalent final predation levels for all trials. Differences in nutrient content or odor cues between species may also influence the desirability or detectability of seeds (Vander Wall 2009). Seed size is another factor thought to affect seed predation levels (Hulme 1998). Because the seeds used in this study were relatively large (Table 1), future experiments should test a broader range of seed sizes, along with different densities, to more accurately determine if any real relationships exist between seed size or mass and removal levels under trees and exposed sites.

Higher removal levels for fruits than seeds were reported in New Zealand (Moles and Drake 1999)

and Spain (Hulme 1997). Pulp presence on *Diospyros* seeds and arils on *Bocconia* seeds also resulted in higher removal levels than for most cleaned seed treatments (Table 2; Fig. 2). More *Pleomele* fruits than seeds were removed, but location was not significant (Table 3; Fig. 3). For these species, it is unknown whether fruit removal results in seed destruction or dispersal, although cleaned-seed trials with these species indicate rodents are also removing, and consuming, seeds. Because intact, and presumably viable, *Reynoldsia* seeds have previously been reported from rat droppings (Medeiros et al. 1986), the use of depulped *Reynoldsia* seeds in this study may explain the complete lack of their removal. For *Reynoldsia*, rodents may be more attracted to fruits and could potentially benefit the tree by legitimately dispersing seeds, as they may be doing on a limited basis in other Pacific Island ecosystems (Williams et al. 2000; Shiels and Drake 2010). In general, however, fruit pulp appears to contribute to higher overall removal levels, but further tests with more species are necessary before definitive conclusions can be made about the effects of pulp on seed removal or predation.

In this study, some seeds or fruit placed on the ground experienced higher removal levels than those placed in other treatments. Differences in removal levels from some accessible treatments may be due to the reluctance of rodents to enter artificial structures (Inglis et al. 1996; Moles and Drake 1999). The high removal levels recorded for all rodent-accessible treatments of *Santalum* (Fig. 2), however, suggest that rodents will enter artificial environments to obtain highly desirable seeds. It may also be possible that *Santalum* seeds are particularly easy to detect by olfactory or other cues. Some of the fruit removal from open ground treatments may be due to the foraging of non-native game birds, including the black (*Francolinus francolinus*) and gray (*F. pondicerianus*) francolin, the ring-necked pheasant (*Phasianus colchicus*) and the common peafowl (*Pavo cristatus*). As game birds can potentially disperse seeds (Cole et al. 1995), seed or fruit removal could result in either dispersal or predation, depending on the agent responsible for removal. Nevertheless, presence of teeth marks on seeds, and gnawed husks, suggest that rodents were responsible for at least some of the seed and fruit removal.

Conclusion

Although almost no fleshy-fruited species are naturally dispersed to exposed sites, (Chimera and Drake 2010), differences in removal levels under trees and in exposed sites could be important for restoration of degraded habitats that employ direct-seeding techniques into open areas or abandoned pastures (Bonilla-Moheno and Holl 2009; Brooks et al. 2009). Even if natural or human-assisted dispersal to exposed sites does allow seeds to escape predation, however, harsher microsite conditions may limit seedling recruitment and survival (Kitajima and Fenner 2001), a situation seemingly occurring at KNAR (Chimera 2004). Nevertheless, seed predation of particular Hawaiian dry forest tree species appears to be one of several factors contributing to lack of seedling recruitment. Although rodents may have limited beneficial effects if removal sometimes results in dispersal (Williams et al. 2000; Vander Wall and Longland 2004), for many Hawaiian species, the effects appear to be predominantly negative. Because this study did not track ultimate seed fate, however, it may be that a rare dispersal event by rodents leads to some recruitment of native species. This could eventually offset earlier seed losses, a scenario documented with primate-dispersed, and rodent-depredated seeds in Uganda, East Africa (Balcomb and Chapman 2003), as well as for both rodent-depredated and dispersed seeds in a mesic forest of the Hawaiian Islands (Shiels and Drake 2010).

Howe and Brown (1999) report that seed predators may selectively consume and destroy seeds of some taxa more than others, thereby giving a competitive advantage to less preferred species. For certain Hawaiian plants, such as the heavily depredated *Santalum*, this is particularly relevant, but for species experiencing moderate predation levels, the effects may be minor. For the invasive *Bocconia* tree, seed removal and predation are not preventing the spread of this species into native forest habitat, a case which may also be true for other widespread and prolific, fleshy-fruited invaders including *Lantana camara* (Verbenaceae) and *Schinus terebinthifolius* (Anacardiaceae) in dry and mesic forests of Hawaii and for *Clidemia hirta* (Melastomataceae), *Psidium cattleianum* (Myrtaceae), *Hedychium gardnerianum* (Zingiberaceae) and others in Hawaiian wet forests

(Wagner et al. 1999; Medeiros 2004; Chimera and Drake 2010). Similarly, on many islands in French Polynesia, several native species are threatened with extinction, in part due to the impacts of rodent seed predation (Meyer and Butaud 2009), whereas invasive trees such as *Miconia calvescens* (Melastomataceae) and others continue to spread in spite of the presence of rodents (Meyer and Florence 1996; Meyer 2004). In certain situations, the negative impacts may be further compounded, as rodents may not only disproportionately destroy seeds of native species, but may also facilitate plant invasions by dispersing intact seeds of non-native weeds such as *Miconia*, *Clidemia* and others (Shiels 2010). In contrast to the situation in Hawaii and French Polynesia, greater predation of non-native Pinaceae seeds versus native seeds by native rodents may confer a form of biotic resistance on an island in Patagonia, Argentina, by inhibiting exotic conifer invasions away from plantations (Nuñez et al. 2008). Such studies suggest that the context in which rodent seed predation occurs can influence the failure, as well as the success, of non-native plant invasions. Because seed predation can also be a major constraint for native tree regeneration in neotropical forests (Guariguata and Pinard 1998), it would be valuable to know to what degree predation limits recruitment of each species. Future conservation and restoration efforts in degraded forest ecosystems of the Hawaiian Islands and elsewhere could therefore begin to address the impacts of seed predation on those species identified as particularly vulnerable.

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