

Disruption of recruitment in two endemic palms on Lord Howe Island by invasive rats

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Abstract Invasive species may have negative impacts on many narrow range endemics and species restricted to oceanic islands. Predicting recent impacts of invasive species on long-lived trees is difficult because the presence of adult plants may mask population changes. We examined the impact of introduced black rats (*Rattus rattus*) on two palm species restricted to cloud forests and endemic to Lord Howe Island, a small oceanic island in the southern Pacific. We combined estimates of the standing size distribution of these palms with the proximal impacts of rats on fruit survival in areas baited to control rats and in unbaited areas. The size distribution of palms with trunks was comparable across baited and unbaited sites. Small juvenile palms lacking a trunk (<50 cm tall) were abundant in baited areas, but rare in unbaited sites for *Lepidorrhachis mooreana*, and rare or absent in 3 out of 4 unbaited *Hedyscepe canterburyana* sites. All ripe fruits were lost to rats in the small fruited *L. mooreana*. Fruit

removal was widespread but less (20–54%) in *H. canterburyana*. Both palms showed evidence of a reduced capacity to maintain a juvenile bank of palms through regular recruitment as a consequence of over 90 years of rat impact. This will limit the ability of these species to take advantage of episodic canopy gaps. Baiting for rat control reduced fruit losses and resulted in the re-establishment of a juvenile palm bank. Conservation of both endemic palms necessitates control (or eradication) of rat populations on the unique cloud forest summits of the island.

Keywords Seed predation · Lord Howe Island · Australia · Palms · Black rat *Rattus rattus*

Introduction

Invasive species disrupt a range of ecological habitats via direct impacts on individuals (either as adults or juveniles) or by altering habitats, ecological processes (Soule 1990; Lonsdale 1999) or disturbance regimes (Mack and D'Antonio 1998). Invasive species are generally competitors, predators, herbivores or pathogens. Endemic populations of plants and animals on oceanic islands often comprise few individuals, occupy highly restricted areas or specialised habitats and cannot recolonise from other areas. These populations are particularly sensitive to

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declines or extinction caused by invasive species (Sakai et al. 2002; Coote and Loeve 2003; Wiles et al. 2003; Blackburn et al. 2004; Towns et al. 2006; Trevino et al. 2007), often in combination with loss of habitat (Hunt 2007; Athens 2009).

In parts of the Pacific, much of the flora and fauna have evolved in the absence of mammalian predators and grazers. The subsequent introduction of such predators, including humans, has led to a number of serious declines or extinctions of species, including birds (Hindwood 1940; Holdaway 1989; Blackburn et al. 2004; Cheke 2006), invertebrates (Priddel et al. 2003; Coote and Loeve 2003; Towns et al. 2006) and plants (Duncan and Young 2000; Campbell and Atkinson 2002). For long-lived plants, extinctions caused by introduced species have rarely been recorded (Prebble and Dowe 2008), and in some cases the life span of individual plants may be longer than the period since the introduction of particular weeds, predators or pathogens. For such plants, continuing impacts may result in population declines, even if these declines are hard to detect. Janzen (1986) described such situations as blurry catastrophes and such species may be candidates for the “living dead” (*sensu* Janzen 1986) where a key part of the life history has been disrupted and successful reproduction has ceased. To identify recent impacts of invasive species on long-lived plants we need to determine if reproduction is sufficient to maintain a stable population.

Past changes to population dynamics in plant species have been inferred using paleoenvironmental records (Hunt 2007; Athens 2009) or standing size distributions across a range of plant communities from arid shrublands (Crisp and Lange 1976; Walker et al. 1986) to rainforests (Ogden 1985), including palms (Enright 1985) and other species on oceanic islands (Allen et al. 1994). To successfully apply these techniques, an understanding of proximal population dynamics is also needed. Assumptions about growth rates or turnover in size or stage classes must be made or estimated from direct observation (Enright 1985; Ogden 1985). Proximate factors limiting fecundity and survival, and the life or size stages at which they act, need to be understood to permit effective conservation management.

In this paper, we assess the impact of introduced black rats (*Rattus rattus*) on two highly restricted endemic palm species (Arecaceae) from Lord Howe

Island in the southern Pacific Ocean. Palms are a useful study group as they are readily counted and age classes may be inferred from leaf scars (Tomlinson 1979). We inferred past impacts on populations by examining standing size structures in combination with some limited data on leaf production. Concurrently, we estimated the proximal impact of seed predation by rats across habitats either baited (to reduce rat numbers) or unbaited. We applied selective caging experiments to exclude vertebrates from gaining access to seeds on the ground. Finally, we combined these two approaches to infer the conservation implication of the invasion of rats on the endemic palm populations and the likely response of these species to rat removal.

Methods

Study site

Lord Howe Island (31°30'S, 159°05'E) is a small oceanic island (0.3–2.8 km wide and 11 km long, 1,455 ha) formed from volcanic activity 6.3–7 million years ago (Hutton et al. 2007). It is situated ~570 km from the east coast of Australia, 1,350 km from New Zealand and 1,250 km from New Caledonia (Pickard 1983a). Almost 80% of the island is protected in a permanent park preserve (Davey 1986). It has been a UNESCO World Heritage Area since 1982 (Department of Environment and Climate Change NSW 2007). Topography on the island is dominated by its two southern mountains (Mt Lidgbird at 777 m and Mt Gower at 875 m). Both mountains are basaltic in origin and Mt Gower is considered to be an eroded caldera (McDougall et al. 1981).

The Lord Howe Island climate is humid-subtropical. It has a mean annual temperature of 19.2°C, ranging from 17 to 25°C in December–February to 14–18°C in June–August (Mueller-Dumbois and Fosberg 1998). Average annual rainfall in the lowlands is 1,645 mm (Australian Bureau of Meteorology), although rainfall in the southern mountains is likely to be much higher (Department of Environment and Climate Change NSW 2007). Rainfall is unevenly distributed throughout the year, with the driest period in late summer (February, average of 100 mm) and the wettest in winter (June/July average of 200 mm).

The island was originally free of mammals (except for small insectivorous bats) when first encountered by humans in 1788 and first settled in 1834 (Hutton 1986). It now has a resident population of about 300 people (Hutton et al. 2007). There is no archaeological evidence of Polynesian occupation of the island prior to 1788 (Anderson 2003) and the Pacific rat (*Rattus exulans*) is not considered to have ever reached the island. Black rats (*Rattus rattus*) were accidentally introduced when a steamship ran aground in 1918 (Billing and Harden 2000). Rat control measures have been sporadic until 1986 when a number of baited areas were established and ongoing baiting was maintained (Billing and Harden 2000). Approximately 8% of the island is currently baited (Billing 2000). This rat control program is now part of an integrated management plan for biodiversity conservation on Lord Howe Island (Department of Environment and Climate Change NSW 2007). The primary aim of the baiting has been to reduce seed predation by rats upon the two species of the endemic lowland palm genus *Howea*, especially *H. forsteriana* which forms the basis of a commercial seedling export enterprise on the island for horticultural trade (Pickard 1980). The baiting program also benefits other species, including seabirds (McAllan et al. 2004), invertebrates (Department of Environment and Climate Change NSW 2007) and plants (Auld and Hutton 2004).

Study species and habitat

We sampled the two endemic mountain palm species from Lord Howe Island. *Lepidorrhachis mooreana* (F. Muell.) O.F. Cook (Arecoideae: Areceae; Dransfield et al. 2008) is a small palm (trunks generally up to 3 m) restricted to the cloud forest vegetation (Pickard 1983a; Harris et al. 2005; Baker and Hutton 2006) on the 27 Ha summit plateau of Mt Gower (about 700–875 m in elevation). It has also been reported from the very small summit of Mt Lidgbird, but this requires confirmation. The species is considered to be rare on Lord Howe Island (Pickard 1983b), with introduced rats and climate change considered to threaten the cloud forest habitat of the species (Baker and Hutton 2006). *Hedyscepe canterburyana* (C. Moore and F. Muell.) H. Wend. & Drude has a trunk of up to 6 m and is generally confined to the higher elevations (600–875 m) of the southern mountains, although on sheltered slopes it can be

found down to 300 m. It is listed as vulnerable under the IUCN red list of threatened trees. It co-occurs with *L. mooreana* on the summit of Mt Gower, but also occurs at lower elevations in forests on several extensive ledges below the summits of both Mt Gower and Mt Lidgbird (Pickard 1983a). Since the two palm species belong to monospecific genera we hereafter refer to them as *Hedyscepe* and *Lepidorrhachis*.

The size and dry weight (air dried at room temperature) of fruits of the species are very different. *Lepidorrhachis* fruits are globular drupes ~1.3 cm in diameter, weighing an average of 1.4 ± 0.04 g ($n = 20$ fruits). Fruits of *Hedyscepe* are large and ovoid, $\sim 3 \times 4.4$ cm, weighing 24.8 ± 0.5 g ($n = 30$ fruits).

Standing size structure

We sampled the size structure of stands of the two species in cloud forest on the Mount Gower plateau. We stratified the sampling between areas that have been baited by the Lord Howe Island Board to control rat numbers and those that have never been baited. Baiting currently involves placement of poison every 3 months at fixed stations throughout the baited area. Baiting has been conducted on Mt Gower for the last 20 years (Billing 2000). Only a small proportion (~7%) of the eastern area of the summit has been baited (1.9 ha of a total 27 ha) and not all the baited or unbaited habitat is occupied by the study species. Although both mountain palms occur across the summit plateau and *Hedyscepe* and *Lepidorrhachis* co-occur in places, there is a tendency for *Hedyscepe* to occupy more sheltered sites and gully slopes while *Lepidorrhachis* is more common on small ridge tops. In each of the baited and unbaited areas we sampled three separate plots for each palm species (12 plots overall). At each plot, we established a 5 m wide transect across the site and sampled all individual palms within the transect. The transects were sampled until we had encountered a minimum of 30 *Hedyscepe* or 50 *Lepidorrhachis* individuals with an emergent trunk. Hence, the number of juvenile plants without a trunk that were sampled varied between plots. Transects ran for a minimum of 20 m up to 35 m, but occasionally to obtain sufficient numbers of plants with trunks we had to sample additional trunked plants beyond this length. These latter plants

were not included in our estimates of plant densities. We measured canopy height (=leaf height in plants lacking a trunk) for all individuals. For plants with emergent trunks, we also scored flowering or fruiting and measured two additional plant size attributes:

1. trunk height to the base of the leaf sheaths; and
2. the number of leaf scars on the trunk.

Occasionally, trunks were covered in mosses and lichens and it was not possible to count the number of leaf scars on the entire trunk. Where this occurred, mainly in *Hedyscepe*, we counted a section of the trunk and extrapolated to the length of the trunk. This assumed even rates of growth between leaf scars. In *Hedyscepe* and *Lepidorrhachis*, there was a pattern of larger intervals between leaf scars at the base of trunks and smaller intervals at the top (after the plants had matured). Consequently, where we had to subsample a trunk, we chose a section that included the transition between smaller and larger intervals between leaf scars. We also calculated the average leaf scar interval per trunked plant from the stem length divided by number of leaf scars.

We additionally sampled one population of *Hedyscepe* at the summit of Mt Lidgbird. The summit of this mountain is very narrow and there is little available habitat. The habitat of *Hedyscepe* palms on this mountain top has not been subject to rat baiting. Sufficient habitat was available to sample one plot, where we ran a 5 m transect along the undulating summit and sampled as per above. It was not possible to sample *Lepidorrhachis* on Mt Lidgbird as no plants could be located.

Hedyscepe also occurs on large ledges below the summits of Mt Lidgbird and Mt Gower. However, to ensure that all our samples were confined to comparable habitat on the mountain summits in cloud forest vegetation, we did not sample in these areas.

Inferring plant age or growth rates

For *Lepidorrhachis*, we tagged leaf bases on 10 mature trunked plants to determine the rate of production of leaf scars over a 31 month period. The length of time a palm had a trunk was then inferred from the mean number of leaves produced per year times the number of leaf scars. All plants sampled were on ridges on the summit of Mt Gower across the gradient in elevation. Loss of tags from

Hedyscepe plants prevented a similar estimation in that species.

Impact of rats on fruit survival

To examine the direct proximal impacts of rats on the palms we established seed predation exclusion experiments on Mt Gower. We ran the experiments on 2 occasions in 2006 (winter–July; and late spring–November). This replication allowed us to examine temporal variation in seed predation rates across the long period of fruit maturation. For both replicate trials, there were developing and ripe fruits available on mature plants of both species. For *Lepidorrhachis*, there were considerably more ripe fruits in July than November, while for *Hedyscepe*, slightly more ripe fruits were available in November. At each time, we sampled 4 sites per species, 2 in rat baited and 2 in unbaited areas. At each site, we established 10 randomised plots of treatments, with the location of each plot constrained by being under a palm with a fruiting infructescence, but such plants were chosen randomly from those available at the site. For *Hedyscepe*, at each chosen palm, we set up 2 batches of 10 mature fruits in a cache, one caged and one uncaged. The caged fruits were covered with a 1 cm² wire mesh cage that was held into place by wire stakes. This excluded rodents and birds. We followed the fates of fruits over a 2 week period. For *Lepidorrhachis*, we observed that green fruits were eaten by rats. In some baited areas, fruits, in which the red fleshy outer layer (the mesocarp and exocarp) had been removed or worn off, persisted on the forest floor (leaving only the seed and endocarp). So for *Lepidorrhachis*, we used caged and uncaged ripe red fruits along with two additional uncaged fruit categories at each plot. These categories were large green fruit and endocarp-only fruit. We observed Lord Howe currawongs (*Strepera graculina crissalis*, a diurnal corvid) remove ripe fruits from infructescences of *Lepidorrhachis* and regurgitate endocarps. As this bird may have removed fruits in our exclusion trials, the inclusion of endocarp-only fruits in the experiment allowed us to compare removal rates for fruits that were attractive to these birds (ripe red fruits) and fruits that were not (endocarp-only). The Lord Howe currawongs may occasionally handle the much larger fruits of *Hedyscepe* (Hutton pers observ.), but no endocarp-only fruits were available on the summit plateau.

In the July trial, the experiments were checked overnight and again at ~ 2 weeks after establishment, with the final data point used in the analyses. In the November trial, we checked removal and fruit loss at plots overnight, at 3–3.5 days and after 2 weeks. We used these temporal sampling data to examine the early rates of fruit loss.

To infer the fates of fruits we explored several possibilities. We spent time observing fruit caches in the day and night to monitor removal agents. We also examined the pattern of fruit mesocarp removal and fruit consumption in situ to infer likely agents.

Data analysis

We compared the population size structure in stands of each palm across baited and unbaited areas. For each species, we used nested 2 Factor ANOVAs (fixed factor rat baiting, with sites nested in rat baiting) to compare each size attribute in trunked plants. Species were not included as a factor as *Hedyscepe* is much larger than *Lepidorrhachis* and as we were interested in the nested site effect within a species. Cochran's Test was used to test for homogeneity of variances. Where heterogeneous variances were detected, the data were log transformed (Underwood 1997). Where ANOVAs were significant, individual means were compared using Student–Newman–Keuls tests (Zar 1974).

For the predator exclusion experiment, for each species, we compared the magnitude of fruit removal/loss across the treatment plots. We used a GLIM with four factors—time of experiment, rat baiting, caging treatment and sites (nested) with a binomial error structure. Removal from a plot was scored if there had been any seed removal as the plot was the unit of replication. In the November trial, we used a failure-time analysis (Fox 2001) to compare the rates of seed removal between baited and unbaited areas and different caging treatments, pooling data across plots and sites.

Results

Standing size structure

In trunked palms of both *Hedyscepe* and *Lepidorrhachis*, there was no significant difference between baited and unbaited areas for all size attributes, but there was

variation among study sites (Table 1). In *Hedyscepe*, there was a significant difference in crown sizes ($F_{4,135} = 3.3$, $P = 0.01$), trunk lengths ($F_{4,177} = 5.4$, $P < 0.001$) and the number of leaf scars per trunk ($F_{4,170} = 2.7$, $P = 0.03$) across sites (Table 1). In *Lepidorrhachis*, there was significant variation among sites in crown sizes ($F_{4,211} = 3.5$, $P = 0.001$) and trunk lengths ($F_{4,294} = 2.8$, $P = 0.025$).

The size distribution of trunked plants was broadly similar across sites, although in *Hedyscepe* there were relatively more individuals in the largest size classes than in *Lepidorrhachis* (Figs. 1, 2). When plants without trunks were compared, there were clear differences between the population structures in the rat baited versus unbaited areas (Figs. 1, 2). Small juvenile palms (< 25 cm) were only present in areas that were baited, with the exception of one *Hedyscepe* site (H2rat; Fig. 1). Large juveniles that did not yet have an aerial trunk and plants with a trunk that had clearly not yet flowered were present at all sites, although they were very scarce at one *Hedyscepe* site where rats were not baited (H1rat, Table 2). The *Hedyscepe* site from the summit of Mt Lidgbird was comparable to the unbaited Mt Gower sites as there were few plants without a trunk (Table 2). Densities of mature (0.06 – 0.4 m $^{-2}$) and juvenile plants (0.05 – 8.3 m $^{-2}$) varied across sites (Table 2).

Trunked *Lepidorrhachis* plants produced an average of 2.6 (± 0.8) leaves each year (range 2.3–3.1). To infer an estimate of the time spent as a trunked *Lepidorrhachis* palm, we assumed plants produced between 2 and 3 leaf scars per year. This would suggest that each site contains a few very old individuals that have had trunks for 100–200 years (cf. Fig. 2). Most of the plants are estimated to have had trunks for less than 70 years.

Impact of rats on fruit survival

Fruit loss varied markedly between baited and unbaited areas. For *Hedyscepe*, there was no significant difference between the replicate experiment times and no significant interactions involving this term. No fruits were consumed in situ in this species. There were significant differences between baited and unbaited areas and between caging treatments, along with significant site variation. Some fruits were removed from all plots at one of the unbaited sites

Table 1 Summary size measurements for trunked palms sampled on Lord Howe Island

Species	Site	Baited for rats	Trunk Length (m)	Mean plant (\pm SE)		
				Crown size (m)	Leaf scars	Leaf scar interval (cm)
<i>Hedyscepe</i>	H1rat	No	4.01(0.34)	2.08(0.19)	193(26)	2.7(0.3)
	H2rat	No	2.73(0.33)	1.98(0.10)	138(32)	3.4(0.3)
	H3rat	No	2.05(0.27)	2.38(0.10)	87(22)	4.2(0.5)
	H4	Yes	2.63(0.33)	2.43(0.10)	115(25)	4.1(0.4)
	H5	Yes	2.39(0.35)	2.38(0.13)	148(34)	4.5(0.5)
	H6	Yes	3.03(0.32)	2.03(0.09)	208(39)	3.1(0.4)
	HLrat	No	2.79(0.21)	1.89(0.07)	170(14)	2.3(0.2)
<i>Lepidorrhachis</i>	L1rat	No	1.37(0.14)	1.73(0.05)	75(9)	2.1(0.2)
	L2rat	No	1.67(0.15)	1.85(0.08)	68(9)	2.5(0.2)
	L3rat	No	1.59(0.12)	1.63(0.07)	70(8)	2.4(0.1)
	L4	Yes	1.73(0.12)	2.02(0.06)	76(9)	2.8(0.2)
	L5	Yes	1.21(0.13)	1.95(0.08)	53(9)	2.9(0.3)
	L6	Yes	1.46(0.11)	1.80(0.05)	75(9)	2.3(0.1)

For each size measurement 30 *Hedyscepe* or 50 *Lepidorrhachis* trunked plants were sampled

(a total 54% of individual fruits removed) and from 85% of plots at the other unbaited site (a total 20% of individual fruits removed). One of the baited sites also had some fruit removed from 85% of plots (a total 22% of individual fruits removed), while the second baited site had removal from 45% of plots (a total 7% of individual fruits removed). There was evidence of rats scraping away the thin mesocarp and trying to remove the fibrous endocarp. Nocturnal observations revealed that rats dragged fruits away from the experimental plots. It is likely that fruits were consumed in caches and such caches with eaten fruits were observed in the habitat.

In *Lepidorrhachis*, there was a significant two way interaction between caging treatment and date of sampling (July or November), along with a significant difference between baited and unbaited areas and a significant nested site effect. In the unbaited areas, uncaged fruits were removed in all plots, except for 2 plots of green fruits. All red fruits and those with the flesh removed (endocarp-only) were taken in both July and November sampling. The removal of green fruits varied from 98% in July to 17% in November. Evidence that rats consumed fruits was indicated by the presence of chewed pieces of pericarps in situ, the presence of fresh rat scats in the plots and our nocturnal observations of rats feeding on fruits. While some ripe red fruits may

have been taken and dispersed by Lord Howe currawongs, it is likely that rats are consuming fruits since there was a loss of both ripe red fruits and endocarp-only fruits in all the unbaited sites. Fruits with the mesocarp removed should not be attractive to currawongs. At these unbaited sites, no adult plants had ripe fruits on infructescences and no fruits with the mesocarp removed (endocarp-only) were present on the ground. In contrast, ripe fruits were common both on infructescences and on the ground in the baited areas. In baited areas, we found that there was some removal of ripe red fruits in all plots in November (a total 64–94% of individual fruits removed across sites) and in 85% of plots in July (a total 35–40% of individual fruits removed across sites). For fruits with only an endocarp, there was more variation between the two sampling seasons, with removal in 95% of plots in November (a total 24–96% of individual fruits removed across sites) compared to only 30% of plots in July (a total 6% of individual fruits removed across sites). Removal of green fruits was comparable across sampling seasons, 65% of plots in November (a total 14–25% of individual fruits removed across sites) and 55% of plots in July (a total 12–13% of individual fruits removed across sites). The losses in November at one baited site were directly attributed to rats as evidenced by large amounts of fruit remains in situ. This

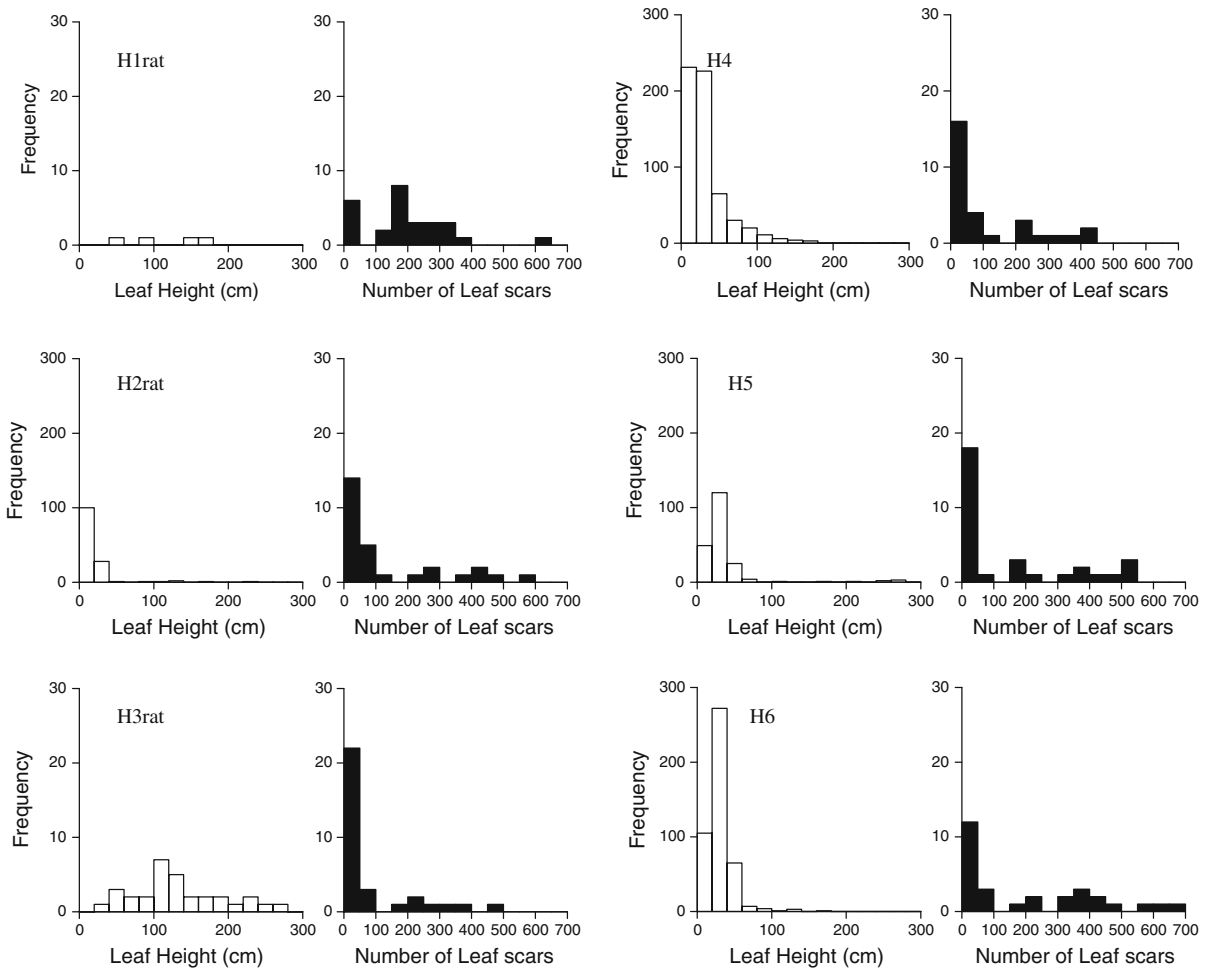


Fig. 1 Size distributions for *Hedyscepe canterburyana* of plant height for juvenile plants lacking a trunk (*open bars*) and the number of leaf scars in trunked individuals (*filled bars*). *rat* No rat baiting conducted at the site. *Note:* Y axis scale varies across sites

may reflect re-colonisation of this site by rats at the time.

In the November trial, there was some initial (overnight) rapid removal of ripe fruits of *Hedyscepe* in unbaited areas and then a slow rate of removal in both baited and unbaited areas (Fig. 3). In *Lepidorrhachis*, loss of ripe red fruits was rapid where rats were not baited (Fig. 4), with some 90% fruits lost within a day and all fruits gone within 3 days. Most of these fruits were consumed in situ by rats over the first night of the experiment, again supporting the conclusion that consumption by rats rather than fruit removal and dispersal by Lord Howe currawongs explains fruit losses. The loss of all endocarp-only fruits within 3 days was also likely

due to rat predation since these fruits are not attractive to currawongs (Fig. 4).

Discussion

The introduction of rats (*Rattus rattus*) to the oceanic Lord Howe Island is likely to have increased the risk of extinction for the two endemic mountain palms. This is a consequence of rat predation of fruits which has the potential to limit recruitment in both palm species. Past observations highlight the lack of ripe fruits on *Lepidorrhachis* plants unless mesh caging was applied to exclude rats from developing fruits (Moore 1966; Pickard 1980). The paucity of small

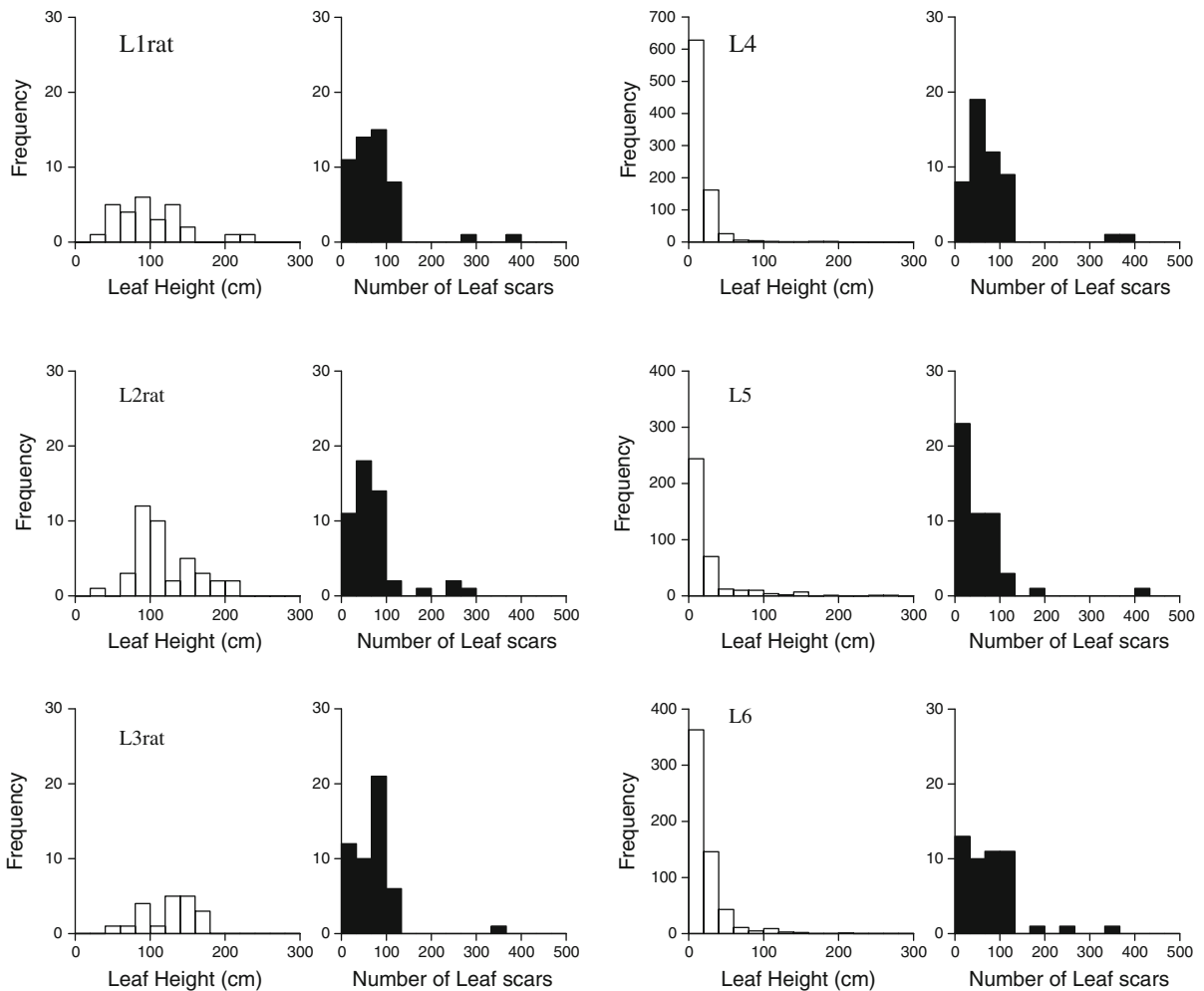


Fig. 2 Size distributions for *Lepidorrhachis mooreana* of plant height for juvenile plants lacking a trunk (*open bars*) and the number of leaf scars in trunked individuals (*filled bars*). *rat* No rat baiting conducted at the site. *Note:* Y axis scale varies across sites

juvenile plants in areas which have not been baited for rat control, both in our study plots and more generally throughout this unbaited area, supports the more general contention that the introduction of rats affects plant recruitment in a range of island ecosystems (Campbell and Atkinson 2002; Delgado García 2002; Towns et al. 2006; Meyer and Butaud 2009; Traveset et al. 2009). It is possible that rats also reduce seedling and juvenile growth as they have been observed eating palm leaf sheaths and causing leaf fall in both juvenile and adult palms consistent with similar damage observed on plants elsewhere (Traveset et al. 2009). The impact of rats is greatest in *Lepidorrhachis*, where fruit losses reached 100% and small juvenile plants (<50 cm) were extremely rare

in the presence of rats. Any possible seed escape in *Lepidorrhachis* via dispersal by the Lord Howe currawong is negated by the loss of endocarp-only fruits (matching regurgitated fruits) in unbaited areas. For *Hedyscepe*, observed fruit losses were less (total of 20–54%), and while some seed escape may be occurring, only one out of four sites sampled on the mountain tops has an appreciable number of small juveniles (<50 cm; Table 2). Differences between the two palm species may relate to the fact that the fruits of *Hedyscepe* are up to 18 times bigger than *Lepidorrhachis* and rats may have more difficulty eating into *Hedyscepe* fruits as they have a thicker and very fibrous endocarp wall. Neither palm species can be considered the “living dead” (sensu Janzen

Table 2 Plant densities across sampled plots for *Lepidorrhachis mooreana* and *Hedyscepe canterburyana*

Species	Site	Baited for rats	Density (m ⁻²)				
			Trunked plants		Juveniles with no trunks		
			Mature	Juv	Height (m)		
					<0.5	0.5–1	>1
<i>Hedyscepe</i>	H1rat	No	0.10	0.02	0	0.01	0.01
	H2rat	No	0.13	0.02	0.85	0.01	0.03
	H3rat	No	0.11	0.14	0.03	0.03	0.18
	H4	Yes	0.14	0.07	4.02	0.56	0.19
	H5	Yes	0.06	0.09	1.52	0.07	0.06
	H6	Yes	0.08	0.03	2.91	0.11	0.03
	HLrat	No	0.40	0.11	0.01	0.02	0.04
<i>Lepidorrhachis</i>	L1rat	No	0.34	0.06	0.04	0.09	0.10
	L2rat	No	0.24	0.06	0.01	0.09	0.15
	L3rat	No	0.35	0.04	0.01	0.04	0.11
	L4	Yes	0.19	0	8.13	0.13	0.08
	L5	Yes	0.12	0.10	2.38	0.19	0.11
	L6	Yes	0.25	0.04	5.41	0.28	0.14

All sites on Mt Gower, except HLrat from Mt Lidgbird

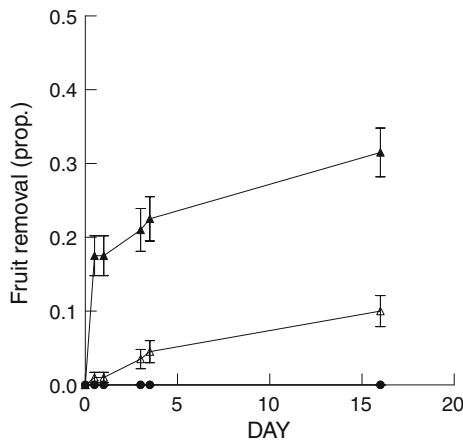


Fig. 3 Rate of fruit loss in *Hedyscepe canterburyana*, pooled across sites. Data are 1-(Kaplan–Meier estimates) with standard errors. Filled symbols are sites with no rat baiting, open symbols are sites with rat baiting. Vertical bars are standard errors. Treatments are: Cage (circle); uncaged ripe fruit (triangle). No fruits were removed in the caged treatment

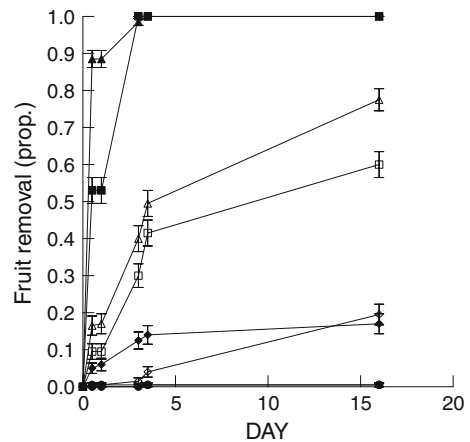


Fig. 4 Rate of fruit loss in *Lepidorrhachis mooreana*, pooled across sites. Data are 1-(Kaplan–Meier estimates) with standard errors. Filled symbols are sites with no rat baiting, open symbols are sites with rat baiting. Vertical bars are standard errors. Treatments are: Cage (circle); uncaged ripe fruit (triangle); uncaged green fruit (diamond) uncaged endocarp-only fruit (square)

1986) as there are juvenile plants over 50 cm in height at all sites, independent of the current rat baiting program on the island. Some episodic recruitment may occur as a result of sporadic seed escape from rats, possibly in relation to natural fluctuations of abundance within the rat population.

Rats reached Lord Howe Island some 90 years prior to this study and are reported to have spread rapidly (Billing and Harden 2000). Consequently, rat predation could have affected palm recruitment for a number of decades. Is this reflected in the estimated

age structure of *Lepidorrhachis*? Plant age in palms has been inferred by the number of leaf scars (Sarukhán 1980; Enright and Watson 1992). In *Lepidorrhachis*, there were few plants (~6% of the population) with more than 120 leaf scars (Fig. 2). This represents some 40–60 years of trunk growth. The remainder of the trunked palms are more or less evenly distributed up to 100 or 120 leaf scars (Fig. 2). If individual mortality was constant across these size classes then this would suggest a declining population and may reflect a long term impact of rats on recruitment. Estimating plant age requires additional data on the time required for juvenile plants to grow large enough to produce a trunk, and this may vary with habitat quality and disturbance regime. This pre-trunk period typically takes decades in some palm species (e.g. 35–60 years, Enright 1985; Enright and Watson 1992), but is currently unknown for *Lepidorrhachis*. Further data on juvenile survival and growth are needed to clarify the age structure of the population.

Recovery of vegetation following removal of rats is not always straightforward (Mulder et al. 2009; Towns 2009). Rats may impact on nutrient cycling (through impacts on seabirds, Mulder et al. 2009) and the impacts of mice may increase if rats alone are removed (Angel et al. 2009). In our study area on Mt Gower, there has only been limited rat control in the last 20 years. There is a lack of small juveniles in unbaited areas at all sampled *Lepidorrhachis* sites and at 75% of the *Hedyscepe* sites. Baited areas are distinguished by the abundance of young juvenile palms, implying a restoration of plant recruitment and a re-establishment of the juvenile bank of palms (sensu Silvertown 1982). Successful growth to maturity of juvenile palms will probably be influenced by local canopy gap formation after tree death or tree fall in storms.

Long-term conservation of the endemic palm genera in this study may be compromised by a reduced capacity to establish a juvenile bank and to adapt to a changing climate. Both species occur in the unique cloud forests on the island (Harris et al. 2005) and changes to moisture regimes (e.g. through a reduction in cloud cover) with a changing climate may limit establishment opportunities in the future. Targeted control, or eradication of rats is essential to maximise the potential for long-term conservation of these species.

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