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Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree

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ABSTRACT. The role of white-tailed rats (*Uromys caudimaculatus*) as dispersers of seeds of the Australian tropical rain forest tree *Beilschmiedia bancroftii*, (Lauraceae) was investigated by following the fates of seeds and seedlings over 2 y. Fruits of this tree are too large to be consumed by any avian frugivore except the southern cassowary (*Casuarius casuarius*), and the only other native mammal capable of dispersing the seeds is the musky rat kangaroo (*Hypsiprimnodon moschatus*). However, neither of these species has been documented to disperse the seeds of this tree. During a mast year, white-tailed rats cached seeds an average of 13 m from parent trees in a variety of microsites. Although none of the 61 cached seeds followed in this study survived to germination, comparison of seed, cache and seedling distributions suggested that most seedlings arose from rat-cached seeds. White-tailed rats cached seeds in both mast and non-mast years, but the time seeds remained on the forest floor and in caches was significantly shorter in non-mast years, suggesting that synchronous seed production increases the probability that some caches survive to germination. Because white-tailed rats are the most common and widespread native mammal capable of dispersing large-seeds, this study suggests that they may play an important role in the seed and seedling dynamics of large-seeded tree species in Australian tropical rain forests.

KEY WORDS: *Beilschmiedia bancroftii*, masting, predator satiation, rodent, seed predation, seed size, *Uromys caudimaculatus*

INTRODUCTION

Seed predation and dispersal by rodents has important implications for seedling germination and survival and can potentially affect the distribution, abundance and community composition of adult trees (Forget *et al.* 1994,

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Forget & Sabatier 1997, Howe *et al.* 1985, Schupp 1988, Sork 1987). In some cases, the relationship between rodent seed dispersers and the trees whose seeds they disperse has been suggested to be mutualistic (Forget 1990, Hallwachs 1986, Leigh *et al.* 1993, Smythe 1989). Recent evidence has supported the hypothesis that the absence of these dispersers has significant negative impacts on tree recruitment (Asquith *et al.* 1999). Most research on the role of rodents as seed dispersers in tropical rain forest systems has centred on the neotropics; the importance of similar relationships in other tropical areas has been less well studied.

In the tropical rain forests of eastern Australia, several tree species produce seeds protected by stony endocarps that are too large to be effectively dispersed by animals other than the southern cassowary (*Casuarius casuarius*), musky rat kangaroo (*Hypsiprimnodon moschatus*) and white-tailed rat (*Uromys caudimaculatus*). Of these, the white-tailed rat is the most common and widespread and can completely remove the entire seed crop of some tree species in a matter of days or weeks (Harrington *et al.* 1997, Moore 1995). Some of these seeds are cached (Harrington *et al.* 1997, Moore 1995), but the pattern and characteristics of caches has not been documented. Given the high rate of seed removal, recruitment by many of these trees would apparently be possible under only four scenarios: (1) seeds escape predation in mast years due to predator satiation (Janzen 1971, 1976; Silvertown 1980), (2) seeds produced in low numbers during non-mast years escape predation because rats fail to find or feed upon such a rare food source, (3) seeds escape during years of low white-tailed rat abundance, or (4) seeds germinate from unrecovered scatter-hoarded seeds. In this paper, these hypotheses were investigated by documenting the rate of seed removal and cache recovery in a mast and a non-mast year during which the abundance of white-tailed rats remained relatively constant. In addition, I documented distances seeds were dispersed, microsites chosen as cache sites and how seed distributions of cached and uncached seeds compared to subsequent seedling distributions.

METHODS

Study site and study species

This study was conducted in *c.* 4 ha of primary upland rain forest in the Lamb Range of northern Queensland, Australia. The study site has never been logged and is surrounded by continuous forest that was selectively logged until the 1970s. The entire area is currently fully protected and designated a World Heritage Area. Elevation at the site ranged from 800–900 m asl. Most of the study area was located on steep slopes that rose from surrounding creek drainages. Rainfall is seasonal, with most of the *c.* 3000 mm falling December–April. All trees greater than 10 cm dbh have been mapped and marked on a 1.7-ha long-term study plot in the centre of the study area (Connell *et al.* 1984).

Beilschmiedia bancroftii (Bailey) C. White (Lauraceae) is a large-seeded, monoecious tree species endemic to the rain forests of northern Queensland from sea level to 1200 m (Hyland & Whiffen 1993). Of the approximately 120 species of trees that occur in the 1.7-ha plot, *B. bancroftii* ranks 9th in number of trees present and 12th in basal area (J. H. Connell, *pers. comm.*). Fruiting is reported to occur between August and March, corresponding to the latter part of the dry season and the early part of the wet season (Hyland & Whiffen 1993). Trees on our study plot have been monitored since 1995 and have produced fruits only once, beginning in October 1996 through March 1997 (P. T. Green, *pers. comm.*). Since that time, none of the trees has produced fruits. Some trees were flowering in October 1999 (P. T. Green, *pers. comm.*). Therefore, because seed development takes *c.* 1 y from flowering, the interval between seeding events will be at least 4 y.

The mature fruits are green to orange in colour and measure up to 75-mm × 60-mm in size. The fleshy exocarp is 2–5 mm thick and relatively dry. When ripe, the exocarp often forms a hollow sphere in which the single, stony endocarp moves relatively freely. The endocarp wall is hard, 2–2.5 mm thick, and contains the succulent, creamy-white cotyledons. The exocarp often splits when the fruit strikes the ground and the seed often separates from the exocarp upon impact. Based on 180 seeds collected at the study site, seed mass ranged from 16–90 g, with a mean of 51 g. Time to seed germination can be quite long, ranging from 4 mo to 9 y (Harrington *et al.* 1997) with most germinating in 1–2 y (A. Irvine, *pers. comm.*). Fruits of this species are too large to be swallowed by birds other than cassowaries. Cassowaries do not regurgitate the seeds of fruits they ingest, but rather pass them through the gut and deposit them in the droppings (T. C. Theimer, *pers. obs.*). However, *B. bancroftii* seeds have not been recorded in cassowary dung (Stocker & Irvine 1983). Nor have they been reported to be eaten by the other major mammalian frugivore and seed scatterhoarder of these rain forests, the musky rat kangaroo (A. Dennis, *pers. comm.*). However, white-tailed rats have been documented to eat and cache seeds of this species (Harrington *et al.* 1997, Moore 1995).

White-tailed rats (*Uromys caudimaculatus*, Muridae, Krefft) are relatively large (500–900 g), scansorial rodents found in rain forest, sclerophyll forest and non-forest habitats of northern Queensland, Australia and New Guinea (Moore 1995). Their diet includes fruits, seeds, fungi, invertebrates and small vertebrates and their eggs. Little has been published about the behaviour and ecology of these animals, although individuals apparently may forage over an area of 4 ha or more (Moore 1995).

Rodent trapping

The minimum number of white-tailed rats using the study plot was estimated annually by live-trapping. One hundred and twenty trap stations were arrayed in a 10 × 12 grid (*c.* 4 ha) with trap stations spaced 20 m apart. An Elliott box trap (11-cm × 11-cm × 30-cm) was set at every station for a total of

120 traps, and a wire Tomahawk cage trap (17-cm × 17-cm × 48-cm) was set at every second station for a total of 60 traps. Thus, every station had an Elliott box trap and every other station had both an Elliott box trap and a wire cage trap. In September and October 1997, August and September 1998, and October and November 1999, traps were initially run for two consecutive nights, then for two nights 2 wk later and for another two nights one mo later. All animals captured were marked with a uniquely numbered ear tag.

Crop size and natural seed fall

In January 1997, 10 *B. bancroftii* trees were selected as the subject of this study and their position mapped relative to the 20 × 20-m trapping grid. Among these 10 were all trees larger than 45 cm DBH that occurred on a 1.8 ha long-term study plot in the centre of the study area (n = 6), along with four other trees outside of this plot that were producing at least some fruit. No other *B. bancroftii* trees produced fruit on the roughly 4-ha area during the 2 y of this study. An index of relative crop size at each tree was determined in late February 1997 by counting the number of seeds in two 50-m × 1-m wide transects. One transect extended directly uphill from each tree's base and the other extended in the opposite direction downhill. This index was not intended as an estimate of total seed abundance, but rather was used to document the striking differences among trees in the relative number of seeds available to white-tailed rats. The transect downhill from each tree was also used to estimate the distances that seeds would naturally fall from the parent. This estimate was biased toward the greatest distances seeds would move on their own, as the canopies of most trees extended downhill and seeds tended to roll downhill after striking the ground. The area beyond 50 m below each tree was searched for seeds for an additional 50 m to ensure no long-distance seed movement was missed.

Seed removal

Beginning in early February 1997, six *B. bancroftii* seeds, each with the fleshy exocarp removed, were placed at the base of each study tree. Trees varied markedly in the amount of natural seed fall, so these six seeds were among as many as hundreds of seeds present under trees that had fruited heavily, or were the only seeds present under trees that produced no seeds of their own. Each seed was uniquely numbered using indelible ink and a small bobbin of thread (1.5-cm × 4-cm, *c.* 4 g (Penguin Thread Co., Victoria Australia)) was glued to the endocarp. These bobbins were wound so that thread exiting from the centre of the bobbin unwound freely. The end of the thread was tied to a metal stake at the tree base so that thread unwound from the bobbin on the seed as the seed was carried away from the stake. Seeds were replaced as they were eaten or removed until March 1997, by which time a total of 193 seeds had been placed under parental trees (Table 1). The mean number of days until seed removal was calculated for each tree based on the first set of six seeds placed at each tree. Spearman's rank correlation was used to determine whether mean days to removal was correlated with crop size index for each tree. The distance and direction from the parental tree was recorded for each seed cached, as well as the microsite in which the seed was cached. Microsite categories included: (1) tree buttresses, (2) base of tree saplings or lianas, (3) near or under logs, (4) in the canopy of trees or (5) in the open at least 1.5 m from the nearest tree, sapling, rock or log. Seeds at parental trees and seed caches were monitored every 3–7 d from February–April 1997. Remaining caches were monitored again beginning in September 1997 and were monitored biweekly until December 1997. Because seeds and caches were not monitored daily, days to removal for each marked seed at adult trees and each seed in a cache was conservatively estimated as the difference between the date when the seed was initially placed or caches initially established and the last date seeds were known to be present.

Seedling germination

In December 1997, 1 y after the initial masting event, seedlings of *B. bancroftii* began to appear on the study plot. From January 1998 until June 1999, newly germinated seedlings were mapped as they were found during bimonthly surveys and their fates followed until October 1999 and the distance and direction to the nearest adult recorded.

Comparison of mast and non-mast years

In January 1998, six bobbined, individually numbered seeds, without exocarp attached, were placed at the base of each parental tree as in 1997 and seed and cache fates were followed. At this time, however, none of the *B. bancroftii* trees in the area were producing seeds and no uncached seeds had been available to rats for *c.* 6 mo. The seeds used in this experiment had been stored in a dark cupboard in the laboratory since March 1997. The nutrient content of these seeds may have been altered by the long storage time, but no other seeds were available because no trees produced fruit in 1997 on our study plot or at any other rain forest sites visited. Once removed from the base of parent trees, experimental seeds were not replaced, so a total of only 60 seeds was placed in this non-mast year. Days to removal was determined for all 60 seeds. Distance, direction, microsite and days to removal were recorded for all caches as in 1997. Wilcoxon signed-ranks tests were used to compare the mean days to removal, distance to cache and days in cache for each tree in 1997 versus the same tree in 1998. Values for 1997 were calculated based on data from the initial 60 seeds placed at parent trees. Because different trees failed to yield any cached seeds in one or the other year, only six of the 10 trees could be compared for cache distance and time-in-cache.

RESULTS

Rodent trapping

Twenty adult white-tailed rats were captured during the 1997 trapping session, 13 were captured in 1998 and 14 were captured in 1999. Seven of the animals captured in 1998 were recaptured from the previous year, and eight of the 14 animals captured in 1999 had been captured in the previous year. Three of the latter had also been captured in 1997.

Seed removal

During the mast year of 1996–97, seeds from natural seedfall were present on the ground below adult trees from October until I left the plot in April 1997. However, when I returned in September 1997, all seeds that had fallen naturally below trees had been removed or were eaten in place. Days to removal for marked seeds ranged from 1–37 d (mean = 12.6 d ± 13.2) for the initial cohort of 60 seeds placed in February 1997 (Table 1). Seed removal rate of this cohort was not correlated with crop size index (Spearman's $r_s = 0.103$, $n = 10$, $P = 0.777$). In fact, a tree that produced no seeds of its own that was located over 50 m from the nearest fruiting conspecific had seed removal rates as high or higher than other trees (Table 1).

Of the 193 seeds placed at the base of parent trees from February–March 1997, roughly equal numbers were eaten at the parent tree (n = 59), cached (n = 61), or had the bobbin removed and their fates were unknown (n = 65). The remaining six seeds were carried up trees or vines into the canopy. The 61 cached seeds were carried 1–55 m from the parent tree (mean = 13.4 ± 10.4 m, Figure 1). Of these, 13 were cached at the base of saplings (DBH < 10 cm), 15 were cached at the base of trees (DBH > 10 cm), eight were cached under rocks or logs, and 25 were cached in the open at least 1.5 m from the nearest tree, sapling, rock or log.

Of the cached seeds, 35% were left on the surface and covered with litter, 47% had between one and three-quarters of the seed buried in soil and were

Table 1. Diameter at breast height (dbh), index of crop size, the number of experimental seeds placed at each tree, the mean (± SD) days to removal of the first six experimental seeds placed at each tree, and the number of caches discovered for 10 *Beilschmiedia bancroftii* trees in the study plot (Queensland, Australia).

Tree	dbh (cm)	Crop index	Seeds placed	Days to seed removal	Caches
1	79	180	17	4 ± 3	0
2	56	170	16	6 ± 2	4
3	77	90	15	34 ± 8	2
4	62	85	10	42 ± 18	5
5	73	45	27	6 ± 8	10
6	85	36	17	1 ± 0	10
7	46	35	16	2 ± 1	9
8	80	20	19	20 ± 12	3
9	99	5	32	12 ± 12	8
10	67	0	23	5 ± 3	10

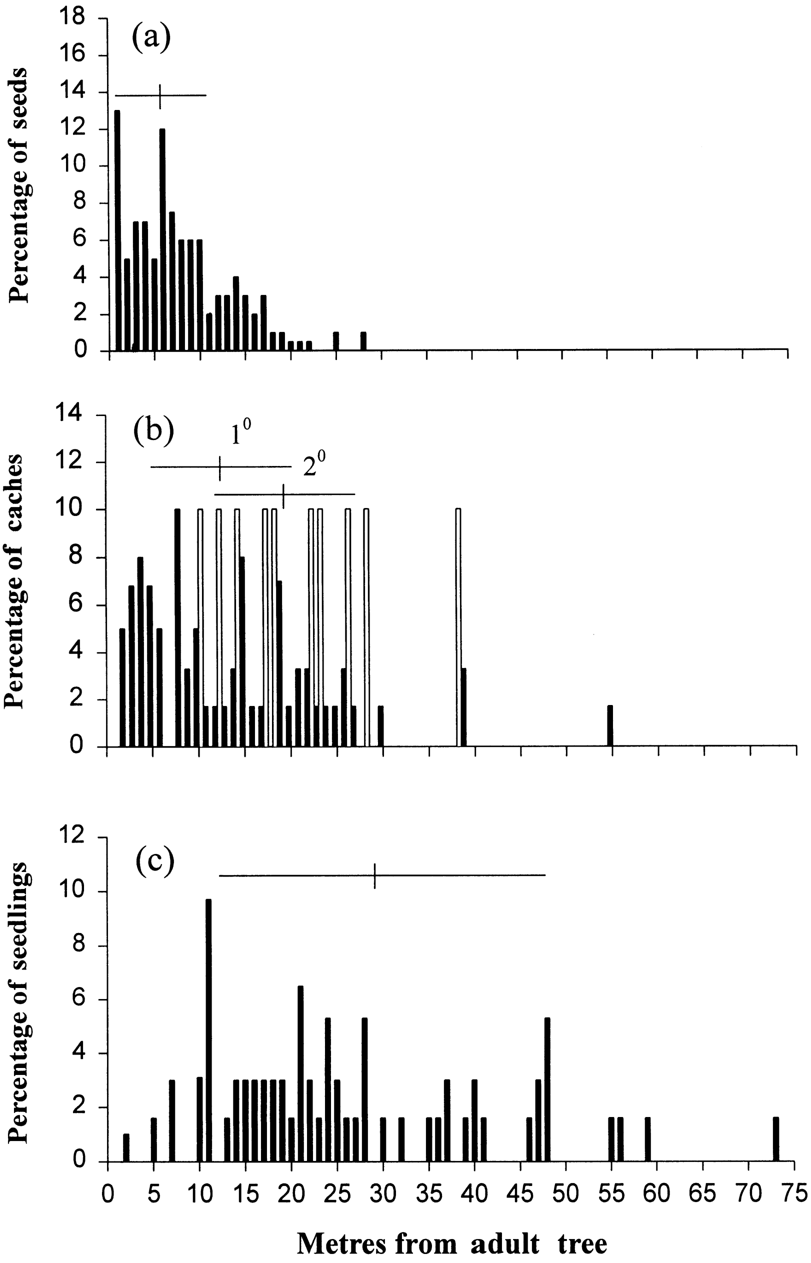

Figure 1. Percentage of (a) seeds falling naturally beneath adult trees, (b) primary (1st) and secondary (2nd) caches and (c) seedlings occurring at different distances from adult *Beilschmiedia bancroftii* trees on the northern Queensland, Australia study plot. In each case, the vertical line above the bars represents the mean distance and the horizontal line represents 1 SD above and below the mean.

covered with litter and 18% were completely buried, often under 1–2 cm of soil and covered with litter. Three seeds remained in caches for over 300 d, while most seeds were removed in less than 100 d. Two of the former were cached in open microsites and were completely buried, while the third was under a large log. Ten of the 61 cached seeds were removed from the initial cache and recached. Secondary caching may have been more common, however, as there was often no evidence of chewed endocarps in the area of primary cache sites when the seed was recovered. The distance of the second cache from the parent tree (19.2 ± 8.6 m) was significantly greater than the distance of the initial cache (13.9 ± 10.9 m) based on these 10 seeds ($z = -2.429$, $P = 0.015$, Figure 1).

Seedling recruitment

Seventy-five *B. bancroftii* seedlings were found in the study area between December 1997 and October 1999. Newly germinated seedlings stood *c.* 30–50 cm tall with two leaves. All but two of these seedlings arose from seeds that were completely buried in the soil, as indicated by removing the soil at the base of the seedling until the seed was reached. Seedlings were significantly farther from the nearest adult *B. bancroftii* tree (27.1 ± 18.5 m) than primary cache sites were (13.9 ± 9.9 m, $t = 5.52$, $df = 122$, $P < 0.005$; Figure 1). Most seedlings (63%) were found upslope of the nearest adult, and 20% were found within 2 m of a known cache site (Figure 2). A census of seedlings in June 1999 showed that 52% died since germinating, with most of this mortality putatively due to white-tailed rats unearthing and consuming the succulent cotyledons and in many cases apparently eating the leaves of the uprooted seedling as well. Other seedlings died as a result of vertebrate herbivory, with the upper stem nipped cleanly at *c.* 30 cm, apparently by pademelons (*Thylogale stigmatica*). Ten seedlings germinated from buried seeds inside a set of vertebrate exclosures that were erected in November 1996. These seeds had presumably been cached by rats prior to the erection of the fences. None of these seedlings has as yet suffered mortality.

Comparison of mast and non-mast years

When the fates of the initial set of 60 seeds placed under trees in the mast year of 1997 were compared to the set of 60 seeds placed under the same trees in the non-mast year of 1998, the number of seeds eaten, cached and of unknown fate were virtually identical (Table 2). However, the time for seeds to be removed from beneath parents was significantly shorter in the non-mast year ($z = -2.701$, $P = 0.007$, $n = 10$; Table 2), as was the time that cached seeds remained in caches ($z = -1.997$, $P = 0.046$, $n = 6$; Table 2). The distance from parents that seeds were cached was also significantly different between years, but in this case the distance to caches was greater in the non-mast year than in the mast year ($z = -2.201$, $P = 0.028$, $n = 6$; Table 2).

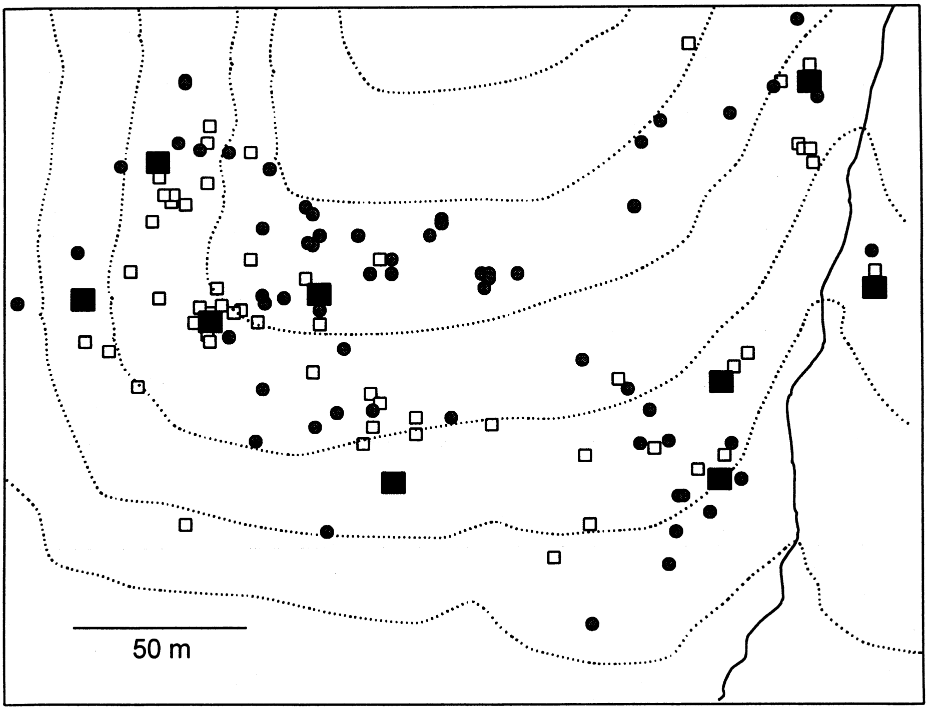

Figure 2. Map of nine adult *Beilschmiedia bancroftii* trees (large, solid squares), cache sites made by white-tailed rats (open squares), and seedling germination sites (shaded circles) at the rain forest study site in Queensland, Australia. Contour intervals are modified from Connell *et al.* (1984) and are intended to roughly illustrate the general increase in elevation from the bottom to the top of the map, the ridge on the left side of the plot and the creek along the right side. Seedling transect lines extended over 100 m beyond the top of the map, and no reproductive *B. bancroftii* trees were noted in that area during the mast year of 1997 (P. T. Green, *pers. comm.*). The 10th tree was located off the map at upper right and no seedlings were found in its vicinity.

DISCUSSION

Although none of the cached seeds followed in this study survived to germination, several lines of evidence suggest that most seedlings germinated from rat-cached seeds. First, given the long germination time required by this tree species and the rapid removal rates by rats, few uncached seeds would have time to germinate before discovery by rats, unless rat populations were severely depressed. On the study plot, all uncached seeds had disappeared from the

Table 2. A comparison of the fates of *Beilschmiedia bancroftii* seeds placed under the same 10 adult trees in a mast year (1997) and a non-mast year (1998). Means ± SD are given for days to removal, days in cache and distance to cache.

Year	Number			Total	Days to removal	Days in cache	Distance to cache (m)
	Cached	Eaten	Unknown				
1997	21	12	27	60	12.5 ± 13.0	48.5 ± 48.1	10.6 ± 6.3
1998	20	13	27	60	1.5 ± 0.8	8.1 ± 1.7	25.7 ± 12.3

plot 6 mo after the 1997 masting event, whereas the first seedling was not discovered on the plot until 12 mo after the masting event. The rapid seed removal rates documented in this study were similar to those in several other Australian rain forest sites studied by Harrington *et al.* (1997), indicating that removal of entire crops by rats before germination is not unusual. Live-trapping on my plot indicated that seedling emergence was not dependent on the absence of rats. Although the number of rats using the plot between 1997 and 1998 fell from 20 to 13, the latter number was large enough to result in the high seed removal rates documented in the non-mast year of 1998 and probably maintained significant pressure on cached seeds as well.

Second, 97% of all seedlings arose from buried seeds, and 65% of all seeds cached by white-tailed rats were at least partially buried. In contrast, of 40 *B. bancroftii* seeds that fell naturally into a vertebrate exclosure during the mast year of 1997, none has become more than 25% buried in the soil after over 2 y of exposure to the natural conditions of rainfall and litter movement, including two cyclones that passed over the site (T. C. Theimer, *pers. obs.*). Burial of seeds by rodent seed dispersers has been shown to enhance germination in several neotropical trees (Asquith *et al.* 1999, Forget 1990, Smythe 1989, Sork 1987) and the same may be true for *B. bancroftii* seeds buried by white-tailed rats.

Third, given the lack of other potential dispersers for this tree species, any significant movement away from the parent would be limited to those seeds moved downhill by gravity. However, even on the relatively steep slopes of my study site, the seed shadow of undispersed seeds downhill from parent trees was still significantly smaller than that of the seedlings that subsequently germinated. More striking was the large proportion of seedlings that germinated uphill of parents or in other directions that would have been improbable for seeds to travel by other means.

Finally, in several cases, seedlings emerged within a few metres of known cache sites. White-tailed rats often cached seeds at the base of trees, saplings or logs, as is the case for neotropical rodents like agoutis (Hallwachs 1986, Kiltie 1981, Smythe 1989). However, nearly half of the caches found in this study were in relatively open microsites more than 1.5 m from any natural object. Seedling microsites were even more biased toward open areas, with all but two emerging more than 1.5 m from the nearest structure. This suggests that either rats do not recover caches in open microsites as efficiently as those near objects, or that germination is less likely in microsites near objects.

As for several neotropical large-seeded trees and their rodent seed dispersers (Forget 1990, Hallwachs 1986, Leigh *et al.* 1993, Smythe 1989), *B. bancroftii* incurs a high cost in the number of both seeds and seedlings that are lost to rat predation. For this tree species, white-tailed rats appear to be the major means of dispersal other than gravity, and the lack of rat dispersal would apparently result in an eventual distributional shift downhill. In contrast, most of the adult trees on my plot were located on slopes or ridges, suggesting that seed movement uphill, whether by rats or some other agent, has apparently operated in the past. The fauna of Miocene and Pliocene Australian rain forests was far more diverse than that of today (Archer *et al.* 1991), and the dispersal system of *B. bancroftii* may have evolved under the influence of a very different set of dispersal agents. However, white-tailed rat fossils dating from the Pleistocene have been documented in New Guinea (Flannery 1995), and these animals have probably been present in Australian rain forests for a similar length of time.

The rapid rates of seed removal and cache recovery in the non-mast year of 1997–98 suggest that masting in this species may be necessary for caches to survive long enough to germinate. In the non-mast year, the only *B. bancroftii* seeds available to rats were the 60 experimental seeds placed in sets of six at the base of each adult tree. Even at these low seed densities, and with putatively fewer rats on the plot, seeds were removed from parent trees and from caches more rapidly than in the mast year. This suggests that *B. bancroftii* trees would not escape the effects of rats even in those years when *B. bancroftii* trees produced few fruits or in years when only a few trees fruited. In mast years, white-tailed rats may remove the entire seed crop, but the large number of caches apparently overcomes the rats' ability to remember or discover all caches made.

Although most seedlings in this study apparently arose from rat-cached seeds, the seed, cache and seedling distributions indicate that primary cache sites may not be the best predictor of future seedling emergence patterns. Most primary caches were closer to parent trees than sites of seedling emergence. This pattern could have arisen in several ways. First, secondary cache sites were significantly farther from parent trees than primary cache sites, and were more similar to distances at which seedlings were found. This suggests that many seedlings may arise from secondarily cached seeds rather than those cached initially. Vander Wall & Joyner (1998) showed that secondary and tertiary caches made by chipmunks were successively farther from the parent tree, and eventually resulted in a more uniform distribution of seeds. Likewise, Peres *et al.* (1997) hypothesized that secondary caches made by agoutis might also explain the distribution of adult Brazil-nut trees (*Bertholletia excelsa*).

Second, this pattern could have arisen if survival of cached seeds and seedlings near adult trees was lower than survival of those farther away. Distance effects on seed and seedling survival have been investigated in many neotropical tree species (e.g. Augspurger 1984, Blate *et al.* 1998, De Steven & Putz 1984, Forget 1992, Schupp & Frost 1989, Terborgh *et al.* 1993), but these effects are apparently stronger for invertebrate seed and seedling predators than for vertebrates (see Hammond & Brown 1998 for a recent review). The effect of invertebrate seed predators on *B. bancroftii* seeds is unknown, although *B. bancroftii* and several other large-seeded laurels with hard endocarps apparently suffer low levels of insect attack (P. Juniper, *pers. comm.*). There are few native vertebrate seed predators capable of chewing through the tough endocarp, but non-native pigs can crush and destroy the seeds, and burial by white-tailed rats may be important in allowing seeds to escape from these animals in areas where pigs are common. The early seedling mortality I documented was primarily due to herbivory by white-tailed rats and pademelons, animals that probably forage over relatively large areas compared to the distance most seeds are dispersed.

Finally, this pattern simply could be due to the greater difficulty in detecting primary caches made farther from the parent tree. A seed carried a long distance had a greater probability of the bobbin thread breaking and therefore would have been recorded as a seed of unknown fate rather than as a primary cache site.

White-tailed rats appear to be one of the few extant, native Australian mammals capable of dispersing the seeds of large-seeded tree species like *B. bancroftii*. Several other trees common in Australian rain forests (e.g. *Endiandra palmerstoni*, *Athertonia diversifolia*, *Pouteria castonosperma*) have seeds of large size and relatively long germination times and are fed upon and scatterhoarded by white-tailed rats (Harrington *et al.* 1997). For those whose fruits are swallowed by cassowaries, these large birds may be an important mode of long-distance dispersal, much as tapirs are in neotropical rain forests (Fragoso 1997). However, any seeds dispersed by cassowaries would most likely be secondarily dispersed by white-tailed rats, as rodents often rapidly removed seeds in cassowary dung (T. C. Theimer, *pers. obs.*). Any interaction between white-tailed rats and the other native mammalian seed disperser, the musky rat kangaroo, remains unknown, although rat kangaroos may cache seeds in different microsites and thereby create an independent seedling shadow in areas where they co-occur (A. Dennis, *pers. comm.*). This study suggests that, if the interaction with *B. bancroftii* is representative, white-tailed rats could act as a major determinant of seedling shadows for many of the large-seeded tree species in Australian tropical rain forests.

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