

SHORT COMMUNICATION

## Intraspecific variation in seed size affects scatterhoarding behaviour of an Australian tropical rain-forest rodent

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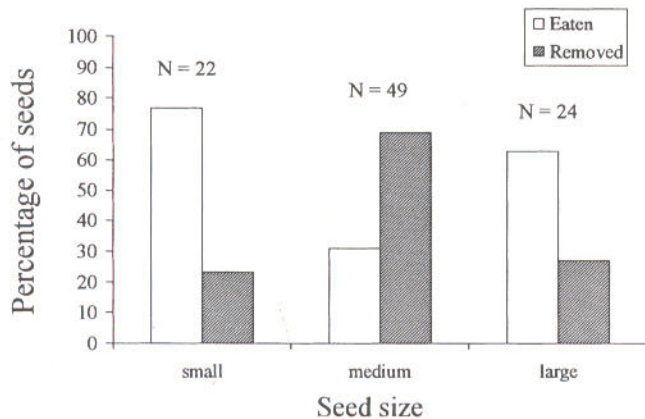
Vertebrate seed dispersers could impact the evolution of seed size or alter the pattern of seedling recruitment if they responded differently to seeds of varying size (Jordano 1995). For example, models of seed caching by birds and mammals predict that seeds of higher nutritive value should be placed farther from parent trees and in lower densities than lower quality seeds (Clarkson *et al.* 1986, Stapanian & Smith 1978, Tamura *et al.* 1999). Comparisons of seed removal rates among tropical tree species in South-East Asia (Blate *et al.* 1998) and Australia (Osunkoya 1994) failed to show a relationship between seed size and removal rate, although the probability that a seed was scatterhoarded by agoutis (*Dasyprocta punctata*) in a neotropical rain forest increased with interspecific seed size (Forget *et al.* 1998). However, interspecific comparisons are often confounded by differences among species in seed characteristics other than size. Studies of intraspecific seed size variation have shown that both red acouchis (*Myoprocta acouchy*) (Jansen *et al.* 2002) and agoutis (Hallwachs 1994) cache larger seeds more often than smaller seeds, and transport larger seeds greater distances. Spiny pocket mice (*Heteromys desmarestianus*) also preferentially removed larger *Astrocaryum mexicanum* (Palmae) seeds over smaller ones, but smaller seeds were buried farther from the seed source (Brewer 2001). These studies suggest that differences in seed size could affect which seeds are ultimately dispersed and the environment in which those seeds must establish.

In the tropical rain forests of eastern Australia, several

tree species produce seeds so large that they can be effectively dispersed only by a relatively small suite of dispersers: the ground-feeding, frugivorous southern cassowary (*Casuaris casuaris*), the terrestrial, frugivorous musky rat kangaroo (*Hypsiprinnodon moschatus*), and the semi-arboreal, omnivorous white-tailed rat (*Uromys caudimaculata*). Cassowaries swallow fruits whole and pass the seeds undamaged in the faeces (Stocker & Irvine 1983). Musky rat kangaroos scatterhoard fruits, feeding on the flesh and leaving most seeds intact (Dennis & Johnson 1995). White-tailed rats also scatterhoard, but do so primarily with seeds, as they are one of the few animals capable of chewing through the hard seed wall to obtain the fleshy cotyledons (Harrington *et al.* 1997, Moore 1995).

I investigated how variation in seed size of the Australian rain-forest tree *Beilschmiedia bancroftii* (Lauraceae) affected scatterhoarding behaviour of white-tailed rats. *Beilschmiedia bancroftii* is a monoecious tree species endemic to the rain forests of northern Queensland (Hyland & Whiffen 1993). It produces large fruits with a soft pericarp surrounding a stony endocarp 2–2.5 mm thick that contains the creamy-white cotyledons. White-tailed rats can remove or eat the entire crop of *Beilschmiedia bancroftii* seeds in a matter of weeks or months (Harrington *et al.* 1997). Because germination takes 4 mo – 9 y (A. K. Irvine, pers. comm.), few, if any, seeds remain on the surface long enough to germinate in areas where white-tailed rats are present (Harrington *et al.* 1997, Moore 1995, Theimer 2001). Likewise, seeds deposited on the surface in cassowary dung are likely to be secondarily handled by rats (T. C. Theimer, pers. obs.). These rats are common throughout the intact tropical rain forests of Australia (Moore 1995), are less affected by

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**Figure 1.** The number of *Beilschmiedia bancroftii* seeds in each of three seed-size categories either removed from the parent tree and cached or eaten at the tree by white-tailed rats.

fragmentation than cassowaries or musky rat kangaroos (Crome & Moore 1990, Laurance 1994), and therefore may be an increasingly important dispersal agent for this tree species.

In January 1997, ten adult *Beilschmiedia bancroftii* trees were selected on a c. 4-ha study site of primary upland rain forest in the Lamb Range of northern Queensland, Australia (Connell *et al.* 1984, Theimer 2001). *Beilschmiedia bancroftii* trees on this study plot have been monitored since 1995 and produced fruit only once, from October 1996–March 1997 (P. T. Green, pers. comm.).

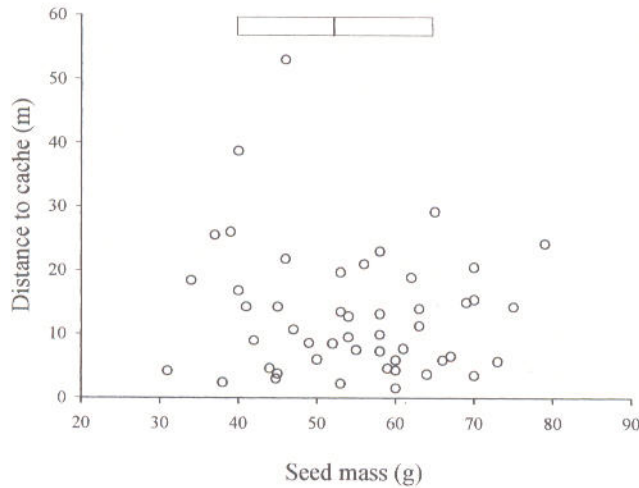
In late February 1997, when seed fall was at its peak, the relative size of seeds produced by each tree was determined by weighing 20 haphazardly selected seeds from beneath the canopy of each tree. Rats were removing seeds at this time and could have biased the size of seeds available under trees. However, because several trees were fruiting heavily at this time, seed removal by rats at any one tree was relatively light. Seed mass across the plot varied almost three-fold, ranging from 28 g to 85 g (mean =  $51.2 \pm 12.3$  SD).

Beginning in early February 1997, six individually marked and weighed *Beilschmiedia bancroftii* seeds were placed at the base of each study tree, with three seeds on the uphill side and three on the downhill side of the trunk. Each set of three seeds represented the range of seed masses available across the plot, with one seed in each trio weighing more than one standard deviation below the mean (< 38 g), one weighing more than one standard deviation above the mean (> 64 g) and one weighing within one standard deviation of the mean. All seeds placed at trees had the flesh removed, so that seed removal could be attributed to rats rather than the frugivorous musky rat kangaroo. Each seed had a small bobbin of thread glued to the endocarp, with the free end tied to a metal stake at the tree base. Within a few days, seeds were either eaten

in place, removed from under the tree after the bobbin was removed or were moved some distance with the bobbin attached. The latter could be followed to determine their fate. The distance from the parental tree was recorded for each seed cached. When a seed was removed or eaten in place, it was replaced with a seed of similar size, so that seeds in each of the three size classes were present together under each tree. The number of seeds available on either end of the size spectrum was limited (very large and very small seeds were rarer than seeds weighing near the mean), so the experiment was terminated when the supply of these very small and large seeds was exhausted and a total of 147 seeds had been handled by rats. Of these, 49 were removed and cached, 46 were eaten at the parent tree and 52 had the bobbin removed and the fate could not be determined.

Very small and very large seeds were eaten at the parent tree more than expected by chance, while intermediate-sized seeds were more likely to be cached ( $\chi^2 = 16.7$ ,  $df = 2$ ,  $P = 0.005$ , Figure 1). None of the seeds cached in this study survived to germination. However, of 75 seedlings that germinated in the following year, 40 were found soon enough after germination to determine an initial seedling height. The fate of these seedlings was followed for the first 6 mo after germination. The five seedlings with an initial height greater than one standard deviation above the mean, and the four seedlings with heights one standard deviation below the mean, all died over the 6-mo monitoring period, compared with 57% survival for the remaining 31 seedlings of intermediate height. Although based on a small sample, this suggests that if larger seeds give rise to larger seedlings, as in several other rain-forest trees (*Virola surinamensis* (Myristicaceae): Howe & Richter 1982; *Beilschmiedia pendula* (Lauraceae): Wenny 2000), larger *Beilschmiedia bancroftii* seedlings do not have a survival advantage over intermediate-sized seedlings.

Although seed size affected which seeds were removed and which were not, seed size did not affect the distance that seeds were initially cached by white-tailed rats ( $r$ -square = 0.008,  $F = 0.483$ ,  $df = 1, 47$ ,  $P = 0.499$ , Figure 2). If larger seeds represent a higher quality resource than smaller ones, theoretical models of seed caching predict that larger seeds should be cached greater distances than smaller ones (Clarkson *et al.* 1986, Stapanian & Smith 1978, Tamura *et al.* 1999). Tree squirrels (*Sciurus* and *Tamiasciurus*) (Hurley & Robertson 1987, Jacobs 1992, Tamura *et al.* 1999), red acouchies (Jansen *et al.* 2002) and agoutis (*Dasyprocta punctata*) (Hallwachs 1994) apparently respond to seed size in this way. However, as pointed out by Jansen *et al.* (2002), 'there must be a seed mass beyond which handling and transport become increasingly difficult and expensive ...'. The seeds used in this study weighed 4–13% of the mean body mass of white-tailed rats on my study plot (650 g), and may cap-



**Figure 2.** The distance *Beilschmiedia bancroftii* seeds of varying masses were cached from the parent tree as a function of seed mass. The box at the top of the figure represents the mean mass  $\pm$  1 SD of seeds produced on the study plot.

ture this upper limit of the seed size continuum. Seeds and artificial fruits used in experiments on other dispersers were a smaller percentage of the disperser's body mass, at least in those studies where relative masses were given (agoutis: 1–7% (Hallwachs 1994); acouchies: 1–8% (Jansen *et al.* 2002); squirrels: 1–6% (Tamura *et al.* 1999)). These studies suggest that white-tailed rats might show preferences for larger seeds in tree species with overall smaller seed masses compared to *Beilschmiedia bancroftii*. Alternatively, the lack of relationship between seed mass and distance to cache in this study may have resulted from variation among white-tailed rats in how they responded to seeds of varying sizes. Age, predation risk and whether an animal is foraging near or far from its core area could all affect which seeds are removed and how far they are transported (Hallwachs 1994). For the plant, the cumulative effect of all animals removing seeds ultimately determines the seed distribution, and for *Beilschmiedia bancroftii*, it appears the cumulative effect of rat dispersal is a distribution around parents that is independent of seed size.

In neotropical forests, seed removal rates by rodents, and the ratio of seeds eaten in place versus those removed, varies seasonally depending upon availability of other fruits (Forget 1990, 1996; Forget *et al.* 2002, Hallwachs 1994, Smythe 1978). Although rate of seed removal and ratio of eaten:cached seeds remained relatively constant over the 2 mo of this study (February seeds eaten = 35%; March seeds eaten = 39%), I did not collect data during the initial 3 mo of seed fall. Many of the trees on the study plot fruit at multi-year intervals, and variation in the amount and the suite of fruit/seed species available varies greatly from one year to the next (Connell *et al.* in press). Investigating how variation in fruit availability affects seed-size sensitivity over time remains an important question in this system. Likewise, how white-tailed rat

responses to seeds of varying size interact with the responses of other dispersers in the system will ultimately determine the direction of selective forces acting on the trees. Given that two of the important seed dispersers of large-seeded Australian tropical rain-forest trees are now absent or rare in forest fragments (Harrington *et al.* 1997, Laurance 1994) understanding the role of white-tailed rats in these altered habitats becomes increasingly important.

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