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Comparison of insects and vertebrates as removers of seed and fruit in a Western Australian forest

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Abstract

Removal from the forest floor of seed or fruit of the six commonest species of trees in upland areas of the northern jarrah forest of Western Australia was studied experimentally. The smallest seeds (Eucalyptus marginata, Allocasuarina fraseriana) *were taken by insects (presumably ants). Heavier seeds or fruits* (E. calophylla, Banksia grandis, Persoonia longifolia, P. elliptica) *were taken more often by vertebrates (presumably small mammals). Seeds of* E. calophylla *and* B. grandis *were most preferred by vertebrates, possibly because they have the highest relative concentrations of nitrogen and phosphorus.*

Introduction

Although there have been many studies or observations of seed-taking by animals in Australia (e.g., Gardner 1923; Jacobs 1955; Grose 1957; Greaves 1958; Ashton 1979; Berg 1975; Christensen & Schuster 1979; Shea *et al.* 1979), few have simultaneously evaluated the contributions of both insects (ants) and vertebrates (mammals, lizards and birds). We are aware of only three such Australian studies (Cunningham 1960; Kimber unpubl.; Conway unpubl.), and not many more from outside Australia (e.g., Lawrence & Rediske 1962; Brown *et al.* 1975; Mares & Rosenzweig 1978; Heithaus 1981). Most research emphasizes either ants or vertebrates. It is therefore important to examine if seed removal ascribed to either group could represent seed removal by both insects and vertebrates.

We became interested in seed removal in the jarrah (*Eucalyptus marginata* Donn ex Sm.) forest when, in 1980, known numbers of seeds of *Banksia grandis* Willd. were broadcast in quadrats and less than 3% germinated. Laboratory studies of germination had earlier shown that germination was exceptionally high (> 90%) over a range of temperatures. Hence it seemed likely that animals might play a role in the population ecology of *B. grandis*. In subsequent experiments in which removal of seed would have been a nuisance, broadcast seed of several species of tree in the jarrah forest was placed within cages surrounded by an insecticide-treated buffer (Abbott 1984). This arrangement prevented seed theft.

In this paper we distinguish the part played by small and large animals in removing from the forest floor, seed or fruit of the six most common and widespread species of tree in the upland areas of the northern jarrah forest. These are *E. marginata*, *E. calophylla* Lindl. (both overstorey) and *B. grandis*, *Allocasuarina fraseriana* (Miq.) L. Johnson, *Persoonia longifolia* R. Br. and *P. elliptica* R. Br. (all understorey). None of these species provides inducements for ants to disperse their seeds.

Materials and methods

Fresh seed or fruit was obtained from various stands of jarrah forest near Jarrahdale (32° 20′S, 116° 40′E). A randomized complete block design was used, with four treatments each replicated five times in five blocks. The sampling unit was a 60 cm × 60 cm quadrat. These were marked out in March 1983 in a stand of unlogged forest 15 km north-east of Jarrahdale. The soil surface was raked clean of leaf litter and all vegetation in or near the quadrat was clipped to ground level. Treatments were 2 m apart and arranged along the contour, and the blocks of treatments were placed about 50 m apart. Treatments were:

(1) Quadrat covered with a wire cage 50 cm × 50 cm × 15 cm high, and of mesh size 12 mm (to exclude vertebrates but not ants.).

(2) Quadrat surrounded by a buffer zone 30 cm wide sprayed with insecticide (15% solution of Dieldrin made up with water to 1 l, to exclude ants but not vertebrates).

(3) Quadrat caged and its surrounds sprayed with insecticide (to exclude both ants and vertebrates).

(4) Quadrat left uncaged and its surrounds not sprayed with insecticide (to allow access to both ants and vertebrates).

The surrounds of the relevant quadrats were sprayed three times in March–April 1983. Seeds of *E. marginata, E. calophylla, B. grandis* and *A. fraseriana* were broadcast by hand on 12 April 1983, with 30 seeds per quadrat. Disappearance of seed was monitored by recording germination on 12 May, 8, 21, 30 June, 13, 26 July, 10 August, 9 September and 12 October. Germinants were discarded away from the study area. Because the fruits (drupes) of the *Persoonia* species do not germinate readily (Abbott 1984), we arranged five fruits of each species in the centre of each quadrat as a quincunx, with a small granitic pebble contrasting in colour with the soil placed next to each drupe so as to detect removal of fruits. Disappearance of drupes was monitored on the dates above and also on 16 November 1983.

The degree of preference (percentage) shown by predators for the different species of seed was calculated indirectly as:

$$\frac{100\ (\text{mean number of seedlings in quadrats lacking cage and insecticide})}{(\text{mean number of seedlings in quadrats with cage and insecticide})}$$

The dimensions and weight of seeds or fruits were measured, and their nitrogen (N) and phosphorus (P) contents determined by standard micro Kjeldahl and vanadate-molybdate analyses.

In 1982 we attempted to establish the identity of vertebrates responsible for seed removal. Depots of *B. grandis* seed and *Persoonia* spp. fruits were placed near 20 pitfall traps (diameter 15 cm, depth 30–40 cm) connected by a single drift fence. These traps were established for 237 days. Eight Elliott traps baited with oatmeal/peanut butter were run for 13 days and breakback traps (five mouse-sized and two rat-sized baited with oatmeal/peanut butter) were also put out for 15 days.

Results

No germination was observed on 12 May but the effect of the treatments became obvious on the following two sampling occasions. Most of the seeds had probably been removed soon after being placed in the quadrats.

In the analyses of variance (Table 1), no interactions between caging and insecticide-spraying were significant. Caging had no significant effect on the number of seeds of *A. fraseriana* or *E. marginata* remaining at the conclusion of the experiment (Table 1). In contrast, spraying with insecticide had no significant effect on the number of seeds of *E. calophylla, B. grandis, P. longifolia* or *P. elliptica* remaining.

In agreement with previous experiments (Abbott 1984), the percentage of seed removed from quadrats lacking cages and insecticide-treated buffers was high (81% for *A. fraseriana*, up to 93% for *E. calophylla*). Some 28% of fruit of *P. longifolia* and 36% of fruit of *P. elliptica* was removed.

The calculated index of preference showed that seeds of *E. calophylla* were most favoured (8.6%), followed by *B. grandis* (13.6%), *E. marginata* (20.0%) and *A. fraseriana* (42.6%). Least favoured were the drupes of *P. elliptica* (66.7%) and *P. longifolia* (81.8%). Seeds of *E. calophylla* and *B. grandis*

TABLE 1. Mean number of seeds (or fruits) remaining at the conclusion of the experiment

Species	Treatment: Uncaged		Treatment: Caged		Cage			Insecticide		
	No insecticide	With insecticide	No insecticide	With insecticide	+	−	*P*	+	−	*P*
A. fraseriana	5.8^{a}	11.0^{b}	8.0^{a}	13.6^{b}			NS	12.3	6.9	0.009
E. marginata	2.4^{a}	8.8^{b}	7.6^{ab}	12.0^{b}			NS	10.4	5.0	0.021
E. calophylla	2.0^{a}	0.8^{a}	19.8^{b}	23.2^{b}	21.5	1.4	0.001			NS
B. grandis	3.2^{a}	4.2^{a}	21.0^{b}	23.6^{b}	22.3	3.7	0.001			NS
P. longifolia	3.6^{a}	2.6^{a}	4.8^{b}	4.4^{b}	4.6	3.1	0.004			NS
P. elliptica	3.2^{a}	1.8^{a}	4.0^{b}	4.8^{b}	4.3	2.6	0.016			NS

Treatment means and the probability (*P*) of accepting the null hypothesis of no difference in treatment means after a one-way ANOVA are shown for each species. Treatment means for each species followed by the same letter are not significantly different ($P > 0.05$) by Duncan's multiple range test. NS : $P > 0.05$.

TABLE 2. Some characteristics of the seeds or fruits of the six species studied.

Species	Mean weight (g)	Dimensions (mm)	Absolute (mg) and relative (%) concentration of N (on wet-weight basis †)	P
A. fraseriana	0.005	8.3 × 2.4	0.05 (10%)	0.01 (2%)
E. marginata	0.020	4.5 × 3.0	0.16 (8)	0.04 (2)
E. calophylla	0.113	12.9 × 7.2	5.39 (48)	0.85 (8)
B. grandis	0.091	29.4 × 8.2	4.51 (50)	0.44 (5)
P. longifolia *	0.962	12.1 × 10.8	7.01 (7)	0.91 (1)
P. elliptica *	1.449	17.0 × 9.5	4.17 (3)	0.33 (<< 1)

* Fresh drupe with green pericarp. † Courtesy of L. Wong, Institute of Forest Research.

are of intermediate mass and have the highest relative amounts of N (48–50%) and P (5–8%) in comparison with the other seeds and fruits tested (Table 2).

The specific identity of the animals responsible for seed removal in this study was not established. Ants, skinks and birds were observed to be abundant, and katydids also were noted occasionally. One individual bird, *Strepera versicolor* (Grey Currawong), was caught in an Elliott trap. Only one individual mammal, *Cercatetus concinnus* (Pygmy Possum), was captured; this was in a pitfall trap. However, this species does not eat seed. The presence of other small mammals was evidenced by seed husks of *E. calophylla* and tooth marks on aluminium tags used to mark seedlings in the same stand. The only granivorous species of mammal to be expected in the study area (a ridge typical of the northern jarrah forest) are the introduced House Mouse (*Mus musculus*; O. Nichols, pers. comm.) and Ship Rat (*Rattus rattus*; Wardell-Johnson 1982). Although the local diets of mammals occurring in the northern jarrah forest have not been studied, most of the indigenous species likely to be present are carnivores or herbivores. This may indicate that before the importation of mice and rats, seeds of *E. calophylla*, and *B. grandis* rarely were removed.

Discussion

We have shown experimentally with the aid of two types of barrier that both insects and vertebrates remove a large proportion of the seeds and fruits offered. This agrees with previous studies. Cunningham (1960) showed that both fencing and spraying of plots with insecticide resulted in improved germination of *Eucalyptus regnans*. Experiments were conducted by P. Kimber (unpubl.) in which samples of 100 *E. marginata* seeds were placed in either flywire envelopes, birdwire cages, or on the ground. The percentage removed was 2.9%, 95.5% and 67.1% respectively, indicating that insects (presumably ants) took more seed than mammals. An unpublished study by C. Conway (J. Majer pers. comm.) used cracked wheat and bird seed in several stands of jarrah forest; both ants and mammals were recorded eating seeds.

The balance between vertebrate and invertebrate removal of seeds or fruits should depend on several factors, including the size of the species of ant present and the mass, width, hardness and nutritive value of the seeds. Also, abundance of ants may be reduced by small mammals (Brown & Davidson 1977), thereby affecting removal of certain seeds. In Australia, seeds are rapidly removed by ants (Majer 1980, 1982; Drake 1981).

Our finding that seed or fruits of different species are not equally attractive supports earlier comparative studies (Withers 1978; Drake 1981; Majer 1982). We found that insects removed only the smallest seeds ($\leqslant 0.02$ g) and vertebrates tended to take the heavier seeds and fruits. In Arizona, rodents preyed selectively on larger seeds (~ 1.5 mg) and ants on smaller seeds (0.04 mg; Inouye *et al.* 1980). A study in Queensland found that ants tend to take seeds or fruits < 10 mg mass (Drake 1981). The size of seed handled by ants depends on the size of the species of ant involved (Davidson 1977). It is reasonable to expect that these limits will vary locally depending on the size of ants and small mammals present. In addition, some compromise involving energetic efficiency should be involved (Brown *et al.* 1975). Although small seeds are easily transported, they are low in energy in contrast to large ones which are high in energy but more difficult to transport. There should therefore be some optimal seed mass. The most preferred seeds in our study were intermediate in mass and held the highest nutritive reward per gram of wet-weight. We did not measure the energy value of the seeds and fruits.

Ants are undoubtedly the insects responsible for removal of seeds in our experiments but it is not known which features of the seeds of *A. fraseriana* and *E. marginata* make them attractive to ants, as both lack an elaiosome. Removal (dispersal) of seeds by ants may be advantageous in the sense that removal by vertebrate seed harvesters is prevented (Culver & Beattie 1978). However, this is unlikely to be true for the species we studied, as insects and vertebrates showed practically exclusive preferences for the species of seeds offered.

Future research in the jarrah forest should focus on the fate of seeds taken by ants, especially the question of how many of those removed subsequently germinate. Removal of seeds of a sample of the hundreds of understorey species deserves attention and studies on the species considered in this paper need to be extended to other localities in the jarrah forest. The impact of fire on the abundance of ants and mammals, and whether this decreases or increases the numbers of seeds removed should also be investigated.

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References

Abbott I. (1984) Emergence, early survival, and growth of seedlings of six tree species in Mediterranean forest of Western Australia. *For. Ecol. Manage.* **9**, 51–66.

Ashton D. H. (1979) Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in Central Victoria. *Aust. J. Ecol.* **4**, 265–77.

Berg R. Y. (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Aust. J. Bot.* **23**, 475–508.

Brown J. H., Grover J. J., Davidson D. W. & Liebermann G. A. (1975) A preliminary study of seed predation in desert and montane habitats. *Ecology* **56**, 987–92.

Brown J. H. & Davidson D. W. (1977) Competition between seed-eating rodents and ants in desert ecosystems. *Science* **196**, 880–2.

Christensen P. E. S. & Schuster C. J. (1979) Some factors affecting the germination of Karri (*Eucalyptus diversicolor* F. Muell.) seed. Res. Pap. For. Dep. W.A. No 51.

Culver D. C. & Beattie A. J. (1978) Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *J. Ecol.* **66**, 53–72.

Cunningham T. M. (1960) The natural regeneration of *Eucalyptus regnans*. School For. Univ. Melb. Bull. No. 1.

Davidson D. W. (1977) Species diversity and community organization in desert seed-eating ants. *Ecology* **58**, 711–24.

Drake W. E. (1981) Ant-seed interaction in dry sclerophyll forest on North Stradbroke Island, Queensland. *Aust. J. Bot.* **29**, 293–309.

Gardner C. A. (1923) Untitled. *Aust. For. J.* **6**, 220.

Greaves T. (1958) Ants affecting the germination of trees. A review of existing information, with some observations. *Inst. For. Aust. Newsletter* **2**, 1–3.

Grose R. J. (1957) A study of some factors associated with the natural regeneration of Alpine Ash, *Eucalyptus delegatensis* R. T. Baker, syn. *E. gigantea* Hook f. For. Comm. Vic. Bull. **4**.

Heithaus E. R. (1981) Seed predation by rodents on three ant-dispersed plants. *Ecology* **62**, 136–45.

Inouye R., Byers G. S. & Brown J. H. (1980) Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* **61**, 1344–51.

Jacobs M. R. (1955) *Growth Habits of the Eucalypts*. Forestry & Timber Bureau, Canberra.

Lawrence W. H. & Rediske J. H. (1962) Fate of sown Douglas-Fir seed. *For. Sci.* **8**, 210–18.

Majer J. D. (1980) The influence of ants on broadcast and naturally spread seeds in rehabilitated bauxite mined areas. *Reclam. Rev.* **3**, 3–9.

Majer J. D. (1982) Ant-plant interactions in the Darling Botanical District of Western Australia. In: *Ant-plant Interactions in Australia* (ed R. C. Buckley), pp. 45–61. Junk, The Hague.

Mares M. A. & Rosenzweig M. L. (1978) Granivory in North and South American deserts: rodents, birds, and ants. *Ecology* **59**, 235–41.

Shea S. R., McCormick J. & Portlock C. C. (1979) The effect of fires on regeneration of leguminous species in the northern jarrah (*Eucalyptus marginata* Sm) forest of Western Australia. *Aust. J. Ecol.* **4**, 195–205.

Wardell-Johnson G. (1982) A vertebrate fauna survey of the western high rainfall forest of the Serpentine area. Typescript, Forests Dept Library, Como.

Withers J. R. (1978) Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II The differential seedling establishment of *Eucalyptus ovata* Labill. and *Casuarina littoralis* Salisb. *Aust. J. Bot* **26**, 465–83.

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