

# Ants, rodents and seed predation in Proteaceae

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Many species of Cape Proteaceae have seeds dispersed by ants. Ants may reduce seed predation by rapidly transporting and burying seeds in their nests. Three field experiments using ant and vertebrate exclosures were set up to determine whether predation of *Mimetes pauciflorus* and *Leucospermum glabrum* fruits is significant, whether ants reduce it, and whether the food body (elaiosome) is important in the interaction. Results showed that seed predation could be as high as 100%, but that ants usually discover and remove seeds before vertebrates. Significantly fewer seeds were dispersed by ants when elaiosomes were removed. Vertebrate removal rates also declined. Laboratory experiments with caged small mammals showed that intact seeds were found more readily than seeds from which elaiosomes had been removed and that seed discovery improved with experience. Different species varied in their ability to detect seeds. Our results suggest that seed dispersal by ants has a direct effect on the number of seeds entering the soil seed bank by reducing predation, that myrmecochorous seeds produce a signal which attracts both ants and small mammals, and that once seeds are buried in ant nests predation is probably minimal.

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Verskeie Kaapse Proteaceae se sade word deur miere versprei. Aangesien miere die sade vinnig opspoor en in hulle neste begrawe, verlaag hulle waarskynlik predasie deur ander organismes. Drie eksperimente is in die veld uitgevoer waartydens miere en/of vertebrate uitgesluit was, om vas te stel of vertebrate *Mimetes pauciflorus* en *Leucospermum glabrum* vrugte kan opspoor en sal vreet, of miere die predasie verlaag, en of die voedselliggaampie (elaiosoom) 'n belangrike rol in hierdie verband speel. Resultate toon dat saadpredasie deur vertebrate baie hoog is en dat tot 100% saadverlies voorkom. Miere ontdek en verwyder egter gewoonlik sade voordat vertebrate dit vind. Beduidend minder sade word deur miere versprei en/of deur vertebrate opgevrete indien die elaiosoom verwyder word. Laboratoriumeksperimente met sade wat op verskillende dieptes begrawe is, het getoon dat kleinsoogdiere sade met elaiosome makliker vind as sade sonder elaiosome en dat hulle meer sade uitgrou met opeenvolgende pogings. Die effektiwiteit van saadopsporing deur die kleinsoogdiere het gewissel van spesie tot spesie. Sade met elaiosome produseer 'n reuk wat deur beide die miere en muise erken word. Nadat sade in miemeste begrawe is, is saadpredasie waarskynlik minimaal. Miere het dus 'n direkte invloed op die aantal sade wat tot die saadbank toegevoeg word deurdat hulle sade begrawe en soende saadpredasie verlaag.

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Myrmecochory, the mutualistic dispersal of seed by ants, is common in fynbos, and particularly well developed in the Proteaceae (Slingsby & Bond 1983; Bond & Slingsby 1983). The fruits of *Leucospermum*, *Mimetes*, *Orothamnus*, and *Paranomus* typically have large elaiosomes (food bodies) which attract ants and are eaten by them. Ants discover, transport and bury the fruits in their nests extremely rapidly.

One benefit of the ant-plant interaction may be seed escape from predators. Elaiosome-gathering ants do not eat myrmecochorous seed which is usually smooth coated, thick walled and difficult for ants to manipulate after the elaiosome is eaten (Berg 1975; Bond & Slingsby 1983). Ant dispersal may, however, result in reduced predation by vertebrates, because of rapid seed burial in ant nests (O'Dowd & Hay 1980; Heithaus, Culver & Beattie 1980; Heithaus 1981; Culver & Beattie 1978).

We studied the role of ants in reducing predation on Proteaceae seed in hygrophilous fynbos by addressing the questions:

- (i) Do vertebrates, especially small mammals, eat significant numbers of Proteaceae seed?
- (ii) Does seed dispersal by ants reduce seed loss to vertebrates?
- (iii) Do elaiosomes attract ants or small vertebrate seed predators?
- (iv) Can small mammals locate buried seed?

## Field experiments

### Methods

*Leucospermum glabrum* and *Mimetes pauciflorus* both occur in hygrophilous fynbos of the Outeniqua mountains. Both have achenes (hereafter referred to as seeds) with prominent elaiosomes formed by fleshy swellings beneath the pericarp at the base of the fruit and below the style. The entire pericarp is often eaten by ants. Both species are killed by fire and regenerate only from seed stored in the soil.

The study was conducted on Tierkop (33°55'S/22°31'E), in the Outeniqua mountains, near George. The vegetation was a dense 12-year-old shrubland, mid-height ca. 1 m and dominated by *Penaea cneorum*, *Grubbia tomentosa*, *Erica arachnoidea*, and *Restio compressus* with scattered *M. pauciflorus* and *L. glabrum* on steep, mesic, south-facing aspects. Soils were moist loams with a black, organic matter rich A horizon overlying Table Mountain Sandstone at 40–60 cm.

The rate of seed removal by ants was compared with rate of seed loss to vertebrates using exclosure experiments. Exclosures were replicated at 10–15 stations placed at least 10 m apart in a grid. At each station, three exclosure treatments were used:

- (i) Ants were excluded from access by a) glueing seed to wooden blocks (ca. 10×10 cm) with a colourless,

(odourless to humans when dry) household glue or, b) placing seed in a Petri dish with the rim smeared with Formex, a sticky grease.

- (ii) Vertebrates were excluded by a) wire mesh enclosures the size and shape of inverted waste paper baskets or b) by securing a lid 5 mm above a Petri dish so that ants had access to seeds but vertebrates did not.
- (iii) Controls excluding both ants and vertebrates were used to test the efficiency of the enclosures using a combination of the above.

Eight to 10 seeds were used for each treatment.

We report the results of three experiments the first of which used freshly collected seed of *L. glabrum* and was conducted from 3–5 December 1981. The second was from 11–13 December 1981, also using *L. glabrum*, but with seed that had been refrigerated for three days (until the weather cleared). Seed with elaiosomes present was used at 10 stations, each alternating with another 10 at which we used seed from which elaiosomes had been removed (by hand). The third experiment used freshly collected, intact seed of *Mimetes pauciflorus* and was conducted from 10 to 11 March 1982. Wire mesh and glued seed enclosures were used in the first and third experiment and Petri dish enclosures in the second.

Non-parametric tests are used in statistical tests since seed predation data do not meet assumptions of normality and equality of variance. We have however used standard measures of dispersion.

## Results

Ants responded very rapidly to fresh seed with elaiosomes, as is usual for myrmecochorous fynbos Proteaceae (Slingsby & Bond 1983). Many seed depots were swarming with ants before the layout of enclosures was completed. Response was not as rapid with the seed that had been stored in a refrigerator before use. Ants are very sensitive to weather conditions and activity ceases if the vegetation is wetted by mist or rain. The *Mimetes* experiment was dry for only 3 h before rain set in. Ant activity ceased and the experiment was stopped after 24 h. Small mammals however remain active and have been trapped in all kinds of weather conditions (Breytenbach 1982).

Neither enclosure method was completely effective. The Petri-dish method was more effective at excluding both ants and vertebrates, but ants had difficulty removing seed from the lidded enclosures. Ants worked persistently on seeds glued to wooden boards and some were prised loose. Nevertheless, the effect of ants and vertebrates can be compared by referring to controls from which both species were excluded, or by

counting vertebrate predation only from depots at which opened seed husks were found.

Small mammals seem to be the major vertebrate seed predators. All seed remnants were typical of those produced by small mammals in laboratory feeding experiments. Granivorous birds are rare in the southern Cape mountain fynbos and none were seen in the study area.

Results of the three experiments are shown in Tables 1–3. Ants removed more than 95% of intact seed within 24 h (from depots to which they had access) in the first and last experiment and 79% in the second. Small mammals ate a large proportion of the seed unavailable to ants but were slower at discovering seed in the first and last experiment (Tables 1 & 3:  $p < 0,01$  for ants versus small mammals after one day, both experiments, Fisher's Exact Test). Small-mammal activity could be easily identified by neatly opened or crushed seed husks near depots. They also typically removed all seed from a depot once it had been discovered. In the second experiment, seed predation exceeded seed removal by ants from the first day (Table 2:  $p < 0,05$  after one day, Fisher's Exact Test). Since this experiment was repeated at the same stations and within a few days of the first, small mammals may have learnt the location of the depots.

### Importance of elaiosomes

Rates of seed removal by ants were significantly reduced when elaiosomes were removed (Table 2:  $p < 0,01$  after one day, Fisher's Exact Test). Some ant dispersal still took place, however, since ants were able to eat and transport seed by adhering pericarp fragments that had not been removed. Both the pericarp and fleshy swellings of *Mimetes* and *Leucospermum* fruits therefore function as 'overall elaiosomes' (Slingsby & Bond 1983). Interestingly, small-mammal predation was also

**Table 1** Experiment 1: Comparison of *L. glabrum* seed removal rates from ant versus small-mammal enclosures, 3–5 December 1981. The mean number of seeds removed (and S.D.) are given for 15 stations starting at 10 seeds per station for each treatment

	Number of days		
	1	2	3
Accessible to ants only	9,3(2,05)	9,9(0,26)	9,9(0,26)
Accessible to small mammals only	2,5(3,96)	5,3(4,42)	8,6(2,69)
Control (accessible to neither)	1,5(2,83)	2,9(2,75)	4,9(3,74)

**Table 2** Experiment 1: Comparison of *L. glabrum* seed removal rates from ant versus vertebrate enclosures using seed with (+) and without (–) elaiosomes, 11–13 December 1981. The mean number of seeds removed (and S.D.) is given for 10 stations starting at 10 seeds per station for each treatment

Treatment	Number of days					
	1		2		3	
	+	–	+	–	+	–
Accessible to ants only	7,9 (2,69)	2,7 (2,67)	9,1 (2,18)	3,4 (3,31)	9,2 (2,2)	3,5 (3,31)
Accessible to vertebrates only	9,0 (3,16)	6,7 (4,57)	10,0 (0)	10,0 (0)	10,0 (0)	10,0 (0)
Control (accessible to neither)	0,1 (0,32)	0,0 (0)	0,2 (0,42)	0,0 (0)	0,6 (1,26)	1,5 (3,37)



**Table 3** Experiment 3: Comparison of *M. pauciflorus* seed removal rates from ant versus small-mammal exclosures, 10 – 11 March 1982. There were 10 stations with 8 seeds/station for each treatment. Unless otherwise indicated values in parentheses are *S.D.*

	Accessible only to		
	ants	vertebrates	neither (control)
Mean number of seed removed per station	7,9(0,32)	4,6(2,27)	3,1(1,97)
% Seed removed	99	58(28,75)*	39

\* Value includes seed counts only from those depots with direct evidence of small mammal predation.

initially slower if elaiosomes were removed (Table 2:  $p < 0,01$  after one day, Fisher's Exact Test).

#### Ant community

Table 4 lists ants observed attempting to remove seed at depots. *Meranoplus peringueyi*, *Rhoptromyrmex* sp. (?) and *Pheidole capensis* were the most adept at carrying seeds and transporting them into their nests. *Camponotus niveosetosus* attempted to collect seed, but discarded them if other ants appeared and was not proficient at manipulating seed. *Crémátogaster peringueyi*, a tree-nesting species, was dominant at several depots. This species feeds on elaiosomes and then discards the seed on the soil surface where it is still vulnerable to predators. *Myrmecaria*, *Meranoplus* and *Pheidole* were all observed carrying seeds to their nests and burying them. We were unable to observe what proportion was ejected from nests because of the density of the vegetation.

**Table 4** Experiment 1: Ants observed manipulating seed glued to wooden blocks. The number of stations at which each species was recorded are listed. Loose seed was removed too rapidly to observe ants at all stations. *M. peringueyi*, *P. capensis* and *Rhoptromyrmex* (?) sp. were amongst the earliest visitors

	Day			
	0	1	2	3
<i>Camponotus niveosetosus</i>		8	10	3
<i>C. cleobolus</i>		–	–	1
<i>Crémátogaster peringueyi</i>		3	2	–
<i>Meranoplus peringueyi</i>	+	2	1	–
<i>Myrmecaria nigra</i>		2	1	1
<i>Pheidole capensis</i>	+	1	–	–
<i>Rhoptromyrmex</i> sp. (? = WB7)	+	1	2	1
Total stations with ants present		14	11	5

#### Laboratory experiments

##### Methods

Field experiments showed that both ants and small mammals remove seeds with elaiosomes more rapidly than seeds from which the elaiosomes had been removed. This suggests that the elaiosome releases an olfactory signal. We tested the ability of six small-mammal species to locate buried seed with and without elaiosomes and the influence of depth of burial on seed discovery in laboratory experiments. All the species used

are granivorous and occur in southern Cape fynbos (Breytenbach 1982). Three 20 cm deep containers filled to 15 cm with sand, were placed in each cage. In one of these containers, seeds were buried at 5 levels with 5 seeds at each level: ca. 0,2 cm, 2 cm, 5 cm, 10 cm, and 15 cm deep. Seeds of either *L. glabrum* and/or *M. pauciflorus* were used as representatives of myrmecochorous seed with elaiosomes intact or removed, and *Protea repens* a serotinous species with no elaiosome, was used as a control. Each trial with myrmecochorous seed was conducted over a 10-day period whilst they lasted for five days in the case of the *P. repens* trials.

Record was kept of the number of seeds taken daily at each depth, as well as whether digging took place in any of the containers without seed. Animals were housed singly in cages and fed on rat pellets before and during the trial.

In a preliminary trial it was established that the animals' ability to retrieve buried seed improved over time. Consequently each trial was conducted with an inexperienced animal. All animals were caught in the southern Cape mountains where myrmecochorous plants feature prominently.

#### Results

Except for *Dendromus mesomelas* and *Elephantulus edwardii* effectivity in recovering seed increased over time (Figure 1). The experimental animals were able to find seeds with elaiosomes more easily than those from which the elaiosome had been removed (Table 5, Figure 2). The difference was particularly pronounced for seeds buried at a depth of 5 cm or more. Species varied in their ability to locate seed. *Acomys subspinosus* and *Aethomys namaquensis* were the most proficient at recovering intact seed from all depths.

Most of the small mammals removed *P. repens* seed (not ant dispersed) at rates comparable to myrmecochorous seeds from which the elaiosomes had been removed. *Praomys verreauxii*, however which feeds predominantly on *Protea* seeds in the wild (Breytenbach 1982), was more efficient at finding *P. repens* seeds than myrmecochorous seeds from which the elaiosomes had been removed, whilst *Aethomys* showed the reverse (Figure 2).

It was not possible to distinguish between casual walking and/or digging marks in the loose sand in the different containers. Generally small excavations were made in all containers. Deep excavations however only occurred in the containers with seed.

**Table 5** The mean number of myrmecochorous seeds with (+) and without (–) elaiosomes dug out by various small mammal species from all five depths every day (see text), using five seeds at each depth, over five days for each treatment.

Species	Elaiosome	n	Mean	SE	G test of independence	
					independence	P
<i>A. subspinosus</i>	+	3	22,9	0,92	388,8	0,001
	–	3	11,6	1,4		
<i>P. verreauxii</i>	+	3	18,1	1,3	175,1	0,001
	–	3	9,7	0,86		
<i>A. namaquensis</i>	+	3	21,7	1,91	202,1	0,001
	–	3	13,5	1,22		
<i>R. pumilio</i>	+	5	12,2	1,5	79,9	0,001
	–	5	8,2	0,45		
<i>D. mesomelas</i>	+	1	5,2	1,98	0,01	ns
	–	1	5,0	1,69		
<i>E. edwardii</i>	+	2	16,5	1,46	79,6	0,001
	–	2	9,5	1,57		

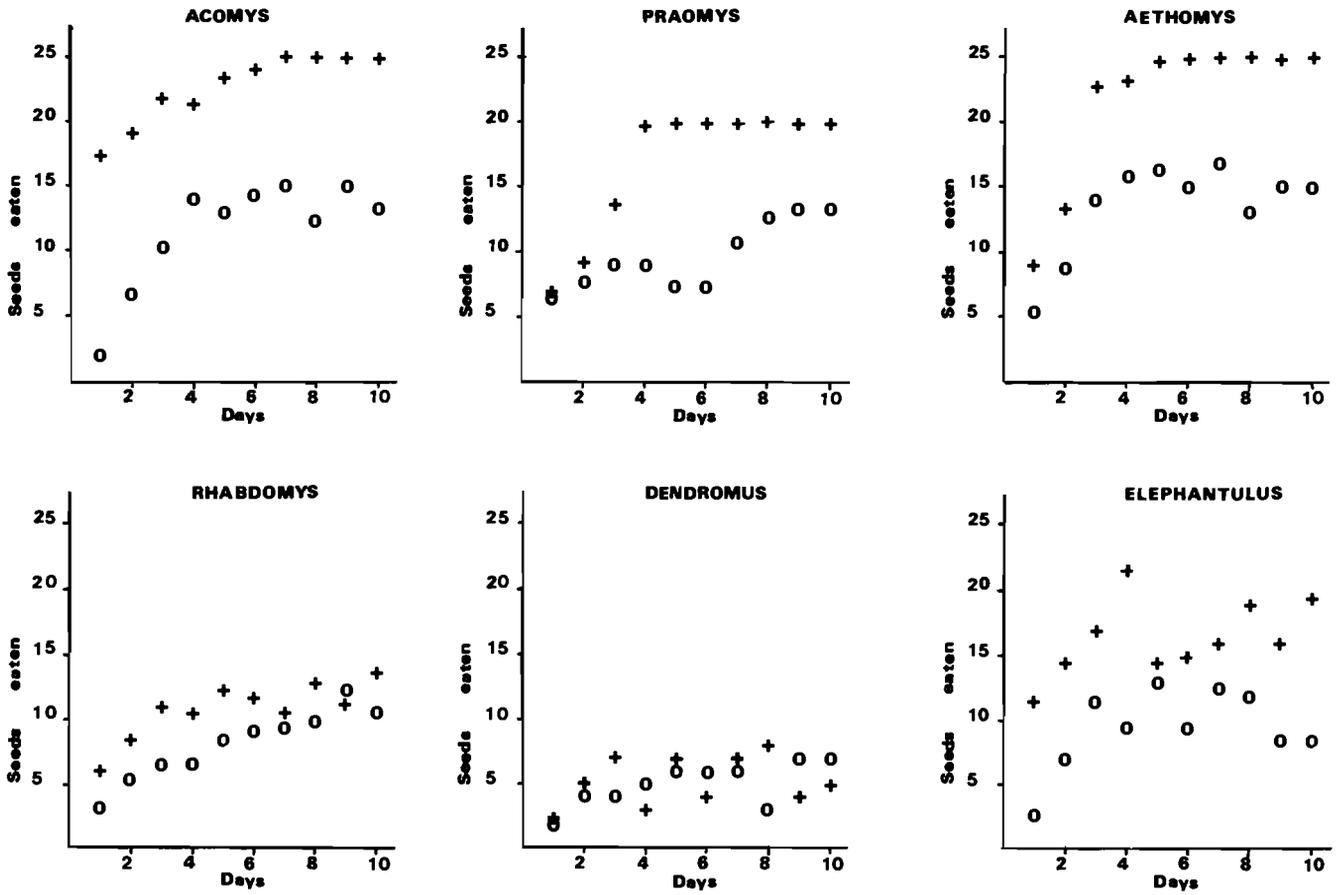


Figure 1 The mean number of seeds of *L. glabrum* and *M. pauciflorus* removed by each individual for each species for each day. The number of test animals for both seeds with (+) and without (0) elaiosomes were the same and were: *Acomys* (3), *Praomys* (3), *Aethomys* (3), *Rhabdomys* (5), *Dendromus* (1) and *Elephantulus* (2).

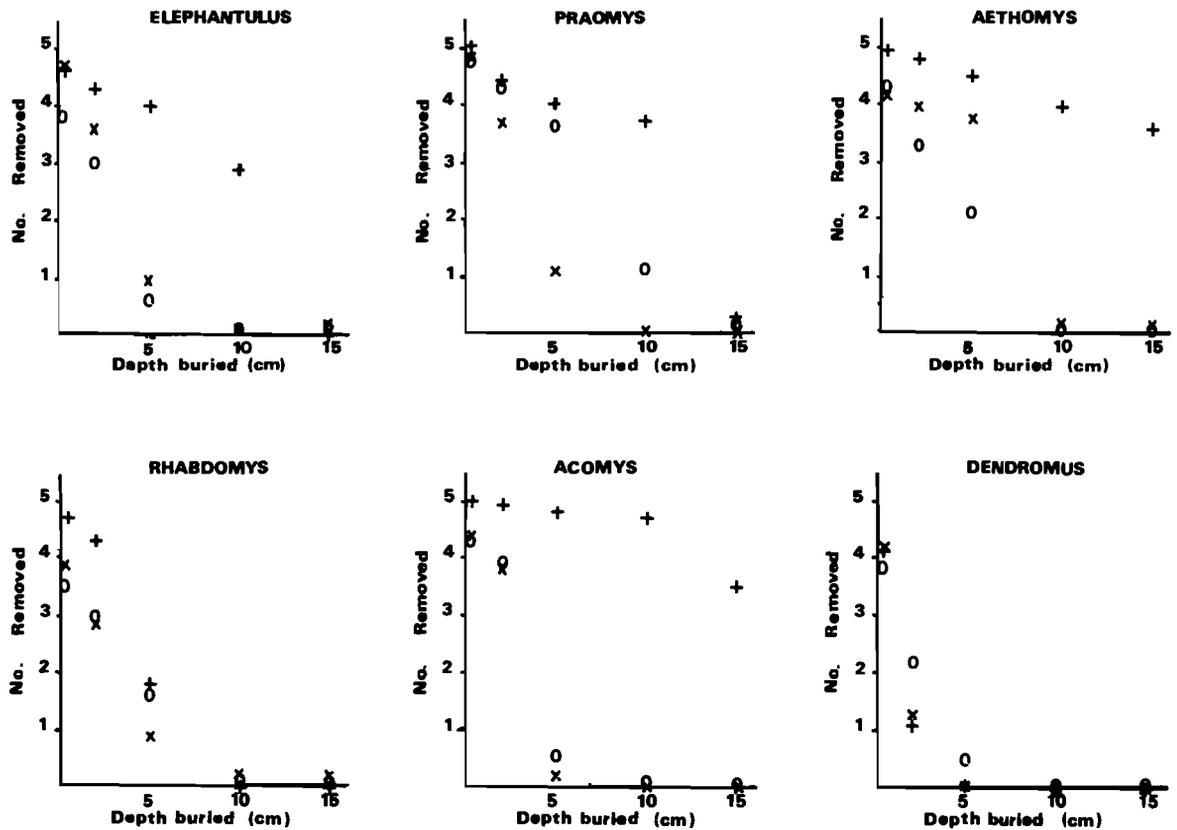


Figure 2 The mean number of seeds of *L. glabrum* and *M. pauciflorus* (with (+) and without (X) elaiosomes) and *P. repens* (0) removed by each individual for each species at each depth. The number of test animals in the *P. repens* trials were: *Acomys* (3), *Praomys* (2), *Aethomys* (4), *Rhabdomys* (5), *Dendromus* (1) and *Elephantulus* (2).

## Discussion

The number of Proteaceae seed which survive to germinate after fire is limited by the number of seed produced annually and their subsequent survival as viable seed reserves. Seed production depends both on successful pollination and adequate resources for allocation to seed production. In Australia, Pyke (1982) has shown that seed set in *Lambertia* (Proteaceae) is not limited by pollinators, but probably by resources of the parent. Australian Proteaceae divert large amounts of nutrients to seeds. These may have 30–500 times more phosphorus and 8–100 times more nitrogen than leaves or woody parts of fruits (Kuo, Hocking & Pate 1982; Hocking 1982). This extraordinary commitment to seed quality on impoverished heathland soil is attained at the expense of seed quantity. If Cape Proteaceae are similar, then seeds are precious items. Selection would be intense to reduce seed loss by strategies such as serotiny and myrmecochory.

This study has shown that small mammals eat significant numbers of myrmecochorous seed (if they are not first removed by ants). Ants discovered and transported seed very rapidly so that they were generally safely buried before being discovered by small mammals. If ants were excluded, however, as much as 100% of the seed was eaten by small mammals. Elaiosomes are a functional adaptation for attracting ants and are crucial to the success of the ant–plant interaction.

Other studies have demonstrated complete failure of seedling recruitment if the dispersal mutualism is disrupted, either by removing elaiosomes (Slingsby & Bond 1985) or if indigenous ants are replaced by *Iridomyrmex humilis* (Bond & Slingsby 1984). Our results support Bond & Slingsby's (1984) hypothesis that the cause of recruitment failure is seed predation and that the major benefit of myrmecochory in Proteaceae is seed escape from predators.

Some weaknesses of the interaction are apparent from our experiments. Firstly, if seed release coincides with wet weather, ants will not disperse seed. Field observations suggest that most seed is dispersed under warm, dry conditions but the effects of temperature and humidity on release mechanisms have not been adequately studied. Secondly, not all ants were effective dispersers. Seeds discovered by *Crematogaster* were left exposed to predators after their elaiosomes had been eaten. Successful seed dispersal may therefore depend on the position of the parent plant in the 'ant mosaic' (Gilbert 1980), i.e. its location with respect to the composition of the ant community.

Finally small mammals seemed to learn localities where seed could be found (Experiment 2). Under natural conditions, seed discovery and seed predation by small mammals may therefore be faster than in our experiments. In the race between ants and small mammals, seeds emitting signals to attract ants would be at an advantage. Indirect evidence for coevolved seed signals which attract only fynbos ants has been discussed by Bond & Slingsby (1984).

Ironically fynbos small mammals may have learnt the same cues since they found intact seed more rapidly than seed from which elaiosomes had been removed (Table 2) (see also Heithaus 1981). In laboratory experiments they were able to detect the presence of buried seeds with elaiosomes more effectively than those without (Figure 2 and Table 5). Seed detection also improved with experience. Thus timing of seed fall might have a large effect on the fate of a seed. Most seed dispersal occurs

in mid and late afternoon (Slingsby & Bond 1981; Slingsby pers. comm.) when relatively few rodents are active and this might increase the chance of first discovery by ants.

Though this and previous studies (Bond & Slingsby 1984) have shown that seed predation is significant in a number of different fynbos communities and that ants reduce it, all observations have been on large seeded Proteaceae. Much work remains to be done on how myrmecochory influences seedling recruitment of the many smaller seeded genera in fynbos that are dispersed by ants.

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