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Selective predation on *Protea neriifolia* (Proteaceae) seeds by small mammals

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The ability of small mammals to select *Protea neriifolia* seeds containing embryos (full seeds) was examined. Full and empty seeds were glued to wooden boards and placed at three sites in young fynbos. Small mammals were able to select and remove significantly more full seeds than expected. Seed removal rates varied between the study sites but this was not related to the density of small mammals trapped at those sites. Selective feeding greatly increases the feeding efficiency of small mammals because 90% or more of the seed dispersed after fires may be empty.

Die vermoë van klein soogdiere om *Protea neriifolia* sade met vrugkieme (vol sade) te selekteer is ondersoek. Vol en leë sade is op hout plankies vasgegom en op drie studieterreine in jong fynbos geplaas. Die klein soogdiere het betekenisvol meer vol sade verwyder as wat verwag was. Die tempo van saad verwydering het verskil tussen die studieterreine maar daar was geen verband met die digtheid van klein soogdiere wat gevang was nie. Deur selektief te voed kan klein soogdiere hul voedingsdoeltreffendheid aansienlik verhoog aangesien 90% of meer van die sade wat na 'n brand versprei is leeg kan wees.

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Seed set in fynbos Proteaceae is low, generally less than 10% (Collins & Rebelo 1987). *Protea neriifolia* R.Br. has 270–320 florets per inflorescence (Collins & Rebelo 1987), but seed production is low, typically less than five per inflorescence in Swartboskloof. Many inflorescences contain no viable achenes, hereafter termed seeds, at all (Le Maitre unpub.). Many florets produce empty, sterile seeds which outwardly resemble embryo-filled seeds. However, seeds with a healthy white embryo (hereafter termed full seeds) are firm, but seeds with decayed embryos or without embryos (hereafter termed empty seeds) are easily compressed. Empty seeds may also have a dull appearance compared with the glossy look of full seeds. Ninety-five per cent or more of full seeds selected by the human hand on the basis of feel and appearance will germinate under controlled conditions (Le Maitre 1990). If small mammals can use similar criteria to distinguish full from empty seeds, without first opening them, their efficiency as seed predators would be significantly higher than if they fed non-selectively.

Seed predation by small mammals can have a significant impact on the regeneration of fynbos Proteaceae with canopy-stored seeds, both between and after fires (Bond 1984; Bond, Vlok & Viviers 1984; Breytenbach 1984; Bond & Breytenbach 1985). Most of these studies used small mammal enclosures in field experiments or were done with captive animals. In this paper we report on a field experiment using seeds of *P. neriifolia* and designed to test:
(a) the ability of small mammals to select seeds;
(b) whether removal rates differ between forest, ecotonal and burnt fynbos communities; and
(c) whether the removal rate is related to the abundance of small mammals.

The study was carried out in the Swartboskloof catchment in the Jonkershoek Valley near Stellenbosch, in the south-western Cape. The catchment was burnt on 17 and 18 March 1987. The pre-fire vegetation was a tall (>2 m), 29-year-old shrubland dominated by *P. neriifolia*. This study was carried out concurrently with other experiments which examined the impact of seed and seedling predation on seedling recruitment of *P. neriifolia* after the fire (Botha & Le Maitre 1992).

Seeds of *P. neriifolia* were collected before the fire and sorted by hand. The sorted seeds were stuck onto 120 × 120-mm masonite boards using wood glue. Four full seeds were stuck onto each board. Six empty seeds were glued in a ring around each full seed on half of the boards giving 0,17 full seeds per empty seed on boards with both kinds.

Ten boards, five with each type of seed arrangement, were placed alternately, about 5 m apart, along each of seven lines on 8 April 1987. The lines were spaced about 20 m apart. The first line was situated in riverine forest, the second in the partly burnt ecotonal community (about 2 m from the forest edge) and the remainder in burnt fynbos. A further thirty boards, fifteen of each type, were set out in a similar fashion at two burnt fynbos sites on 11 April 1987. The boards were visited at intervals of one to two weeks and the number and type, full or empty, of any missing seeds were recorded. The experiment continued until 6 July 1987 when it was found that heavy rains had soaked the boards, with the result that seeds had become unstuck or had germinated on the boards.

Small mammals were captured at these sites in the following way. At each of the fynbos sites a 48 × 48-m trapping grid with 49 trap stations (7 × 7 grid) at 8-m intervals was used. At site three the grid was situated about 60 m from the forest margin. Small mammals were also trapped within the riverine forest where ten trap stations were placed about 5 m apart along each bank of the stream. One live trap was set at each station on four consecutive nights. Traps were baited with a mixture of peanut butter, lard and candle wax (1:1:1 by mass) melted together and mixed with rolled oats (2 parts by mass) (Willan 1986), and each one was visited daily. No pre-baiting was done. Small mammal nomenclature follows Meester, Rautenbach, Dippenaar & Baker (1986). Trapping at sites 1 and 2 began on 20 March 1987 and at site 3 on 6 April 1987.

The data on seed removal are summarized in Tables 1 & 2. Overall, significantly more seed was removed from boards with both full and empty seeds, mean 12,13 ± 6,96 than boards with full seeds only, mean 2,91 ± 1,33 (Tukey's Studentized Range test [TSR_t] value = 1,607; P < 0,05). The total number of seeds removed differed significantly between the three sites, being highest at site 2 and lowest at site 1 (TSR_t value = 3,354; P < 0,05, Table 1). The number of full seeds removed did not differ between the types of board, mean of both types = 2,67 ± 1,46 and mean of full only = 2,91 ± 1,33 (TSR_t P > 0,05). The number of full seeds removed differed significantly between sites (Anova F = 4,08; DF = 2; P < 0,05). The total number removed from boards with both types was significantly higher at site 2 than at sites 1 and 3 (TSR_t value = 3,354; P < 0,05), but the difference between sites 1 and 3 was not significant.

Full seed removal at all three sites was significantly higher (Table 1) than was expected, based on the number of full (4) and empty seeds (24) presented on the boards (Chi-square goodness-of-fit test — site 1: χ^2 = 33,33; DF = 1; P < 0,01; site 2: χ^2 = 4,54; DF = 1, P < 0,05; site 3: χ^2 = 15,25; DF = 1; P < 0,01). There were only two occasions, one for a board with full and empty seeds and one for a board with only full seeds, when all the seeds were removed between successive visits. Most of the seeds (75–90%) were removed at the rate of one or two between successive visits. The removal rates of full seeds did not differ between boards with and without full seeds (χ^2 = 4,97; DF = 3; P > 0,05).

Table 1 Seeds removed by small mammals at three sites by 6 July 1987. The experiment was laid out in April 1987. Four full seeds (with embryos) were glued onto each board and an additional 24 empty seeds (with no embryos) were glued onto boards with both types of seed

Site	Board type	Number of boards	Seed type	Mean number missing (±*SD*)	Per cent missing	Missing full/ empty
1	Full only	15	Full	2,69 ± 1,25	67	
	Full & empty	15	Full	2,27 ± 1,83	57	0,53
			Empty	4,27 ± 2,81	18	
			Total	6,53 ± 3,70	23	
2	Full only	15	Full	3,53 ± 1,25	88	
	Full & empty	15	Full	3,29 ± 1,14	82	0,24
			Empty	13,93 ± 5,39	58	
			Total	17,21 ± 5,79	62	
3	Full only	35	Full	2,74 ± 1,36	69	
	Full & empty	35	Full	2,60 ± 1,35	65	0,26
			Empty	9,89 ± 6,06	41	
			Total	12,49 ± 6,84	45	

Table 2 Seeds removed by small mammals at site 3 by 6 July 1987 in three different plant communities: unburnt riverine forest, partly scorched forest-fynbos ecotone and burnt fynbos. Four full seeds were glued onto each board and an additional 24 empty seeds were glued onto boards with both types of seed

Plant community	Board type	Number of boards	Seed type	Mean number missing (±*SD*)	Per cent missing	Missing full/ empty
Forest	Full only	5	Full	3,80 ± 0,45	95	
	Full & empty	5	Full	3,20 ± 0,84	80	0,23
			Empty	13,80 ± 5,31	58	
			Total	17,00 ± 6,04	61	
Ecotone	Full only	5	Full	4,00 ± 0,00	100	
	Full & empty	5	Full	3,80 ± 0,45	95	0,26
			Empty	14,40 ± 9,10	60	
			Total	18,20 ± 9,34	65	
Fynbos	Full only	25	Full	2,28 ± 1,34	57	
	Full & empty	25	Full	2,24 ± 1,39	56	0,27
			Empty	8,20 ± 4,81	34	
			Total	10,44 ± 5,50	37	

A more detailed analysis of full seed removal at site 3 shows that significantly more seeds were removed from boards with full seeds in forest and ecotonal communities than in burnt fynbos (TSR_t value = 3,475; P < 0,05, Table 2). Significantly more full seeds were removed from boards with both types in the ecotonal community than in the other two communities (TSR_t value = 3,475; P < 0,05) but the number of empty seeds removed did not differ significantly between sites. All the seeds on boards with only full seeds in the ecotonal community had been removed by 6 July, the highest value at any site (Table 2).

The rate of seed removal was also particularly rapid in the ecotonal community. The mean number of full seeds removed was already 3,80 (95%) by 21 May on boards with both types or only full seeds compared with an average of 1,00 in the fynbos and 2,24 in the forest community.

The highest selection coefficient, number of full seeds taken per empty seed, of 0,51 was recorded at site 1 (Table 1). Selection coefficients were lower, but still significantly higher than expected, at sites 2 and 3 (Table 1) and the forest and ecotonal communities at site 3 (Table 2).

The number of small mammals captured at each site varied during the period of the experiment (Table 3). The mean trapping success was highest in the forest (10,6%), followed by site 1 (4,4%), site 3 (1,9%) and site 2 (0,7%), but the differences were not significant (F = 2,55; DF = 3; P > 0,05). Captures in the forest refuge and at site 3 were highest in June which is in sharp contrast to the fynbos sites where the trapping success rates were lowest in June (Table 3).

Table 3 Number of small mammals and individuals captured at the three study sites in fynbos and one in the forest refuge. Trapping in the forest refuge at site 3 only began on 8 April 1987. Forty-nine trap stations were used in the fynbos sites and twenty in the forest refuge. For more information on the trapping see Botha & Le Maitre (1992)

Site	Trapping period	Species	Number of captures	Number of individuals	Trap success (%)
1	19–23 March	*Myomyscus verreauxii*	1	1	7,7
		Rhabdomys pumilio	13	7	
		Otomys sp.	1	1	
	8–12 April	*Rhabdomys pumilio*	4	3	4,1
		Myosorex varius	4	2	
	7–11 June	*Rhabdomys pumilio*	1	1	1,5
		Otomys sp.	1	1	
		Crocidura flavescens	1	1	
2	19–23 March	*Rhabdomys pumilio*	2	2	1,5
		Crocidura flavescens	1	1	
	8–12 April	*Rhabdomys pumilio*	1	1	0,5
	7–11 June	No captures	0	0	0,0
3	19–23 March	No captures	0	0	0,0
	8–12 April	*Rhabdomys pumilio*	1	1	1,5
		Myosorex varius	2	2	
	7–11 June	*Aethomys namaquensis*	1	1	4,1
		Myomyscus verreauxii	1	1	
		Rhabdomys pumilio	6	5	
Forest	8–12 April	*Crocidura flavescens*	2	2	3,8
		Myomyscus verreauxii	1	1	
	22–26 June	*Myomyscus verreauxii*	9	3	17,5
		Aethomys namaquensis	4	3	
		Crocidura flavescens	1	1	

The results of this experiment show that small mammals are able to feed selectively when presented with a mixture of outwardly similar full and empty seeds of *Protea neriifolia*. Although they removed many more empty than full seeds from boards with both seed types, the number of full seeds removed was only slightly lower than that from boards which only had full seeds. They also selected significantly more full seeds than would be expected if they could not identify full seeds. Most seeds were removed at the rate of one or two between successive visits, suggesting that the animals collect seeds and move on rather than settling down to systematically consume all those available on the board at the time.

Seed removal from boards with both types differed between study sites and communities. Of all the seeds removed, it was highest in the partly burnt fynbos-forest ecotonal community (65%, Table 2), followed by the forest community and then site 2 with 61% and 62%, respectively (Tables 1 & 2). The lowest removals were recorded at site 1 (23%, Table 1). These differences in seed removal were not consistently related to the number of small mammals trapped. Small mammal numbers were highest in the forest refuge (mean trapping success 10,6%) and lower in the adjacent fynbos (1,9%, site 3) (Table 3) but many seeds were removed from site 2 which had the lowest number of small mammals (Table 3). Some of these differences may have been due to bait selection by small mammals (Willan 1986). The bait used in the live traps was the preferred overall choice but may give low capture rates for the insectivorous shrews (*Crocidura* and *Myosorex*) which are known to feed on *Protea* seeds after fire (Breytenbach 1982).

Bond & Breytenbach (1985) found that the ability of small mammals to find buried seeds improved with time. It is possible that one or more of the animals learned to find the full seeds on the boards and this influenced the results of this experiment. Seeds of *Protea repens*, *P. nitida* and several other species are hard and woody and it is not possible to sort these accurately by hand (Horn 1972). Small mammals may be markedly less efficient when feeding on these seeds, but this remains to be proved. Is it possible that woodiness of the seed is a response to selective seed predation by small mammals? This question is not a simple one to answer because there are no reliable, non-destructive methods for pre-determining the ratio of full to empty seeds. Maybe someone can come up with an ingenious solution to this problem. Whatever the solution, future studies will have to take cognisance of the behaviour and learning patterns of individual small mammals.

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