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Scatter-hoarding of Cape Proteaceae nuts by rodents

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ABSTRACT

Most large-seeded shrubs and trees from Mediterranean shrublands are either serotinous (canopy stored seeds) or myrmecochorous (ant-buried). It has been hypothesized that these traits evolved to prevent access to the seeds by rodents. Here we present the first field evidence of a third guild, scatter-hoarding of nuts in the genus *Leucadendron* (Proteaceae) from the south-west Cape. The rodent concerned is *Acomys subspinosus*, a small (< 20 g) south-west Cape endemic murid. Seeds are typically buried singly, less than 2 cm deep and at distances of up to 5 m from seed depots. This finding has implications for the understanding of the evolution of myrmecochory and serotiny in shrublands. It extends the evolution of cached-nuts to a new family and is one of the first records of scatter-hoarding, outside of forests, in the southern hemisphere.

Keywords: Cape Mediterranean shrublands, myrmecochory, rodents, scatter-hoarding, seed dispersal, serotiny.

INTRODUCTION

Seeds stored in closed-cones (serotiny) or seeds buried by ants (myrmecochory) are two traits found in thousands of large-seeded species in Mediterranean fire-prone shrublands, such as Cape 'fynbos' and Australian 'kwongan' (Le Maitre and Midgley, 1992; Cowling *et al.*, 1997). They are considered to have evolved to minimize seed predation by rodents in nutrient-poor landscapes (Bond and Breytenbach, 1985; Slingsby and Bond, 1985; Le Maitre and Midgley, 1992). This hypothesis ignores the existence of a small, but widespread, group of large nut-seeded species that are neither myrmecochorous nor serotinous (Le Maitre and Midgley, 1992). In this instance, seeds are merely released *en masse* onto the soil. Since these species appear to be both desirable (large size) and unprotected against easy access by rodents, there has been some debate as to whether these species are possibly rodent-dispersed (Midgley, 1989; Vlok, 1995), but as there has been no field study, data are lacking. Our aim was to provide these field data on the dispersal of a single nut-fruited species.

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MATERIALS AND METHODS

We used the relatively large seeds of the non-serotinous species *Leucadendron sessile* (Proteaceae; mean seed mass = 0.29 g, $n = 50$). Since seeds of this species have no elaiosomes and are very large, they are probably non-myrmecochorous. To determine whether released seeds of these types of species are removed by animals (as opposed to being ignored and thus passively dispersed or, alternatively, being predated *in situ*), we placed five seeds at 25 depots spaced 10 m apart at each of two sites in mature Cape fynbos. All depots were within the *L. sessile* distribution range on the Sir Lowrys Pass area about 50 km from Cape Town (34°09′S 18°55′E).

Next, to determine the likely disperser, we eliminated granivorous birds and ants (both are diurnal) as candidates by placing further groups of five seeds under large flat boards in the late afternoon (18.30 h). Ten boards, each 45 × 45 cm, were placed 5 cm above ground level. Seed removal from underneath the boards was checked early the following morning (07.30 h) before ant activity commenced. To determine the fate of dispersed seeds, we tagged seeds by glueing 20 cm lengths of brightly coloured dacron fishing line onto the seeds using fast-setting glue. Tagged seeds were placed in groups of five, with groups being separated by 10 m and sites by at least 100 m. There were 18, 14 and 20 groups respectively at the three sites.

To determine the likely rodent dispersers, we live-trapped at two sites using *L. sessile* seeds as bait. Twenty ‘Sherman’ type traps were used at each site. Traps were set in the late afternoon and emptied early the following morning.

A further perspective on burial depth was obtained by excavating all 3-month-old *L. sessile* seedlings from a nearby (1.5 km) stand (in a 60 × 60 m plot) burned the previous year. Seeds predominantly germinate after fire and seed burial depth can be determined from length of hypocotyl (Brits, 1987). Before the burn, we had estimated seed loads and after the burn we determined seedling : parent ratios by walking 2 m wide transects. These data will provide a rough indication of seed escape rate (seed load per female/seedlings per female) and also of relative recruitment rates.

RESULTS

Initial seed removal at both sites was high (91.4%) and only 0.5% of husks were left within a 0.5 m radius around depots that we inspected. Seed removal from underneath boards was again high, with 90% seeds removed. Removal rates of tagged seeds were similarly high (64/90, 65/70 and 95/100 seeds removed) and less than 2% of seeds remained as husks at depots. Our mean retrieval rate of tagged seeds was only 41.5%, partly because the vegetation was dense but also probably because of either long-distance dispersal or dispersal into deep burrows. Dispersal distances >2 m occurred in 73.2% of relocated seeds; nearly all relocated seeds (98%) were buried <2 cm deep and 64% of tagged seeds were buried singly (i.e. scatter-hoarded). The Cape spiny mouse, *Acomys subspinosus*, was the dominant capture (8 *Acomys* and 1 *Rhabdomys pumilio*).

At the burned sites, mean seed burial depths (2.1 cm, $n = 122$) determined from seedlings coincided with that of the above tagged seeds. Less than 2% of seedlings emerged from >4 cm depth, confirming that very few seeds are larder-hoarded in burrows. The product of mean numbers of cones per female (15.9, $s = 18.2$, $n = 50$) and mean number of seeds per cone (8.4, $n = 75$) yielded a mean individual seed-load of 134.7 seeds. Post-fire mean seedling : female adult (244 : 50) ratio was 4.9 : 1, suggesting an escape rate of 3.6% (134.7/4.9).

DISCUSSION

Acomys subspinosus was the only nocturnal rodent present and captives are known to be able to bury and retrieve seeds in laboratory conditions (Bond and Breytenbach, 1985; Vlok, 1995; personal observations). It is thus the likely scatter-hoarder. *Acomys* is a widespread, but poorly known, small (20 g), fynbos, endemic, granivorous murid (Skinner and Smithers, 1990). It is the dominant species in arid areas (Botha, 1989), where nut-fruited *Leucadendron* species such as *L. pubescens* predominate, as well as where nut-fruited rare conifer species (*Widdringtonia cedarbergensis*) occur (Botha, 1989). The extent to which the distribution of *Acomys* limits the distribution of nut-fruited species requires further research.

Nut-fruits without any obvious dispersal attributes occur in other families, such as *Ceratocaryum argenteum* in the Restionaceae (H.P. Linder, personal communication). It is thus likely that scatter-hoarding is fairly widespread. We also observed field burial of tagged winged serotinous seeds (*L. laureolum*), myrmecochorous seeds (*L. conocarpodendron*) and even of sunflower nuts.

Seed predation by rodents is considered to be the crucial determinant of post-fire seed-to-seedling ratios in Cape Proteaceae (Bond, 1984; Bond and Breytenbach, 1985). However, some field experiments that apparently demonstrated this may be flawed because removal of seeds by rodents and subsequent dispersal was previously unexpected. For example, Christian (2001) assumed that removal of seeds of a myrmecochorous species placed at depots was only due to ants and that the presence of chewed seed husks left at a depot reflected the extent of rodent predation. Both these assumptions are potentially erroneous. Also, since seed dispersal distances by *Acomys* can be several metres, recruitment data from depots (e.g. Botha, 1989; van Hensbergen *et al.*, 1992, Christian, 2001) may be underestimates. Clearly, the ‘avoiding-rodent-access’ paradigm must be re-evaluated as the main reason for the evolution of serotiny and myrmecochory. Our results suggest that rodent-burial is similar in depth to that of ant-burial (Brits, 1987) and post-fire regeneration rates are comparable to those of serotinous species (Bond, 1984). Further differences in dispersal distances and dispersal microsites, as well as of the distribution patterns of the different dispersers, is required to explain the evolution of different dispersal guilds.

Here we have provided the first field evidence that some Cape species are rodent-dispersed. This is among the first records of scatter-hoarding in murid rodents (as opposed to heteromiids) in the southern hemisphere outside of tropical forests (vander Wall, 1990; Forget and vander Wall, 2001). It also extends the evolution of scatter-hoarded nut-seeds to the Proteaceae, a typical southern plant family unrelated to typical nut-fruited families such as the Fagaceae (vander Wall, 2001).

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