The influence of ants on the dispersal distance and seedling recruitment of *Leucospermum conocarpodendron* (L.) Buek (Proteaceae)

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Leucospermum conocarpodendron (L.) Buek has seeds (achenes) which are dispersed by ants. Removal of the elaiosomes (ant attractant food bodies) had no effect on the germination in nursery experiments. In replicated field experiments, however, removal of the elaiosomes resulted in complete failure of seedling emergence after fire. Sixty-one seedlings emerged from sample piles of intact seed compared with only one where elaiosomes were removed. Seedlings tended to emerge in groups (median of three seedlings per group) and mostly near the sample sites. Dispersal distances were short. The median seedling distance from sample marker pegs was 1,7 m, the mean was 2,52 m and the maximum 9,84 m. The two dominant elaiosome gathering ants, *Pheidole capensis* (Mayr) and *Anoplolepis steingroeveri* (Forel), were equally effective dispersers but seedlings associated with *A. steingroeveri* nests were more clustered. The ecological implications of obligatory dependence of *Leucospermum conocarpodendron* on seed burial by ants are discussed together with the biogeographic implications of the absence of long-distance dispersal mechanisms in myrmecochorous Proteaceae.

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Leucospermum conocarpodendron (L.) Buek het sade (dopvrugte) wat deur miere versprei word. Die verwydering van die elaiosomes (mierlokkende voedsel-liggaam) het geen invloed op die ontkieming in kwekery-eksperimente nie. In veldeksperimente met replikate het die verwydering van elaiosomes, saailingopslag geheel en al onderdruk na brand. Een-en-sestig saailinge het opgeslaan uit 'n monster volledige sade terwyl net een opgeslaan het na die elaiosomes verwyder is. Saailinge het verskyn in groepe (mediaan drie per groep) meestal naby monsterareas. Verspreidingsafstand was kort. Die mediaan-saailingafstand vanaf monstermerkpenne was 1,7 m en die gemiddelde 2,52 m en die maksimum 9,84 m. Die twee dominante elaiosome-versamelende miere, *Pheidole capensis* (Mayr) en *Anoplolepis steingroeveri* (Forel) was ewe effektiewe verspreiders maar saailinge geassosieerd met *A. steingroeveri*-neste was meer in groepe bymekaar. Die ekologiese implikasies van verpligte afhanklikheid van *Leucospermum conocarpodendron* op die begrawe van saad deur miere word bespreek saam met die implikasies van die afwesigheid van langafstand verspreidingsmeganismes in mierverspreide Proteaceae.

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Introduction

Though dispersal interactions between plants and animals are common, there is little direct evidence for the benefits plants gain from dispersal by animals. The ability to disperse long distances is not necessarily advantageous — most of the seed may fall in an unsuitable habitat. Poor dispersers, in contrast, have the safer option of merely replacing their parents *in situ*. Some local dispersal may be advantageous in that seed can escape predators, pathogens and competitors (Janzen 1970; Howe & Smallwood 1982) or simply locate openings created by the death of parents (Hamilton & May 1977).

Myrmecochory is a mutualistic interaction between plants whose seeds have elaiosomes (food bodies) attached and ants which are attracted by the elaiosomes. Ants transport the seed, usually to nests where the elaiosome is eaten but the seed is left buried and intact (Sernander 1906; Van der Pijl 1982; Berg 1975). Unlike birds or mammals, ants do not carry seed for long distances but, by carrying the seed to their nests, they can improve the chances of successful establishment considerably (Culver & Beattie 1978; O'Dowd & Hay 1980; Heithaus 1981; Handel 1978; Davidson & Morton 1981).

More than half the species of Cape Proteaceae are myrmecochorous, including two-thirds of the taxa regarded as threatened because of narrow endemism, small population size or habitat destruction (Slingsby & Bond 1983; Hall *et al.* 1980). In this article we discuss the importance of myrmecochory in the life cycle of members of the Proteaceae and in their biogeography. We address the questions:
(i) Does myrmecochory significantly enhance seedling recruitment and, if so, (ii) is the effect merely due to improved germination if elaiosomes are removed?
(iii) What pattern of seedling distribution is produced by ant dispersal and does this change with different ant partners?
(iv) Does ant dispersal limit the mobility of plant populations and, therefore, the distribution patterns of myrmecochorous species?

Methods

Leucospermum conocarpodendron (L.) Buek has achenes with elaiosomes covering the fruit which is typical of several genera of the Proteaceae, e.g. *Leucospermum, Diastella, Mimetes, Orothamnus, Paranomus* (Slingsby & Bond 1983). It differs from many congenerics by being a small tree or tall shrub and surviving fire by sprouting from roots or, in older plants, from the crown (Rourke 1972). The fruits (hereafter referred to as seeds) are the largest in the genus (*ca.* 10 mm) but are discovered and transported to nests as speedily as all taxa with similar fruits (Slingsby & Bond 1981; Slingsby &

Bond 1983).

L. conocarpodendron seed set is relatively high. 1 200 fresh fruits were collected in January 1982 from populations in the vicinity of Kleinmond, Caledon district. Elaiosomes of 600 of these were removed by hand and then exposed to the Argentine ant, *Iridomyrmex humilis* Mayr, until all traces of elaiosomes had been eaten and field tests with indigenous ants yielded neutral responses.

The influence of elaiosomes on seed germination were tested by planting 100 fresh seeds with intact elaiosomes in seed trays in an open nursery on 5 January 1982. A second group of 100 with elaiosomes removed was planted in adjacent trays six days later. Seeds were planted in white sand at a depth of 30 mm. Seeds were not pre-treated before planting. Trays were regularly watered with tap water.

The influence of ants on seedling recruitment was assessed by field experiments established in mixed ericoid-restioid fynbos (Map unit J of Boucher 1978) on gently sloping foothills above the Palmiet River (34° 19′S, 18° 58′E). Although natural populations of *L. oleifolium* (Berg.) R.Br. occurred in the area, no *L. conocarpodendron* was present within 300 m of the test site. Seedlings of the two species are easily distinguishable at the cotyledon stage. Soils were stony, moderately deep, pale sands over quartzite.

Twenty experimental sites were located in the area and marked with steel pegs. Ten were randomly located on west-facing and ten on east-facing aspects. The minimum distance between pegs was 30 m. Fifty fresh seeds, with elaiosomes intact, were placed at each of five of the east-slope and five of the west-slope marker pegs. Six days later, 50 seeds with elaiosomes removed were placed at each of the remaining pegs. Treatments were randomly allocated within each aspect category. Seeds were placed in a pile around each marker peg.

The area was burned in a prescribed fire on 5 May 1982. All seedlings emerging after the fire were counted and distance and direction from the nearest marker peg were recorded. Observations of seedling emergence in both field and nursery trials were terminated on 30 July 1982.

Results

Seedling emergence in nursery trials was first observed on 13 April, about 14 weeks after planting, and had ceased by 30 May. There was no significant difference in percentage germination between seeds with elaiosomes (24%) and seeds without (22%) (Fishers Exact Test, $p>0,4$). The relatively poor germination percentages are typical of myrmecochorous Proteaceae seed which has not been pre-treated (Van Staden & Brown 1977; Brits & Van Niekerk 1976; Horn 1962).

The results suggest that elaiosomes have no direct effect on seed germination. Similar studies on other ant-dispersed species report either no change in germination after seed handling by ants (e.g. Culver & Beattie 1978) or increased germination (Horvitz 1981). In some cases, germination was enhanced if seeds were buried by ants but the effect could not be duplicated by experimental removal of elaiosomes or seed scarification to mimic ant behaviour (Culver & Beattie 1980).

The influence of ant dispersal on seedling recruitment

Seedling emergence in field experiments was first observed on 1 July, eight weeks after the fire, and had ceased by 16 July. Seedling numbers differed greatly between the two treatments (Table 1). Only one seedling emerged from sample sites with seeds with the elaiosomes removed (from a hole made by the marker peg), compared with 61 from sites with intact seed (t test for depots, $t=7,36$, $p<0,001$). Seedling numbers did not differ significantly between west and east aspects ($t=0,85$, $p>0,4$).

Table 1 Seedling emergence from sample sites with elaiosomes intact or removed. Fifty seeds were placed at each site, with five replicates of each treatment on west aspects and five on east aspects

	Elaiosomes present		Elaiosomes removed	
	mean	SD	mean	SD
West aspects	5,4	1,67	0,0	0,00
East aspects	6,8	3,27	0,2	0,45
Combined	6,1	2,56	0,1	0,32
Total seedlings	61		1	
% Emergence	12,2		0,02	

The results clearly demonstrate the functional significance of elaiosomes and imply a critical role for myrmecochory in maintaining *Leucospermum conocarpodendron* populations.

The percentage seedling emergence from treatments with intact seed was half that of nursery trials. This relatively small difference suggests that myrmecochory efficiently places seeds in suitable microsites for germination and protects them from seed predators. Unfortunately, no similar studies for alternative dispersal types are available for comparison, nor were we able to compare post-emergence seedling mortality with different systems (such as serotinous species of *Protea*). Many of the *L. conocarpodendron* seedlings were eaten, probably by rodents, within a few weeks of emergence.

The spatial pattern of seedlings

Seedlings were spaced either individually (>100 mm between neighbours) or were clustered in tight groups (<20 mm between neighbours). Of the seedlings which emerged from intact seed depots, 12 stood alone and the remainder were in 15 separate groups of two to six seedlings each with a median of three per group (Figure 1). The grouping of seedlings is, presumably, a direct result of the dispersal of seed into the galleries of only a few ant nests.

The relationship of seed density to distance transported was strongly skewed and leptokurtic (Figure 2). The median distance was 1,78 m, the mean was 2,52 m with a maximum of 9,84 m and a minimum of 0,31 m. No overlap between sample sites was apparent and distances conform closely to field observations on ant dispersal (Bond & Slingsby 1983; Slingsby & Bond 1981 and unpublished observations). Since sites were established randomly with respect to ant nests, the low dispersal distances imply high densities of ant colonies. Ant nests may not be randomly located with respect to *L. conocarpodendron* individuals so that natural seed patterns may differ slightly from these results.

Populations of *L. conocarpodendron* would be expected to migrate slowly downhill if dispersal was by gravity alone. Thirty-six seedlings were located uphill and 25 seedlings downhill from the marker pegs. The median seedling distance from the pegs was 1,78 m uphill and 1,85 m downhill ($p>0,1$), Mann-Whitney two sample test). These observations suggest that ants carry seed in all directions irrespective of slope.

The influence of different ant species

The major elaiosome gathering ants in the Kleinmond area are *Anoplolepis steingroeveri* Forel, *A. custodiens* Smith and *Pheidole capensis* Mayr (personal observations). *A. custodiens*

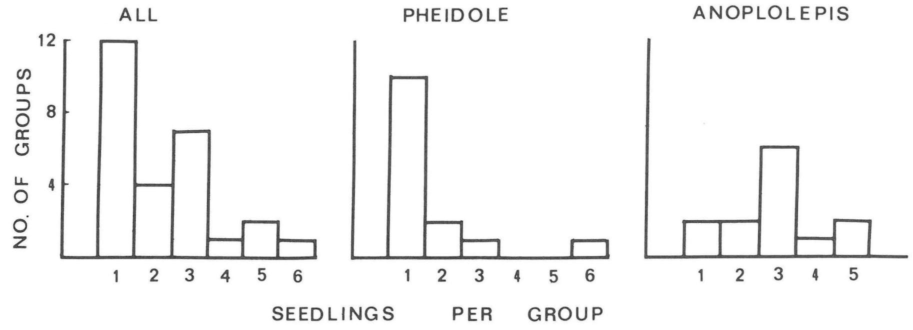

Figure 1 Grouping of *Leucospermum conocarpodendron* seedlings after dispersal by ants. Seedlings were always associated with ant nests of either *Pheidole capensis* or *Anoplolepis steingroeveri.* The overall frequency distribution of group size is shown together with distributions associated with each ant species. 'Groups' of one are seedlings with no immediate neighbours.

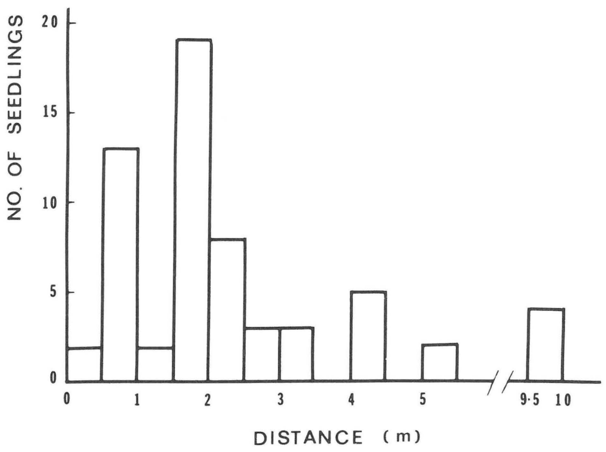

Figure 2 Dispersal distance of *L. conocarpodendron* seedlings. The distance (in m) of each seedling from seed pile marker pegs was measured. Dispersal statistics are $\bar{x}$ 2,52 m; SD 2,27; g1 (skewness) 2,12; g2 (kurtosis) 4,22; max. 9,84 m; min. 0,31 m.

and *A. steingroeveri* appear to have different substrate preferences. The former was absent from our study sites. In most of our field observations, *Anoplolepis* spp. displace *Pheidole* spp. from myrmecochorous seeds and transport and bury them far faster.

All seedlings were associated with nests of *Anoplolepis steingroeveri* or *Pheidole capensis.* Twenty-three seedlings (distributed as four groups and 10 alone) were associated with *Pheidole* nests and 38 seedlings (11 groups and two alone) with those of *A. steingroeveri.* Although *P. capensis* is a smaller ant, the mean distance of seedlings from the marker pegs was greater (but not significantly so) with *P. capensis*-associated seedlings than with *A. steingroeveri*-associated seedlings (*Pheidole capensis,* mean=2,54 m, $s=3{,}26$; *Anoplolepis steingroeveri,* mean=1,19 m, $s=1{,}02$, $p<0{,}1$, $p>0{,}05$, *t* test).

Seedling spacing patterns differed significantly depending on the associated ant species. Seedlings associated with *P. capensis* nests were not aggregated having a median 'group' size of one compared with three for *A. custodiens* nests (Mann-Whitney two sample test, $p<0{,}01$). This suggests that *P. capensis* colonies or nest entrances are more densely distributed or that *A. steingroeveri* aggressively displaces *P. capensis* before the latter can remove all the seed.

Since the *Leucospermum conocarpodendron* seed successfully germinated from the nests of both species, it is buffered against changes in the composition of ant communities. Seedlings emerging from *Anoplolepis* nests may, however, suffer more intense intraspecific competition.

Discussion

Our results suggest that *Leucospermum conocarpodendron* has an obligatory dependence on its ant dispersers. Seedling regeneration failed completely when elaiosomes were removed but increased sixty-fold with intact seed. We have observed a similar dependence on ants by *Mimetes cucullatus* (L.) R.Br. (Bond & Slingsby 1984) and it seems probable that most Proteaceae with similar fruits rely equally heavily on mutualistic ant dispersers.

The specific benefits of myrmecochory have been disputed. Westoby & Rice (1981) have argued that although distances transported are small, they may nevertheless be significant, particularly if the chances of successful establishment vary as a function of distance from parents (Janzen 1970). Most studies, however, have emphasized the consequences of seed placement in ant nests. Seed burial favours seed escape from vertebrate predators (Heithaus 1981; O'Dowd & Hay 1980; Culver & Beattie 1978; Berg 1981). Alternately, seedling growth may benefit from nutrient-enriched, ant nest soils (Davidson & Morton 1981; Westoby *et al.* 1982; Culver & Beattie 1983) or from reduced competition with other species (Handel 1978).

Treatment differences in this study were already apparent at seedling emergence — before seedlings were independent of nutrient reserves stored in cotyledons. The major benefit of myrmecochory for this and similar members of the Proteaceae (e.g. *Mimetes cucullatus*) (Bond & Slingsby 1984) must, therefore, be increased seed survival until germination rather than subsequent seedling growth after germination. We have observed very high seed predation rates with similar species of Proteaceae if ants are prevented from removing seed (Bond & Slingsby 1984; Bond & Breytenbach, unpublished). Escape from seed predators has, therefore, probably been significant in the evolution of fynbos myrmecochory.

Leucospermum conocarpodendron is well buffered against species changes in the ant community since *Anoplolepis steingroeveri* and *Pheidole capensis* were equally effective dispersers. Both these species and *A. custodiens* are ubiquitous in mesic to arid phases of fynbos. The dispersal mutualism would, therefore, be relatively reliable unless the balance between ant and rodent activity shifts strongly to the latter. An example of just such a shift occurs in small areas of fynbos invaded by *Iridomyrmex humilis,* the Argentine ant. This invader replaces the native ant fauna and completely disrupts the dispersal and seedling recruitment of *Mimetes cucullatus* (Bond & Slingsby 1984). Similar recruitment failure would be expected with *L. conocarpodendron* from the results reported here. Other myrmecochorous Proteaceae are probably also at risk, especially in coastal fynbos where the patchwork of man-altered landscapes provides foci from which *Iridomyrmex* can invade (Skaife 1961; Prins 1978).

Long distance dispersal and distribution patterns

Some typical characteristics of the Cape flora, narrow endemism, vicariant species, high species turnover between regions (e.g. Kruger & Taylor 1979; Rourke 1972; Taylor 1980; Goldblatt 1978) imply poor dispersal ability. Fruit structures associated with long distance dispersal are rare in fynbos compared with adjacent strandveld and semi-arid shrublands. For example, fleshy fruits dispersed by birds are extremely rare in fynbos and Asteraceae typically have no, or highly reduced, pappi (Dyer 1975; Milewski & Bond 1982; Bond & Slingsby 1983; Siegfried 1983).

Leucospermum conocarpodendron fruits are large and heavy and, except for elaiosomes, lack any obvious structures to aid dispersal. Other species of Proteaceae dispersed by ants have smaller fruits but share the same nut-like structure (Rourke 1972; Slingsby & Bond 1983). Opportunities for chance long distance dispersal of ant-dispersed seed are very limited. There are no seed-cacheing rodents in fynbos and we have not observed birds feeding on myrmecochorous fruits. With the probable exception of the Proteaceae species, many ant-dispersed plants (e.g. *Agathosma* spp.) appear to synchronize seed release with seed maturity so that premature removal and non-destructive transport of seed by birds or rodents would usually lead to germination failure (Blommaert 1972; Slingsby & Bond 1981). Myrmecochorous seed is ill adapted to wind dispersal. Seed surfaces are typically smooth and rounded, minimizing surface area (e.g. Berg 1975; Bond & Slingsby 1983). Furthermore seed burial in nests anchors seeds against subsequent movement by wind or water.

Seedling distribution patterns observed in this study suggest that myrmecochory favours local recruitment at the expense of population mobility. Populations would tend to spread as a distinct front, contrasting with wind (e.g. *Pinus pinaster* Ait.) or bird dispersal (e.g. *Acacia cyclops* A. Cunn. ex G. Don) where single individuals can advance in leaps ahead of the main population (*cf.* Harper 1977). Where ant colonies are common and workers forage for limited distances, plant population advance will be confined to corridors of suitable habitat with no means of crossing intervening barriers of hostile terrain. The converse, population fragmentation, would also occur easily unless gene flow is maintained by pollination.

Short distance dispersal might enhance speciation rates because of the ease with which populations can become geographically isolated. In contrast, extinction rates would tend to be reduced because of the slow spread of potentially superior competitors. It is perhaps no coincidence that both Cape and southwestern Australian fynbos equivalents share an unusually high incidence of myrmecochory (Berg 1975), an unusually low incidence of adaptations for long distance dispersal (Carlquist 1974; Bond & Slingsby 1983; Milewski & Bond 1982) and the richest temperate floras in the world (Goldblatt 1978; Hopper 1979).

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