

Dispersal of elaiosome-bearing seeds of six plant species by native species of ants and the introduced invasive ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae) in the Western Cape Province, South Africa

A B R Witt* & J H Giliomee

Department of Entomology and Nematology, Faculty of Agricultural and Forestry Sciences, University of Stellenbosch, Private Bag X1, Matieland, 7602 South Africa

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According to the literature, areas dominated by small ant species, such as the introduced invasive *Linepithema humile*, are characterised by low dispersal rates for plant species with large seeds. The selection and subsequent dispersal of elaiosome-bearing seeds collected from six species of plants, varying in size, shape and mass, by *L. humile* and five native ant species of different size, was investigated in the Western Cape Province, South Africa. Larger seeds were generally taken last by all ant species monitored, except *Polygala myrtifolia* seeds which, despite being larger than those of *Agathosma ovata*, were selected first more often and dispersed more readily by all ant species. *L. humile* failed to disperse any of the larger elaiosome-bearing seeds such as those of *Podalyria calyptata*, *Paranomus reflexus* and *Leucospermum cordifolium*, unlike *Pheidole capensis*, which has similarly-sized workers and a large soldier caste. Nest entrance measurements revealed that large seeds such as those of *P. reflexus* and *L. cordifolium* were too large to be accommodated in the nests of small ant species as well as most of the large ant species. In these cases, seeds were discarded on the soil surface where some of the benefits of myrmecochory, including protection of seeds from desiccation and rodent predation, would not be realised. The study showed that myrmecochorous plants with small seeds will probably not be affected to the same extent as those with large seeds by the displacement of large species of ants by *L. humile*. The inability of native ant species to accommodate large myrmecochorous seeds in nests also brings into question some of the apparent benefits of this ant-plant interaction.

Key words: ants, *Linepithema humile*, myrmecochory, seed dispersal, seed selection

Almost 20 % of the plant species found in the Cape Floristic Region of South Africa (Goldblatt 1978) produce elaiosome-bearing or myrmecochorous seeds, which are attractive to ants (Bond & Slingsby 1983). After dehiscence, these seeds are located by the ants and transported to their nests where the elaiosome, which generally contains lipids, protein, starch, sugars and vitamins (Bennett & Krebs 1987), is chewed off and the seed discarded in the nest or on the soil surface (Horvitz 1981). Ants therefore benefit from this interaction by gaining the nutrients in elaiosomes. Myrmecochorous plants also benefit from their interaction with ants. Seeds within ants' nests are protected from fire and high temperatures (Andersen 1982). Increased germination rates through elaiosome removal, distance dispersal, escape from competitors, and avoidance of seed predators are other possible benefits of myrmecochory (Auld 1986; Ohkawara & Higashi 1994).

Relationships between ants and the plants whose seeds they disperse are believed to be determined by the size and shape of the seed and its elaiosome, as well as the chemical content of the elaiosome itself (Marshall et al. 1979; Davidson & Morton 1981; Davison 1982; Hughes & Westoby 1990). Large ants, in particular, can disperse a wide range of seeds, varying in shape and size, while smaller ants apparently are limited to the dispersal of small seeds (Hughes & Westoby 1990).

The accidental introduction of the Argentine ant, *Linepithema humile* (Mayr) (formerly *Iridomyrmex humilis* Mayr), to South Africa has created an ideal opportunity to determine if a small ant species like *L. humile*, which is not known to disperse seeds in its native range, will disperse small and large seeds equally well. In South Africa, *L. humile* displaces myrmecochorous ant species such as *Anoplolepis custodiens* (Smith) and *Pheidole capensis* Mayr (Bond & Slingsby 1984; De Kock & Giliomee 1989). This study examined the ability of five native ant species and *L. humile* to disperse

*Corresponding author. Present address: ARC-Plant Protection Research Institute, Private Bag X134, Queenswood, 0121 South Africa. E-mail: witta@arc.agric.za

and 'bury' elaiosome-bearing seeds varying in size, shape and mass.

Materials and methods

Study area

The study was undertaken in the Jonkershoek Valley (33.57S, 18.55E), 15 km southeast of Stellenbosch, Western Cape Province, South Africa. The valley has hot, dry summers and a mean annual rainfall of approximately 1600 mm (Wicht et al. 1969). Observations were made in fynbos plant communities where the vegetation is of a graminoid nature. Some areas within the valley have been invaded by *L. humile* while adjoining fynbos areas were uninvaded.

Ant species and nest entrance measurements

Preliminary studies indicated that *A. custodiens*, *P. capensis*, *Tetramorium quadrispinosum* Emery, *Anoplolepis steingroeveri* (Forel) and *Ocymyrmex cilliei* Prins & Roux were the ant species most frequently dispersing seeds. The size of foraging ants of these species and *L. humile* was determined by measuring them from the anterior end of the clypeus to the tip of the abdomen using an ocular micrometer.

Nest entrances of all five native species of ants and *L. humile* were located by placing tuna fish baits at 5 m intervals along transects in areas uninvaded and invaded by *L. humile*. Nest entrances of all six species of ants were marked after following workers from the bait to their nests.

All nest entrances were measured using a vernier calliper. The diameter of the entrance was measured at its widest point and a second measurement was taken perpendicular to the plane of the first measurement. These two measurements were used to calculate the area of each nest entrance using the formula for calculating the area of an ellipse: $\pi \times a \times b$, where a = half of the major axis and b = half of the minor axis (Spiegel 1968).

Seed measurements

Mature seeds of six plant species, *Agathosma ovata* (Thunb.) Pillans (Rutaceae), *Polygala myrtifolia* L. (Polygalaceae), *Phylica pubescens* Aiton (Rhamnaceae), *Podalyria calyptata* Willd. (Fabaceae), *Paranomus reflexus* (E Phillips & Hutch.) N E Br. (Proteaceae) and *Leucospermum cordifolium* (Salisb. ex J Knight) Fourc. (Proteaceae), were collected one to three months prior to

commencement of the study and stored in vials at 4°C until required. These species were selected because they were relatively common in the field, matured at approximately the same time and produce seed that exhibit a range of shapes and sizes. The dimensions and mass of a random sample of seeds taken from each plant species were measured using an ocular micrometer and electronic balance. To obtain a single area value for each species of seed, the width and breadth measurements were used, based on the assumption that they were all ellipsoid in shape, with the same formula as that used for the nest entrance measurements.

Selection and dispersal of seeds

To determine the speed at which the various ant species dispersed seeds and to ascertain if a particular ant species preferentially selects certain species of seeds above others, 10 nests of each of *L. humile*, *P. capensis*, *T. quadrispinosum*, *O. cilliei*, *A. steingroeveri* and *A. custodiens* were located in the valley. Only those nests where the area in the vicinity of each entrance was flat and of a soil texture similar to other nests, were selected. One seed of each of the above six plant species were placed in a group 30 cm from each main nest entrance. The first species of seed to be moved at least 1 cm and the time taken to move a single seed over a distance of 15 cm were recorded. Each group of seeds was monitored for two hours after the first seed had been moved, with each nest being observed only twice during the entire experiment and never on the same day to exclude possible colony satiation. All selection experiments took place when the particular ant species was most active because the movement of ants is largely regulated by soil-surface temperature (Witt & Giliomee 1999). At least one nest of each of the six species of ants was tested for possible seed preferences on the same day. Observations of seed dispersal were undertaken in March 1992.

A selectivity index (Si) to show if the various ant species preferentially selected certain seed species above others was calculated from the observed order of removal of single seeds of each of the six plant species according to the equation:

$$Si = \frac{\sum_{i=1}^6 n_i(7-i)}{120}$$

where n_i is the number of seeds of each plant species moved i th.

Table 1. Measurements of nest entrances of *Linepithema humile* and five native ant species.

Ant species	<i>n</i>	Measurements ^a		
		Widest diameter (mm)	Plane perpendicular to widest diameter (mm)	Area (mm ²) ^b
<i>L. humile</i>	47	2.92 ± 0.21 (1–7)	1.87 ± 0.13 (1–6)	4.72 ± 0.66 (0.79–28.26)
<i>Pheidole capensis</i>	87	4.24 ± 0.31 (1–16)	2.40 ± 0.14 (1–5)	9.28 ± 1.32 (0.79–94.98)
<i>Tetramorium quadrispinosum</i>	25	4.52 ± 0.37 (2–9.5)	2.64 ± 0.19 (1–5)	9.47 ± 1.07 (2.36–22.37)
<i>Anoplolepis custodiens</i>	123	4.78 ± 0.17 (2–13)	3.56 ± 0.10 (2–8)	14.34 ± 0.89 (3.14–65.94)
<i>A. steingroeveri</i>	86	5.21 ± 0.25 (1.5–16)	4.24 ± 0.16 (1.5–9)	19.19 ± 1.54 (1.77–75.36)
<i>Ocymyrmex cilliei</i>	21	5.95 ± 0.30 (4–8)	4.86 ± 0.19 (3.5–6)	23.44 ± 1.73 (12.56–37.68)

^aMean ± SE (range). ^bCalculated according to Spiegel (1968).

Results

Ant species and nest entrance measurements

The nest entrances of *Anoplolepis* spp. were often associated with grasses and dried leaves at the base of *Berkheya* spp. (Asteraceae). Horizontal galleries just below the soil surface frequently emerged through the surface, resulting in multiple nest entrances. The entrances of *P. capensis* nests were generally multiple and distributed around the base of grass clumps, contrary to *O. cilliei* and *T. quadrispinosum* nests which usually only had a single functional entrance. *O. cilliei* nest entrances were found in unvegetated areas exposed to direct sunlight, whereas those of *T. quadrispinosum* were common at the base of rocks, grass clumps, and only occasionally in the open. *L. humile* exhibited a wide range of nest sites with multiple entrances in the open, under dead and decaying leaves and branches, under rocks and at the base of shrubs and grasses.

P. capensis and *L. humile* workers were 2.35 ± 0.03 mm (mean ± SE) (*n* = 20) and 2.58 ± 0.03 mm (*n* = 30) long, respectively. However, soldiers of *P. capensis*, the only ant species observed of which soldiers assisted in seed removal, were 4.64 ± 0.09 mm (*n* = 10) long, which is somewhat longer than the workers of *T. quadrispinosum* (3.26 ± 0.02 mm) (*n* = 10) and almost as long as those of *A. custodiens* (4.76 ± 0.11 mm) (*n* = 60) and *A. steingroeveri* (4.89 ± 0.15 mm) (*n* = 60). *O. cilliei* was the longest of the six ant species, measuring 6.48 ± 0.06 mm (*n* = 12) and also had the largest nest entrances (Table 1) while the nest entrances of *L. humile* were by far the smallest.

Seed measurements

Seed of the six plant species included in this study differed in shape, size and texture of both the elaiosome and the seed itself. Unlike seeds of *A. ovata*, *P. myrtifolia*, *P. pubescens* and *P. calypttrata*, where the elaiosome was a distinct appendage, the outer fleshy layer of *L. cordifolium* and *P. reflexus* acted as elaiosomes. The testa of *P. myrtifolia* and *A. ovata* seeds were thin and fragile, whereas those of *P. pubescens*, *P. calypttrata*, *P. reflexus* and *L. cordifolium* were thick and hard. *A. ovata* seeds were the smallest and lightest, and those of *L. cordifolium* the heaviest (Table 2).

Selection and dispersal of seeds

All ant species, with the exception of *A. custodiens*, readily removed seeds. *A. custodiens* was therefore excluded from the analyses. The first forager of the other five ant species locating the group of test seeds would remove a seed, generally the smallest one in the group, and return to the nest, whereupon large numbers of workers converged on the seeds. Large seeds were usually removed by a number of cooperating workers, especially those with small body sizes. *P. capensis* workers often recruited soldiers to assist in seed removal, whereas single *O. cilliei* workers were capable of moving the large and heavy *L. cordifolium* seeds.

Although *L. humile* workers attempted to move larger seeds they failed to move any of the larger and heavier *P. calypttrata*, *P. reflexus* and *L. cordifolium* seeds over a distance of 1 cm in two hours (Table 3). *P. myrtifolia* seeds were favoured by all the ant species monitored, despite being larger

Table 2. Size and mass of seeds of six plant species included in the study.

Plant species	Measurements ^a			
	Width (mm)	Breadth (mm)	Area (mm ²) ^b	Mass (mg)
<i>Agathosma ovata</i>	1.87 ± 0.01	1.51 ± 0.02	2.21 ± 0.02 (1.78–2.57)	5.19 ± 0.39
<i>Polygala myrtifolia</i>	2.45 ± 0.04	1.98 ± 0.05	3.82 ± 0.13 (1.63–5.17)	10.74 ± 1.27
<i>Phyllica pubescens</i>	3.12 ± 0.05	2.25 ± 0.03	5.53 ± 0.14 (4.02–7.79)	17.39 ± 1.46
<i>Podalyria calyptata</i>	4.22 ± 0.05	2.54 ± 0.03	8.46 ± 0.18 (5.29–10.62)	30.90 ± 1.63
<i>Paranomus reflexus</i>	5.57 ± 0.05	5.57 ± 0.05	24.42 ± 0.41 (18.20–31.12)	60.45 ± 4.33
<i>Leucospermum cordifolium</i>	5.96 ± 0.08	4.77 ± 0.07	22.40 ± 0.52 (13.80–28.36)	80.39 ± 9.59

^aMean ± SE of 40 seeds. ^bCalculated according to Spiegel (1968).

than those of *A. ovata*. None of the four indigenous ant species was capable of moving all of the seed species 1 cm within two hours. *O. cilliei* removed the smallest number of *L. cordifolium* seeds of all the native ant species monitored.

With few exceptions, larger ant species moved seeds faster than smaller species and small seeds were generally moved faster by all ant species observed (Table 4). The elaiosomes of the four smallest seed species were used as a 'carrying handle' by all ants when transporting seeds. The larger ant species managed to lift smaller seeds off the ground whereas larger seeds were generally dragged along the ground by all ant species. It appeared if the smooth elaiosomes enveloping *L. cordifolium* and *P. reflexus* seeds were particularly difficult to grasp. All ant species, with the exception of *O. cilliei*, moved seeds directly to the closest nest entrance. *O. cilliei* often moved seeds further away from the entrance and lodged them under stones or twigs.

By comparing the area of the nest entrances of the various species of ants to that of the species of seeds it is clear that smaller seeds could easily be accommodated in the majority of nest entrances

that were measured (Fig. 1). Seeds of *P. reflexus* and *L. cordifolium*, however, would not fit into the entrances of the smaller and most of the larger ant species. Seeds which could not be taken into nests were generally abandoned outside the nest entrance where the elaiosomes were chewed off. *L. humile* removed the elaiosomes of large seeds in situ.

Discussion

According to Hansen (1978), Davidson & Morton (1981), Andersen (1982), Campbell (1982) and Majer (1982), the size of an ant plays an important role in the selection of seeds. The behaviour of *L. humile* was similar to that observed by Berg (1975) and Auld (1986), who found that small ants were unable to move large seeds and mostly removed elaiosomes in situ. However, smaller seeds of all species were generally also selected and removed first by large species of ants. This was partly due to the fact that most seed clumps were discovered first by a lone forager and that smaller seeds were easier to transport than large ones. In most cases, larger seeds were taken only once more workers were recruited from nests.

Table 3. Selectivity index of five ant species for seeds of six plant species. Ant worker size increases from left to right and seed mass from top to bottom.

Plant species	Selectivity index ^a				
	<i>Linepithema humile</i>	<i>Pheidole capensis</i>	<i>Tetramorium quadrispinosum</i>	<i>Anoplolepis steingroeveri</i>	<i>Ocymyrmex cilliei</i>
<i>Agathosma ovata</i>	0.883 (20)	0.508 (20)	0.717 (20)	0.700 (20)	0.625 (17)
<i>Polygala myrtifolia</i>	0.925 (20)	0.825 (20)	0.842 (20)	0.883 (20)	0.825 (20)
<i>Phyllica pubescens</i>	0.017 (5)	0.658 (20)	0.675 (20)	0.658 (20)	0.817 (20)
<i>Podalyria calyptata</i>		0.558 (19)	0.342 (14)	0.517 (19)	0.367 (14)
<i>Paranomus reflexus</i>		0.392 (18)	0.450 (16)	0.392 (18)	0.258 (12)
<i>Leucospermum cordifolium</i>		0.500 (19)	0.317 (16)	0.350 (19)	0.225 (10)

^aRange of 0–1, with 0 = no seeds moved 1 cm within two hours and 1 = 20 seeds moved within two hours; values in brackets indicate total number of seeds moved 1 cm within two hours.

Table 4. Speed at which *Linepithema humile* and four native ant species moved seeds of six plant species over a distance of 15 cm. Seed mass increases from left to right and ant size from top to bottom.

Ant species	Speed (seconds) ^a					
	<i>Agathosma ovata</i>	<i>Polygala myrtifolia</i>	<i>Phylica pubescens</i>	<i>Podalyria calytrata</i>	<i>Paranomus reflexus</i>	<i>Leucospermum cordifolium</i>
<i>L. humile</i>	359.6 ± 80.4	561.8 ± 95.70	37772.5 ± 723.4	— ^b	—	—
<i>Pheidole capensis</i>	260.8 ± 93.8	220.3 ± 84.8	264.0 ± 46.1	855.2 ± 260.1	533.3 ± 185.8	964.9 ± 275.8
<i>Tetramorium quadrispinosum</i>	37.6 ± 7.5	65.0 ± 10.6	113.8 ± 18.9	262.7 ± 81.5	324.5 ± 45.8	616.0 ± 77.1
<i>Anoplolepis steingroeveri</i>	55.4 ± 11.2	96.6 ± 22.7	84.4 ± 21.3	198.3 ± 45.7	275.0 ± 64.1	456.3 ± 106.3
<i>Ocymyrmex cilliei</i>	6.5 ± 1.1	7.9 ± 1.8	14.4 ± 3.4	11.1 ± 2.1	42 ± 13.4	57.6 ± 11.3

^aMean ± SE. ^bNo seeds moved.

However, larger seeds were sometimes taken first by single workers of the larger ant species, despite smaller seeds still being available in the clump.

P. myrtifolia seeds are larger and heavier than those of *A. ovata*, but were nevertheless selected first and dispersed more readily than the latter. Despite being smaller than *P. reflexus* and *L. cordifolium* seeds, *P. calytrata* seeds were not selected and dispersed as readily as may have been expected. This can probably be ascribed to the size and attractiveness of the elaiosomes

(Davison 1982; Majer 1982). The size and nutritional value of the elaiosome itself, and not necessarily the size and mass of the whole seed, may determine why seeds of one species will be removed in preference to those of another because ants, in theory, only disperse seeds that provide a net energy gain (Brown et al. 1975; Davidson 1978; Davidson & Morton 1981). Unfortunately, the small size of elaiosomes of *A. ovata* precluded calculation of their percentage mass. Visual inspection of *A. ovata* seeds nevertheless indicated

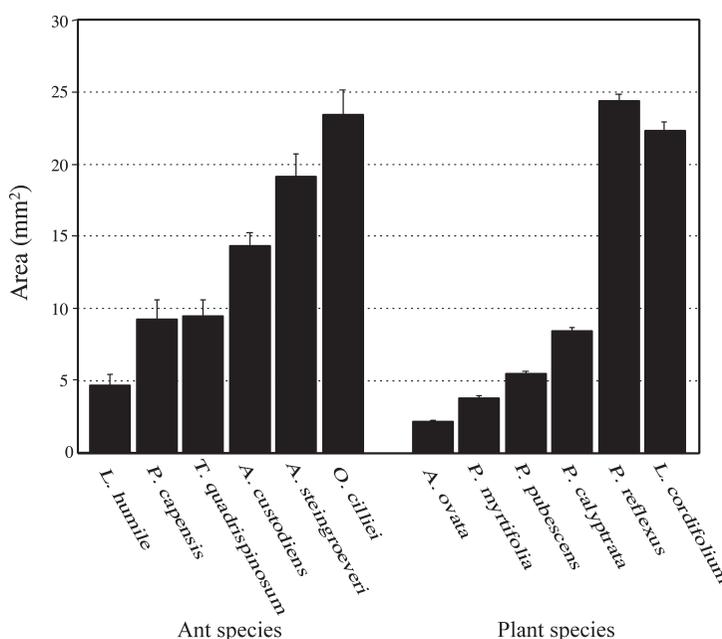


Fig. 1. Mean (±SE) area of nest entrances of *Linepithema humile* and five native ant species, *Pheidole capensis*, *Tetramorium quadrispinosum*, *Anoplolepis custodiens*, *A. steingroeveri* and *Ocymyrmex cilliei*, and of elaiosome-bearing seeds of six plant species, *Agathosma ovata*, *Polygala myrtifolia*, *Phylica pubescens*, *Podalyria calytrata*, *Paranomus reflexus* and *Leucospermum cordifolium*, calculated according to Spiegel (1968).

that their elaiosomes are comparatively much smaller than those of *P. myrtifolia*, which may partly explain why *P. myrtifolia* seeds were preferred to *A. ovata* seeds. Another possible explanation is that the secondary compounds in the elaiosomes, which attract dispersers (Davison 1982; Majer 1982; Buckley 1982; Brew et al. 1989), differed between species. Marshall et al. (1979) ascribed the selectivity of ants to species-specific attractants in the elaiosomes. However, Handel (1976), Culver & Beattie (1978), Majer (1982), Westoby et al. (1982) and Davidson & Morton (1984) found that specificity for certain seeds was very low in myrmecochory.

One of the main benefits of myrmecochory to plants is the burial of seeds in ants' nests where they are protected from fire, high temperatures (Andersen 1982) and seed predators (Auld 1986). Obviously, these benefits cannot be realised if seeds cannot be accommodated in nest entrances. Smaller seeds could readily be accommodated in the entrances of most species of ants monitored, including those of *L. humile*. Despite the displacement of native ant species, including the large *Anoplolepis* spp., by *L. humile*, myrmecochorous plant species with small seeds in invaded areas should still receive the full benefits of this ant-plant interaction. However, based on the results of this study, the inability of *L. humile* to move large elaiosome-bearing seeds could have a detrimental impact on the species composition of fynbos plant communities in invaded areas. This is despite the ability of larger ant species, such as *T. quadrispinosum* and *O. cilliei*, which can coexist with *L. humile* (Witt & Giliomee 1999), to disperse seeds. Neither of these indigenous ant species probably contribute significantly to seed dispersal as they both have low worker densities in most fynbos areas compared to those of *A. custodiens* and *P. capensis* (Donnelly & Giliomee 1985; De Kock et al. 1992). However, measurements of nest entrance of *Anoplolepis* spp. and *P. capensis* indicated that the majority are too small to accommodate large seeds.

Perhaps the major benefit of myrmecochory for many plants, particularly those with large seeds, is not seed burial but merely distance dispersal (Westoby & Rice 1981; Andersen 1982). Yeaton & Bond (1991) found that seed dispersal by ants is a mechanism whereby seeds may be removed from a superior competitor, thereby promoting coexistence. Rodent seed predation will be reduced by

the mere dispersal of the seeds away from the parent plant (Janzen 1970) and the removal of the elaiosomes after dispersal (Heithaus 1981; Bond & Breytenbach 1985). The thick, hard testa of large myrmecochorous seeds like those of *P. reflexus* and *L. cordifolium* may protect the embryo from desiccation and possibly even fire if the seeds were to remain on the soil-surface after dispersal. These aspects require further research, although the inclination of *O. cilliei* to move seeds farther away from the entrance and lodge them under stones or twigs indicates that dispersal rather than burial is the prime benefit of myrmecochory.

From this study it is clear that a small ant species such as *L. humile* is capable of dispersing small seeds but not large elaiosome-bearing seeds. Although some of the larger seeds in *L. humile*-invaded areas may be dispersed by *T. quadrispinosum* and *O. cilliei*, which can co-exist with *L. humile*, the absence of species like *P. capensis* and *Anoplolepis* spp. will result in an overall reduction in the dispersal of large ones. The study also indicated that the dispersal of seeds, especially large seeds, may be the only real benefit of myrmecochory, considering that the nest entrances of most ant species are too small to accommodate bigger seeds. In terms of seed dispersal the displacement of important myrmecochorous ants by *L. humile* seems likely to impact more seriously on large-seeded plant species, which include some of the most spectacular and, in many instances, endemic plants of the Cape Floral Region.

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