

Dispersal for distance? *Acacia ligulata* seeds and meat ants *Iridomyrmex viridiaeneus*

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Abstract Ant seed dispersal distances are typically small, averaging less than 1 m in published studies. Here, a new record (180 m) for ant seed dispersal distance is reported, and preliminary observations are made on the interaction between meat ants *Iridomyrmex viridiaeneus* Viehmeyer (Hymenoptera: Formicidae) and diaspores of the sandhill wattle, *Acacia ligulata* A. Cunn. ex Benth. (Fabaceae) in Kinchega National Park, New South Wales (NSW), Australia. *Iridomyrmex viridiaeneus* moved diaspores over distances of 7–180 m (mean 93.9 m) from the source trees to their nests, removed the arils underground and discarded the seeds over a 3000-m² area surrounding the nest. A germination trial determined that the viability of discarded seeds was 40%, with 80% of the viable seeds in a dormant condition. Although the cumulative effects of *I. viridiaeneus* on *A. ligulata* recruitment require further investigation, this study and others raise the possibility that myrmecochorous systems in the Australian arid zone may be characterized by longer dispersal distances than those in other parts of the world. Long-distance seed movement by ants lends credence to the hypothesis that distance dispersal (in contrast to directed dispersal) could be of benefit to myrmecochorous plants.

Keywords: ant–plant interaction, dispersal distance, dormancy, germination, mutualism, myrmecochory, seed dispersal.

INTRODUCTION

Seed dispersal by ants (myrmecochory) is an important component of reproduction in thousands of plant species worldwide (Beattie 1985). Like other forms of animal seed dispersal, myrmecochory is viewed as a positive association in which individual plants (myrmecochores) increase the likelihood of successful reproduction by recruiting animals (in this case, ants) to spatially redistribute their seed crop. In turn, ants receive nutritional benefits that presumably increase colony fitness. Ant foragers are attracted to food bodies (called arils or elaiosomes) attached to seeds, at least in some cases because aril composition mimics that of insect prey (Hughes *et al.* 1994). The entire unit (seed plus aril) is carried back to the nest, where the aril is removed from the seed and used as food for workers and/or larvae. The seed is then discarded either below or above ground. Benefits to the plant from this association vary widely across plant species (reviewed in Beattie 1985). Most documented cases fall into three categories; the plant benefits because: (i) seeds are deposited underground and are thus protected from fire; (ii) seeds are deposited in a nest microhabitat superior (in terms of nutrients or water) to microhabitats occupied by undispersed seeds; or (iii) seeds are moved from areas of high to low seed predation rates (Beattie 1985). These three categories

may be viewed as types of ‘directed dispersal’ (Howe and Smallwood 1982), in which the benefit is achieved by virtue of the seed’s microhabitat after deposition, independent of the distance travelled.

In Australia, although the first category of plant benefits (protection from fire) has been demonstrated for some species (e.g. Hughes & Westoby 1992), the second and third categories are infrequently found (Westoby *et al.* 1991). This leads to speculation about alternative types of benefits. One hypothesis is that dispersal distance *per se* may provide important advantages to Australian myrmecochores (Andersen 1988). Under this scenario, safe sites for recruitment are patchy and relatively rare. Plants that experience a seed distribution with a long tail, thereby sampling a wide range of sites, would achieve higher fitness (Green 1983; Andersen 1988).

Dispersal distance *per se* has historically been rejected as a potential benefit of myrmecochory because ant seed dispersal distances are thought to be small in comparison with those recorded for birds, mammals and other vertebrates (Andersen 1988). A recent synthesis of more than 2500 distances reported in the world literature by Gómez and Espadaler (1998) shows that ant seed dispersal distances can indeed be small: the authors calculate a mean of 0.96 m, with a range of 0.01–77 m. However, studies of ant seed dispersal distances are far more common in the Northern Hemisphere, despite the fact that nine-tenths of the world’s myrmecochores are found in the Southern

Hemisphere (Gómez & Espadaler 1998). Could this geographical bias result in misapprehension of 'typical' ant dispersal distance and thus cause an inappropriate dismissal of the dispersal for distance hypothesis?

Evidence from two sites (coastal Victoria and Kakadu) indicates that ant-generated seed dispersal curves may have longer tails (10.9 and 13.1 m, respectively) in Australia than elsewhere in the world (Andersen 1988; Andersen & Morrison 1998). Furthermore, the global maximum for ant dispersal distance (77 m) is attributed to the meat ant *Iridomyrmex viridiaeneus* carrying seeds of *Sclerolaena diacantha* in far western New South Wales (NSW), Australia (Davidson & Morton 1981). Until recently, this remained the only study of myrmecochorous dispersal distance in the Australian arid zone, an enormous area known to host a highly diverse ant fauna (Greenslade & Halliday 1982). To encourage further investigation of potentially unique aspects of myrmecochory in the arid zone, I report here on a new record for ant dispersal distance based on observations of *I. viridiaeneus* interacting with *Acacia ligulata* in Kinchega National Park, NSW, Australia. In addition, I describe the densities and distribution of dispersed *A. ligulata* seeds surrounding *I. viridiaeneus* nests, and the viability and dormancy of these seeds. I then discuss the possible contributions of *I. viridiaeneus* to recruitment in *A. ligulata*, and the implications of long-distance seed dispersal by ants for our understanding of myrmecochory in Australia.

METHODS

Study species and study site

Iridomyrmex viridiaeneus is a member of the *Iridomyrmex purpureus* or meat ant group (Shattuck 1993). Meat ants are often the numerical and behavioural dominants in Australian ant assemblages (Greenslade 1976; Andersen & Patel 1994). Although quite variable, nesting areas are often large (up to 10.5 m in diameter), barren of vegetation, and decorated with pebbles (Ettershank 1968; Greenslade & Halliday 1982). The main nest area is often connected to satellite nests via above-ground trails (Ettershank 1968). Distant foraging areas are accessed via semipermanent trails; continuous use of particular trails has been documented over a period of 4 months (Duncan-Weatherley 1953). Meat ants are generalist foragers, incorporating nectar, honeydew, insects and other foods into their diet (Briese & Macauley 1981). They are known to be attracted to arils and to carry seeds considerable distances back to the nest (Davidson & Morton 1981; Smith 1989; Andersen & Morrison 1998).

The sandhill wattle, *A. ligulata*, is one of the most widespread of the Australian wattles, occurring on dunes across the arid zone (Maslin & Hopper 1982; Chapman & Maslin 1992). Diaspores consist of the seed and an expanded coloured funicle (the aril or elaiosome); aril colour is polymorphic (O'Dowd & Gill 1986). Diaspores are collected and dispersed by a variety of ants and birds (Davidson & Morton 1984; Forde 1986; Letnic *et al.* 2000). Germination is episodic following rains and recruitment can be severely reduced by vertebrate herbivores and drought (Auld 1995b; Auld & Denham 2001).

In Kinchega National Park, NSW (32°26'E, 142°11'S), *A. ligulata* populations occur on red earth dunes, sandplains and lunettes (Auld 1995b; Westbrooke *et al.* 2001). Fruits ripen in December and diaspores are dispersed by at least 10 species of birds, predominantly honeyeaters (Meliphagidae), and at least five species of ants, predominantly *Rhytidoponera* spp. (K. D. Whitney, unpubl. data). Typically, *I. viridiaeneus* is responsible for 0–10% of the ant dispersal events from *A. ligulata* experimental seed depots, depending on the timing and location of sampling (K. D. Whitney, unpubl. data).

Research methods

Following initial observations of *A. ligulata* dispersal by *I. viridiaeneus* in 1999, *I. viridiaeneus* colonies were examined periodically during the 2000–2001 and 2001–2002 fruiting seasons (December to February). If the ants were actively collecting diaspores, then more detailed observations were made. This resulted in data for six colonies associated with four *A. ligulata* populations. For these colonies, all foraging trails containing *A. ligulata* diaspores in transport were measured with a measuring tape and compass, and mapped onto an X,Y coordinate system. Each trail was examined from its distal end (which invariably corresponded to a fruiting *A. ligulata* tree or trees) to its origin (at either a main or satellite nest). These examinations confirmed that foraging was taking place only at the distal ends of trails, and that diaspores were taken to nests rather than being deposited en route. Thus, dispersal distances for all diaspores on a given trail were the same, and were calculated as the straight-line distance between the tree and the nest. Mean and median dispersal distances across trails were then calculated (the 'trail-weighted' mean and median). Depending on the relative diaspore traffic on different trails, this trail-weighted mean may, or may not, be an unbiased estimate of the mean distance an *A. ligulata* diaspore is moved by *I. viridiaeneus* (the 'diaspore-weighted' mean).

The density and distribution of *A. ligulata* seeds around two *I. viridiaeneus* colonies (A and B) was compared with that around two control areas at the

end of the 2001 fruiting season (19 February). Control areas were circular and 4 m in diameter (the approximate size of the colony nest areas). The control areas were chosen in the same habitat as the colonies, and at the same distance from the edge of the *A. ligulata* adult population, but did not contain *I. viridiaeneus* colonies or foraging trails. At each area (colony or control), two belt transects of 50 adjacent quadrats (each 0.5 m × 0.5 m) were established, radiating 25 m in random directions from the edge of the colony or the control area. All *A. ligulata* seeds on the soil surface in each 0.25 m² quadrat were counted and collected.

To examine the viability and dormancy of ant-dispersed seeds, I followed a germination procedure for *A. ligulata* provided by Letnic *et al.* (2000). Seeds collected on the transects at colony A were assessed with 30 replicates of five seeds each, but only 10 replicates were available for colony B. It would have been advantageous to examine the viability and dormancy of seeds not processed by ants as a control, but because the ant-dispersed seeds were of unknown (and presumably varying) ages, no appropriate controls were possible. Seeds were first soaked for 24 h in distilled water (7 July 2001), and then placed on moist filter paper in plastic cell culture trays (wells

35 mm diameter). Seeds were misted with distilled water and examined daily for germination over a 10-day period. Trays were kept in the dark except during examination, and temperature was maintained at 24°C. To assess the viability of the ungerminated seeds, on day 10 all seedcoats were scarified with a razor to allow imbibition. To deter fungus growth in the trays, 2 mL of a 1.0-mg mL⁻¹ fungicide solution (Captan, Chevron, San Ramon, CA, USA) was added to each well following scarification. Germination was then scored daily for another 10 days, at which point all seeds had either germinated or started to decompose. Seeds that did not germinate during the 20-day experiment were considered inviable; those that did not germinate until after scarification were considered dormant.

RESULTS

Ant behaviour and dispersal distances

Iridomyrmex viridiaeneus workers collected arillate seeds (diaspores) underneath fruiting *A. ligulata* trees

Table 1. Lengths of *Iridomyrmex viridiaeneus* foraging trails, and straight-line dispersal distances accomplished along those trails for *Acacia ligulata* seeds

Colony	Year	Trail no.	Origin	Trail length (m)	Dispersal distance (m)
A	2000	1	M	183.0	179.8
		2	M	203.0	172.6
		3	M	105.0	103.7
		4	M	166.0	160.2
		5	M	125.0	125.0
		6	M	172.0	136.0
Means				159.0 ± 15.0	146.2 ± 12.1
B	1999	1	M	160.0	134.0
	2000	2	S	110.0	106.6
		3	M	155.0	155.0
		4	S	87.0	87.0
Means				128.0 ± 14.7	120.7 ± 15.0
C	2001	1	M	49.8	47.4
		2	M	29.3	27.1
		3	M	76.8	67.0
		4	M	72.0	56.8
Means				57.0 ± 10.9	49.6 ± 8.5
D	2001	1	M	136.5	117.8
E	2001	1	M	61.1	61.1
		2	M	77.2	71.0
		3	M	91.2	83.0
Means				76.5 ± 8.7	71.7 ± 6.3
F	2001	1	M	52.1	47.8
		2	M	29.1	27.0
		3	M	7.1	7.1
Means				29.4 ± 13.0	27.3 ± 11.8
Overall means				102.3 ± 12.2	93.9 ± 11.1
Overall medians				91.2	87.0

Means (± SE) and medians are 'trail-weighted' (see Methods). Origin: M, main nest; S, satellite nest.

up to 180 m from their nest area (Table 1) and returned the diaspores to the nest. Only arillate seeds and aril pieces were seen being carried by the ants, despite the presence of bare seeds in the foraging areas. Workers ignored fruiting *A. ligulata* en route and foraged only at the distal ends of the trails. One diaspore was watched from its collection under an adult canopy until it was taken underground at the main nest of colony B. Time in transit on the 160-m trail was 41 min.

Averaged across trails, the mean dispersal distance (\pm SE) was 93.9 ± 11.1 m (Table 1). Without data on relative diaspore traffic on different trails, we cannot assess whether this trail-weighted mean is an unbiased estimate of the diaspore-weighted mean dispersal distance. For example, if diaspore traffic is consistently heavier on trails originating at main nests than at satellite nests, the trail-weighted mean probably underestimates the diaspore-weighted mean because satellite nests tend to have shorter foraging trails than their corresponding main nests (Table 1).

All diaspores that were observed being carried onto the surface of the nest were taken below ground. Concurrently with these observations, workers were also observed exiting the nest entrances with *A. ligulata* seeds from which the arils had apparently been removed. These seeds appeared undamaged, and were deposited singly 3–18 m from the edge of the nest. Thus, the distances reported in Table 1 reflect the first leg of a seed's journey (parental tree to nest) once taken by *I. viridiaeneus*. The postprocessing discarding of seeds from colonies results in final deposition up to 25 m (and probably further) from the nest, as will be described later. Depending on the direction of discarding, this behaviour may increase or decrease a given seed's distance from its parent.

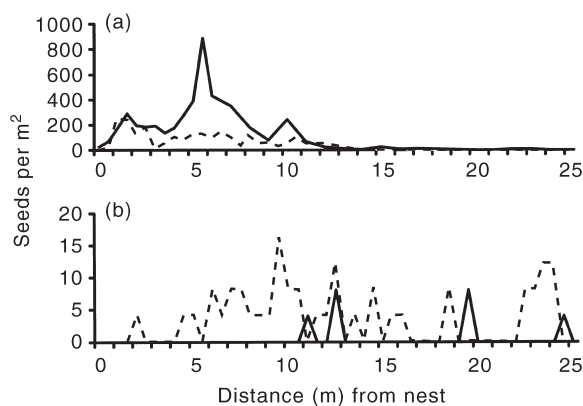


Fig. 1. Distribution of *Acacia ligulata* seeds adjacent to *Iridomyrmex viridiaeneus* colonies. For both colonies, values for the control areas are so low as to be indistinguishable from the x-axis, and are not presented. (a) Colony A; (b) colony B. (---), Nest transect 1; (—), nest transect 2.

Seed density and distribution near ant colonies

Considering colonies A and B together, seed densities averaged 0.12 m^{-2} on the control transects and 40.54 m^{-2} on the nest transects. This 338-fold difference suggests that *I. viridiaeneus* has a major impact on the distribution of *A. ligulata* seeds in the neighbourhood of their nests. Increased seed densities were found even on the distal ends of the nest transects (Fig. 1), indicating that a colony can affect seed densities in an area of 3000 m^2 around the nest. The magnitude and shape of the distribution of seeds discarded from *I. viridiaeneus* colonies is variable (Fig. 1). Colony A had a relatively high density of seeds (mean \pm SE = $79.1 \pm 14.8 \text{ m}^{-2}$), concentrated within the first 15 m of the transects (skewness 1.78, kurtosis 3.96). In contrast, colony B had a much lower density of seeds (mean \pm SE = $2.0 \pm 0.3 \text{ m}^{-2}$), more evenly scattered out to the extremity of the 25-m transects (skewness 1.39, kurtosis 2.27). These differences are reflected in the median distance of a seed from the nest area: 6.0 m for colony A and 12.5 m for colony B.

Seed viability and dormancy

The viability of the ant-dispersed seeds was similar across colonies and averaged 39.7% (Table 2). Most seeds were dormant, as only 20.2% of the viable seeds germinated prior to experimental scarification (Table 2).

DISCUSSION

Potential role of *Iridomyrmex viridiaeneus* seed dispersal in *Acacia ligulata* recruitment

In the present study, the meat ant *I. viridiaeneus* regularly moved *A. ligulata* diaspores from underneath parent canopies to nest sites 7–180 m away. Arils were apparently removed underground, and the resulting bare seeds were scattered up to 25 m from the nest. Approximately 40% of the seeds sampled from nest refuse areas were viable, and most (80%) of these viable seeds were dormant. Given these patterns, what role

Table 2. Percentage of seeds viable, and percentage of viable seeds dormant, for seeds collected from two *Iridomyrmex viridiaeneus* colonies

Colony	Viability (\pm SE)	Dormancy (\pm SE)
A	35.3 ± 5.3	88.0 ± 5.5
B	44.0 ± 7.8	71.7 ± 10.2
Means	39.7 ± 4.3	79.8 ± 8.1

does dispersal by *I. viridiaeneus* play in the recruitment of *A. ligulata*?

Although only 40% of the ant-dispersed seeds were viable, there is at present no evidence that *I. viridiaeneus* damages seeds. Australian *Acacia* seeds are generally well-defended against ants via strong seed coats (Rodgers 1998), and evidence that another ant species (*Rhytidoponera* sp.) has no effect on seed viability and dormancy in *A. ligulata* (Letnic *et al.* 2000) suggests alternative scenarios. The surface seed-banks from which seeds for the assay were drawn probably represent accumulations of several years. In Kinchega, summer temperatures at the soil surface fluctuate daily by as much as 55°C, and maxima regularly exceed 70°C (T. D. Auld, unpubl. data). Heat fluctuations are known to break dormancy in some legumes (Quinlivan 1971), and would result in attrition from the surface seed-bank as seeds germinate. In Kinchega, yearly attrition to germination and death in *A. ligulata* seed-banks has been estimated at 10–30% (Auld 1995a). Such attrition would act to decrease the ratio of viable : inviable seeds on the ground, with the consequence that viability as measured in the present study should be considered a lower bound for the viability of seeds immediately after they are discarded from the nests. Thus, it remains unclear whether *I. viridiaeneus* changes seed viability or dormancy in *A. ligulata*, but we can conclude that a substantial fraction of seeds are dispersed unharmed.

Given that at least some seeds are dispersed in viable condition, are they being delivered to appropriate micro- and macrohabitats for germination and recruitment? Davidson and Morton (1981) considered seedling recruitment of shrubs in the Chenopodiaceae at *I. viridiaeneus* nest microhabitats, and focused on the observation that soils of meat ant nests have lower nutrient content than surrounding soils (Briese 1974, in Davidson & Morton 1981). This led the authors to speculate that *I. viridiaeneus* may be parasitic on the mutualistic relationship between *Sclerolaena diacantha* (Chenopodiaceae) and other ant species. However, at least in the case of *A. ligulata*, seeds are deposited not on the nest surface itself but in surrounding areas, where nutrient content may not be depressed. Inspection around the colonies studied here found both *A. ligulata* seedlings and juveniles, indicating that germination and early establishment are at least possible in the deposition microsites provided by *I. viridiaeneus*. Macrohabitat considerations, however, suggest that the nature of the relationship between *I. viridiaeneus* and *A. ligulata* recruitment may depend on the location of the ant colony. In three of the colonies studied (A, C, D), nests were located in bluebush (*Maireana pyramidata*) open-shrubland, which differs in both vegetation composition and soil structure from the adjacent dune habitats favoured by *A. ligulata* (Beadle 1948; Westbrooke *et al.* 2001). Other *I. viridiaeneus* colonies (B, E, F) were located on

or bordering red sand dunes or white sand lunettes and, thus, may provide dispersal to suitable macrohabitats. Studies of the spatial distribution of *A. ligulata* seedlings, juveniles and adults in relation to long-lived *I. viridiaeneus* colonies would aid in determining how this ant species affects recruitment in the plant.

Overall, the potential importance of the relationship between *A. ligulata* and *I. viridiaeneus* must be gauged against the plant's relationship with numerous other dispersers. Although *I. viridiaeneus* is an infrequent visitor relative to other ants and birds (K. D. Whitney, unpubl. data), even infrequent dispersers may be important if more frequent visitors damage seeds, or deposit them in inhospitable locations. On one hand, some have argued that *A. ligulata* (and other *Acacia* species with large, energy-rich, brightly coloured arils) belong to a 'bird dispersal syndrome' rather than an 'ant dispersal syndrome' (Davidson & Morton 1984; O'Dowd & Gill 1986), which might suggest that ants are an unimportant influence on recruitment. On the other hand, Letnic *et al.* (2000) argued that *A. ligulata* employs a risk-spreading dispersal strategy involving both birds and ants, via differential effects of the two taxa on seed dormancy. To my knowledge, no studies have actually compared the contributions of ants versus birds to recruitment in any *Acacia* species.

Long-distance seed dispersal by ants

The arid zone of Australia comprises approximately 70% of the continent (Stafford Smith & Morton 1990) but has received little attention in terms of myrmecochorous dispersal. There have been just two studies of myrmecochorous dispersal distances in the arid zone (Davidson & Morton 1981; the present study), and nine studies in more mesic regions of the continent (Berg 1975; Shea *et al.* 1979; Gill 1985; Auld 1986; Andersen 1988; Mossop 1989; Smith 1989; Hughes & Westoby 1992; Andersen & Morrison 1998). Although the patterns should be considered provisional, the emerging picture is that myrmecochorous dispersal distance maxima in the arid zone are larger than in more mesic regions of Australia and, indeed, larger than in all other areas of the world. Maxima for the arid zone studies are 77 and 180 m, whereas for the studies in mesic regions, maxima range from 1.9 (Shea *et al.* 1979; Hughes & Westoby 1992) to 50 m (Smith 1989). It should be noted that the latter value was observed for seeds of a non-native garden plant in a house-yard; for a native plant in mesic Australia, the maximum is 13.1 m (Andersen & Morrison 1998). Mean dispersal distances, although less frequently reported, are also larger in the arid zone: 93.9 m (the present study) compared with a range from 0.1 (Auld 1986) to 7.2 m (Andersen & Morrison 1998). Outside of Australia, the documented maximum myrmecochorous dispersal distance is 70 m (Gómez & Espadaler 1998).

That Davidson and Morton (1981) and the present study focus on only a few ant and plant taxa may produce a biased view of myrmecochory in the Australian arid zone. However, the provisional pattern described herein, that is, longer myrmecochorous dispersal distances in the arid zone compared with more mesic areas, cannot be wholly an artefact of the focus on meat ants in the arid zone. Three of the studies in more mesic areas (Berg 1975; Smith 1989; Andersen & Morrison 1998) also examined meat ant dispersal distances, and five of the remaining studies (all but Andersen 1988) examined unidentified *Iridomyrmex* species. An initial focus on seed dispersal by meat ants seems appropriate, as meat ants are an extremely widespread and important component of the ant fauna of the Australian arid zone (Greenslade & Halliday 1982) and thus may interact with a wide variety of plant species.

The data reported here for *I. viridiaeneus* show that ant seed dispersal distances can be of the same magnitude as those produced by vertebrates. For example, the median and maximum seed dispersal distances of 87 and 180 m are comparable to distances measured for some tropical bird species. Westcott and Graham (2000) studied the dispersal of six plant species by the flycatcher *Mionectes oleagineus* in Costa Rican wet forest, and found median and maximum seed dispersal distances ranging from 42–56 and 55–100 m, respectively. In Rwanda, Sun *et al.* (1997) recorded median seed dispersal distances of 117–292 m for six tree species dispersed by four species of turacos (maxima were not reported). Thus, predicted differences in the spatial structure of vertebrate-dispersed versus ant-dispersed plant populations (Horvitz & Le Corff 1993) may not be globally applicable.

It would be of great interest to examine other sites, and other ant–plant associations, to generate a distribution of myrmecochorous dispersal distances in the arid zone. If the dispersal distances reported so far are unexceptional for the region, it follows that Australian arid-zone myrmecochores may have a substantially different genetic and/or spatial structure from those occurring elsewhere in the world. Furthermore, arid zone myrmecochores provide a good opportunity to evaluate the benefits of ant dispersal, including the hypothesis that dispersal distance *per se* can be a benefit of myrmecochory (Andersen 1988). One approach would be to compare the relative distribution of safe sites for representative myrmecochore species pairs that experience long- versus short-tailed seed dispersal curves.

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