SHORT COMMUNICATION

Claire Detrain · Olivier Tasse

Seed drops and caches by the harvester ant *Messor barbarus*: do they contribute to seed dispersal in Mediterranean grasslands?

Abstract To determine whether the harvester ant *Messor barbarus* acts as a seed disperser in Mediterranean grasslands, the accuracy level of seed processing was assessed in the field by quantifying seed drops by loaded foragers. In the vicinity of exploited seed patches 3 times as many diaspores were found as in controls due to seed losses by foragers. Over trails, up to 30% of harvested seeds were dropped, singly, by workers but all were recovered by nestmates within 24 h. Seeds were also dropped within temporary caches with very few viable diaspores being left per cache when ants no longer used the trail. Globally, ant-dispersed diaspores accounted for only 0.1% of seeds harvested by *M. barbarus*. We discuss the possible significance for grassland vegetation of harvester-ant-mediated seed dispersal.

Ants are important seed predators in deserts or semi-arid areas (Tevis 1958; Brown et al. 1979; Davidson et al. 1985; Detrain and Pasteels 2000; Detrain et al. 2000) but they are also widely recognised as seed dispersers in a variety of habitats (Davidson and Morton 1981; Buckley 1982; Beattie 1985; Hughes and Westoby 1992; Levey and Byrne 1993). Evolutionary interactions between ants and plants have even led to seed morphological specialisation such as elaiosomes, which are attractive to ants and encourage dispersal of myrmecochorous plants to a "safe site" for germination and growth (Sernander 1906; Bond et al. 1991; Westoby et al. 1991). The effect of ants on plant dispersal is however not restricted to myrmecochores, since non-elaiosome-bearing seed species that are harvested by ants can ultimately be dispersed at long distances from the parent plant within the galleries or on the refuse pile of their nest (Beattie and Culver 1982; Rissing 1986; Kaspari 1993). Such dispersal of seeds by harvesters may have preceded myrmecochory during the co-evolution of ants and plants (Rissing 1986). Other possible benefits from harvester ants were not considered. Indeed, the "mistakes" they make, i.e. the seeds they lose along the way, may contribute to plant dispersal and may somewhat compensate for the damage caused by predation. Here, we explore whether ant-mediated dispersal of seeds occurs during the return trip of foragers to their nest.

We observed, from April to June 1997, colonies of the Mediterranean harvester ant, *Messor barbarus,* located at Vidauban (southeastern France). Grasses and a variety of annuals dominated the cover of the study site but sclerophyllous trees (umbrella pine) and evergreen shrubs (e.g. lavender, thyme, juniper) were also present. We assessed the dispersal of seeds by *M. barbarus* foragers, which may occur at three stages of their homeward trip. Harvester ants may drop their load before they reach the foraging trail in the vicinity of the exploited seed patch, while they walk on the trail, or when they encounter a temporary seed cache located on the foraging path. As harvester ants can carry whole fruits and remove the seed from the inedible parts inside the nest, the term "seed" refers without distinction to fruits or seeds that are retrieved by the ants.

Seed drops outside the trail, near the exploited seed patch

Outside trails, foragers that dropped their seeds were easily overlooked since the vegetation cover often hid them. Therefore, ant-mediated dispersal of seeds in the vicinity of the discovery site was globally assessed by comparing the numbers of seeds present over the soil surface of trail-centred quadrats to those found in adjacent controls. Sampling was as follows: two 1 m × 0.2 m plots were established approximately 2–3 m apart as

C. Detrain (✉) · O. Tasse
Laboratoire de biologie animale et cellulaire C.P. 160/12, Avenue F.D. Roosevelt 50, 1050 Bruxelles, Belgium
e-mail: cdetrain@ulb.ac.be
Tel: +32-2-6504512
Fax: +32-2-6502445

Table 1. Seed drops outside trails, found over the soil surface of trail-centred or control quadrats after foraging activity had ceased (*n* number of trails observed). The mean (±SD) numbers of seeds found in trail-centred plots were compared to controls by a Student *t*-test for paired samples (significance level 0.05). Only seed species that were observed in at least four different plots are reported in the table

Seed species	Plant family	Total number (%) of seeds in all trail-centred quadrats		Number of seeds per quadrat			
		All seeds	Viable seeds	Control (mean±SE)	Trail-centred (mean±SE)	*n*	Paired *t*-values
Gaudinia fragilis	Poaceae	157 (18.5%)	55 (22.3%)	3.3±1.5	17.4±4.0	9	*t*=4.1 *P*=0.003
Holcus lanatus	Poaceae	157 (18.5%)	2 (0.8%)	0	40.0±27.6	4	*t*=1.4 *P*=0.24
Agrostis pallida	Poaceae	146 (17.2%)	32 (12.9%)	4.5±2.1	17.6±4.7	8	*t*=2.6 *P*=0.037
Juncus capitatus	Juncaceae	122 (14.3%)	72 (29.1%)	3.0±1.3	15.2±11.9	8	*t*=1.15 *P*=0.29
Tuberaria guttata	Cistaceae	90 (10.6%)	19 (7.7%)	3.4±1.2	9.0±5.2	12	*t*=1.2 *P*=0.27
Vulpia myuros	Poaceae	29 (3.4%)	9 (3.6%)	0.7±0.2	4.8±2.4	6	*t*=1.7 *P*=0.14
Crepis	Asteraceae	28 (3.3%)	7 (2.8%)	2.2±1.4	3.5±1.9	8	*t*=2.2 *P*=0.06
Aira sp.	Poaceae	24 (2.8%)	6 (2.4%)	2.5±1.6	6.0±3.0	4	*t*=0.9 *P*=0.42
Mibora verna	Poaceae	7 (0.8%)	7 (2.8%)	1±0.4	2.8±0.9	5	*t*=1.7 *P*=0.17
Moenchia erecta	Caryophyllaceae	7 (0.8%)	7 (2.8%)	1.2±0.5	2.3±0.8	6	*t*=1.9 *P*=0.11
Plantago sp.	Plantaginaceae	4 (0.5%)	4 (1.6%)	1.7±1.2	2.0±0.6	4	*t*=0.3 *P*=0.76
Avena fatua	Poaceae	3 (0.3%)	0 (0%)	0.2±0.2	0.75±0.25	4	*t*=1.0 *P*=0.39
All seed species		851 (100%)		15.4±3.8	53.2±11.1	16	*t*=3.8 *P*=0.002
All viable seed species			247 (100%)	5.9±1.6	16.1±4.8	16	*t*=3.0 *P*=0.009

soon as a new foraging trail was detected. The first plot was centred on the end of the foraging trail; the second (control plot) was chosen in an area of similar exposure, substrate and vegetation cover but in which no seed harvesting by ants occurred. The soil surface of both plots was carefully surveyed: all seeds detectable by eye were counted, removed, stored in vials, identified to species and checked for viability under a binocular microscope. Two successive measures were carried out: firstly at the beginning of foraging when the trail was detected, and secondly when the trail was no longer followed by foragers. Between-plot differences in the amount of plant diaspores provided us with an estimate of seed dispersal exclusively due to the activity of harvester ants. The sampling procedures described above were repeated over 16 different trails.

At the beginning of foraging, the numbers of seeds found in control plots were significantly correlated with those in trail-centred plots (paired samples correlation, $r=0.828$, $P<0.001$), but the correlation was weaker and not significant after several days of harvesting activity when the trail was no longer followed (paired samples correlation, $r=0.463$, NS). Indeed, both the total number of seeds and the number of viable diaspores were, significantly, 3 times higher in trail-centred plots than in controls (Table 1). The same proportion of viable seeds (around 30%) was however found in both plots, suggesting that foragers do not selectively drop seeds with no consumption value. Five species each accounted for at least 10% of all seeds dispersed outside trails, in the vicinity of exploited seed patches (Table 1). They were more frequently found in trail-centred plots than in controls, though this difference was significant for only two species (French oat *Gaudinia fragilis* and *Agrostis pallida)*. When taking into account only diaspores which had kept their reproductive potential, *G. fragilis* and *Juncus capitatis* species accounted together for half of lost seeds. The abundance among seed drops of species such as *G. fragilis, Holcus lanatus, J. capitatis* or *Tuberaria guttata* may be related to their intensive exploitation by harvester ants in spring and early summer (Detrain and Pasteels 2000) suggesting seed dispersal by ants could result from chance losses during food transport.

Seed drops on foraging trails

Preliminary observations showed that, if seeds were dropped on a trail, they were all located at its very end, near the harvested areas. Therefore, we individually followed loaded workers along the last 2 m of trails. We noted whether seeds were dropped and recovered by nestmates within 1 h or within the following 24 h. We also observed whether, after dropping seeds, ants went on their homeward trip or half-turned back towards the exploited seed patch. The rate of seed drops was assessed for eight plant species which either dominated *M. barbarus* seed retrievals (Detrain and Pasteels 2000) or produced cumbersome seeds likely to be lost by ants *(Plantago, Vulpia, Avena)*.

Such seed drops were observed among 17% of the foraging ants and occurred at higher rates (up to one-third of retrievals by ants) for heavy or cumbersome species such as wild oat *Avena fatua* and *Vulpia myuros* (Table 2). All dropped seeds were recovered by nestmates, usually within 1 h (87%). After having dropped their load, most workers (79%) half-turned back instead of going ahead over the trail, and returned to the exploited seed patch.

Table 2. Individual seed drops on trails. For each seed species, the number (and percentage) of drops was measured by following 40 loaded foragers. The rates of seed recovery by nestmates and of U-turns are calculated over the total number of observed seed drops

Plant species	Number (%) of seed drops	% Recovered within 1 h	% Recovered within 24 h	% U-turns after drops
Gaudinia fragilis	4 (10%)	75%	100%	75%
Holcus lanatus	2 (5%)	50%	100%	100%
Juncus capitatus	4 (10%)	75%	100%	100%
Tuberaria guttata	7 (17.5%)	100%	100%	100%
Avena fatua	11 (27.5%)	91%	100%	64%
Plantago sp.	6 (15%)	100%	100%	50%
Vulpia myruos	13 (32.5%)	85%	100%	54%
All species	47 (17%)	87%	100%	79%

Seed drops in temporary caches

We carried out a daily survey of six different nests in order to detect possible seed caches along trails. For each seed cache, we measured its distance from the nest as well as the total trail length. As soon as ants ceased to use the trail, seeds left within the cache were removed, counted, identified to species and checked for viability.

Harvester ants were seen dropping their load on seed piles located on 20% of *M. barbarus* foraging paths (*n* = 75, Table 3). Trails associated with seed caches were nearly twice as long and more ramified (two branches on average) than trails without seed caches (*P* < 0.005 and *P* < 0.02 for length and number of branches respectively). No significant difference was found in their length of use (*P* = 0.34). Only one seed cache was usually found per trail, two being detected on the same foraging path in 3 of 15 cases. Caches were usually located in the last quarter of trail length, on average at 4 m (SD = 3.4) from the exploited seed patch. Among the 18 detected caches, 4 were completely emptied by the ants but most of them still contained seeds when foraging activity had ceased over the trail. Ants left a median number of 21 seeds per detected cache (25th and 75th percentiles: 3.5 and 37 seeds) among which only a few were viable (median: 3 viable seeds, 25th and 75th percentiles: 0 and 9.8 viable seeds). Caches were usually polyspecific and contained a median number of five different seed species (25th and 75th percentiles: 3.25 and 5.4 seed species). The majority of viable diaspores left within caches were of *Vulpia*

myuros and of grasses such as *Mibora verna, Gaudinia fragilis* or *Bromus* sp. Viable seeds of plantain *Plantago* sp., *Juncus capitatis* and *Tuberaria guttata,* which were extensively harvested species (Detrain and Pasteels 2000), were also found within seed caches.

Discussion

As harvester ants collect seeds from one area and retrieve them to the nest, they may act as dispersal agents and thus, alter the spatial distribution of plant species. *M. barbarus* workers are very efficient at transporting seeds from the discovery site to the main foraging trail. Taking into account flows of loaded ants per minute, daily activity cycles and trail lifetime (Detrain et al. 2000), we roughly estimate that around 50,000 seeds are retrieved on average per foraging trail. We show here that only 0.1% of those harvested seeds are lost and dispersed by ants in the vicinity of exploited seed patch before foragers join the main trail. Seeds that are dropped on trails are all recovered by nestmates and thus do not contribute to plant dispersal. The high rate of U-turns among ants that have dropped seeds on the trail suggests that they participate in an active process of indirect load transfer between nestmates (Ratnieks and Anderson 1999; Reyes and Haeger 1999). Another kind of transport relay occurs on lengthy trails, i.e. the dropping of seeds in temporary caches. The viable diaspores left in such caches roughly account for less than 0.01% of harvested seeds. Those few seeds that are not retrieved for consumption are however left in a microhabitat conducive to increased germination since these shallow surface caches may accumulate water and provide more suitable soil temperatures.

Plant species that have cumbersome morphological seed adaptations, such as the awns of grasses, or that produce heavy diaspores less subject to wind dispersal, are more likely to benefit from the presence of harvester ants since their seeds are more easily dropped and dispersed by foragers. Data are still needed on the fate of seeds dropped by the ants and the ability of these seeds to survive and develop into reproducing adults. Although benefits may be rare and difficult to study we should not assume they are unimportant. In a system in which most seeds die and in which favourable microen-

Table 3. Characteristics of trails with or without temporary seed caches. Both types of trails were compared by means of a Student t-test. Significance level: 0.05

	With seed caches mean ± SD	Without seed caches mean ± SD	Statistical test *df* = 73
No. of trails observed	15	60	
No. of branching points	1.2 ± 1.2	0.53 ± 0.8	*t* = 2.5, *P* = 0.014
Trail lifetime (days)	5.9 ± 4.8	4.8 ± 3.6	*t* = 0.96, NS
Trail length (m)	18.1 ± 9.2	10.6 ± 7.5	*t* = 3.2, *P* = 0.002

vironments are limiting, rare events such as seed placement in suitable sites may influence seedling recruitment.

References

Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, New York

Beattie AJ, Culver DC (1982) Inhumation: how ants and other invertebrates help seeds. Nature 297:627

Bond WJ, Yeaton R, Stock WD (1991) Myrmecochory in Cape fynbos. In: Huxley CR, Cutler DF (eds) Ant-plant interactions. Oxford University Press, Oxford, pp 448–462

Brown JH, Reichman OJ, Davidson DW (1979) Granivory in desert ecosystems. Annu Rev Ecol Syst 10:201–207

Buckley RC (1982) Ant-plant interactions: a world review. In: Buckley RC (ed) Ant-plant interactions in Australia. Junk, The Hague, pp 111–141

Davidson DW, Morton SR (1981) Competition for dispersal in ant-dispersed plants. Science 213:1259–1261

Davidson DW, Samson DA, Inouye RS (1985) Granivory in the Chihuahuan desert: interactions within and between trophic levels. Ecology 66:486–502

Detrain C, Pasteels JM (2000) Seed preferences of the harvester ant *Messor barbarus* in a Mediterranean mosaic grassland. Sociobiology 35:35–48

Detrain C, Tasse O, Versaen M, Pasteels JM (2000) A field assessment of optimal foraging in ants: trail patterns and seed retrieval by the European harvester ant *Messor barbarus*. Insectes Soc 47:56–62

Hughes L, Westoby M (1992) Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. Ecology 72:1285–1299

Kaspari M (1993) Removal of seeds from Neotropical frugivore droppings. Oecologia 95:81–88

Levey DJ, Byrne E (1993) Complex ant-plant interactions: *Pheidole* as secondary dispersers and post-dispersal seed predators of rain forest plants. Ecology 74:1802–1812

Ratnieks FL, Anderson C (1999) Task partitioning in insect societies. Insectes Soc 46:95–108

Reyes JL, Haeger FJ (1999) Sequential co-operative load transport in the seed harvesting ant *Messor barbarus*. Insectes Soc 46:119–125

Rissing SW (1986) Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. Oecologia 68:231–234

Sernander R (1906) Entwurf einer Monographie der europäischen Myrmekochoren. K Sven Vetenskapsakad Handl 41

Tevis L (1958) Interrelations between the harvester ant *Veromessor pergandei* (Mayr) and some desert ephemerals. Ecology 39:695–704

Westoby M, Hughes L, Rice BL (1991) Seed dispersal by ants: comparing infertile with fertile soils. In: Huxley CR, Cutler DF (eds) Ant-plant interactions Oxford University Press, Oxford, pp 434–447