Falling or Movement of Seeds and the Presence of an Elaiosome: Its Effect on Ant Reaction (Hymenoptera: Formicidae) in a Myrmecochorous Species, *Euphorbia characias* (Euphorbiaceae)

by

Xavier Espadaler¹ and Crisanto Gómez²

ABSTRACT

When seeds fall from the parent plant or are ejected ballistically as in some myrmecochorous species, the impact produced on the soil may alert seed collectors. Ants can perceive sound transmitted through the ground and could detect the shock waves, the ephemeral movement of the seed or both. Additionally, ants may perceive chemicals from the elaiosome at some distance and be attracted to the seed. The aim of this study was to assess if ants respond to falling seeds and if they are attracted from a distance by the elaiosome. The reaction of four ant species to the seeds of the myrmecochorous *Euphorbia characias* artificially dropped to the ground or to seeds deposited on top of the soil were studied and the retention time of seeds under those two treatments were measured. The four ant species involved (*Tapinoma nigerrimum, Pheidole pallidula, Aphaenogaster senilis* and *Messor barbarus*) did not behave differently in response to either treatment. Retention times of seeds on the soil were similar, whether deposited on soil or left to fall freely from more than a meter height. Elaiosomes did not attract ants from a distance. This is not unexpected since ants that eventually find the seeds can be also seed predators (i.e. granivorous).

Keywords: Ant-seed interaction, elaiosome, myrmecochory, retention time, *Euphorbia characias*

INTRODUCTION

Seeds from myrmecochorous species are dispersed by ants (Beattie, 1985). Those plants may have a single phase dispersal system (Clay 1983; Horvitz & Beattie 1980; Kjellsson 1985), a two-phase dispersal system (Berg 1966; Bülow-Olsen 1984; Byrne & Levey 1993; Kaufmann et al. 1991) and even a three-phase dispersal system (Clifford & Monteith 1989; Aronne & Wilcock 1994). Species belonging to the

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¹C.R.E.A.F. Universitat Autònoma de Barcelona, E-08193, Bellaterra, SPAIN The address for correspondence.
²Departament de Ciències Ambientals, Universitat de Girona, E-17001 Girona, SPAIN. e-mail: ibec5@cc.uab.es
second group usually have a first ballistic dispersal process in which the seed is ejected at some distance after a releasing mechanism involving drying of enveloping structures is put in action (Berg 1975). This distance is assumed to reduce competition between seedlings and adults (Handel 1976; Kjellsson 1991), and is called the escape hypothesis (Howe & Smallwood 1982). Noise from the explosive mechanism is not expected to affect ant behavior since those insects are deaf to air-transmitted vibrations. Ants may use substrate-borne sound in their communication systems (Hölldobler & Wilson 1990). Soil from the nest (Hahn & Maschwitz 1985; Baroni Urbani et al. 1988), nest walls, specially from arboreal species (Markl 1973) or vegetation (DeVries 1990; Roces et al. 1993) are some of the substrates through which vibrations originating from the stridulatory organ can be perceived by ants. Distances are usually about a few cm although drumming Camponotus on a wooden substrate may reach as far as 90cm (Fuchs 1976).

In what follows we do not imply that seed fall does actually produce a detectable noise to the ants. But there is the logical possibility that when seeds fall on top of soil following ballistic dispersal they may produce a noise or a vibration. This could be detected by ants. That noise effect was suggested by Pacini (1990) as the reason seeds of Mercurialis annua (weight 2.5mg) were collected by the ants in a few seconds after being launched from a height of 10-50cm. The shock produced by the seeds impact on the soil was perceived and recognized by Messor structor -a seed predator- which ran to collect the seeds. In the absence of chemical signals immobile objects rarely attract attention of foraging ants but moving objects can be readily perceived by some large-eyed species (Hölldobler & Wilson 1990). Here we explored the hypothesis that the falling of a seed on the soil may affect retention time - time elapsed before an ant retrieves the seed - through its effect on ant behavior, be it by the noise produced when contacting the soil and/or vegetation or by the bouncing or lateral movement of the seed before it remains resting on the soil. Nothing is known concerning eventual differences in sound-detecting organs in ants.

Chemicals present in the elaiosome is another of the factors that affect the initial probability that an elaiosome bearing seed will be encountered by an ant. If chemicals from the elaiosome attract ants from a distance, we expect that seeds with elaiosomes will be found in a shorter time than seeds without the elaiosome. It must be noted that finding a seed does not translate directly into its transport to the nest. Upon encountering a seed an ant may show a graded response: ignore the seed, touch it and leave the seed intact, gnaw the elaiosome in situ.
or transport of the seed. We have tested if the elaiosome affects the time before seeds are found by an ant. The specific questions addressed were: (1) Does falling per se affect retention time before a seed is retrieved by an ant? (2) Does the presence of the elaiosome shorten the time elapsed before a seed is found?

MATERIALS AND METHODS

The study area is located near Barcelona (NE Spain), at the Collserola Park. The habitat is a field abandoned 15 years ago and it is now in a rapid process of colonization by bushes and a few young trees (for a full description see Espadaler & Gómez 1996). Observations were made on May 14, 1996, June 5, 1996 and May 23, 1997. We used seeds of *E. characias* (mean mass ± s.d.: 8.5 mg±0.88; n=40) that were obtained by allowing mature shoots of plants from the same field to desiccate at the laboratory.

**Effect of falling or movement**

Seeds were always manipulated with forceps and were subjected to the following two treatments: 1. Noise treatment: the effect of ballistic dispersal was simulated by letting single seeds fall from a height between 1.1 m and 1.5 m and noting the time until any ant transported the seed. Mean height of fruiting shoots at the site is 69.4 cm; range 29-127 cm (n=116). Retention time for seeds remaining on soil for longer than 30 minutes was included in a single class (>30’) since it is assumed that the effect of falling — if any — would dilute after that time. Thus, retention times are truncated to under 30 minutes. Data from that class were not included in the analysis. 2. Control treatment: a single seed was carefully deposited on top of soil and its retention time was noted. As in the previous treatment, the species of ant and time of day were also noted.

As the four ant species involved in seed retrieval at the site (*Tapinoma nigerrimum, Pheidole pallidula, Aphaenogaster senilis* and *Messor barbarus*) have different degrees of eye development and could correspondingly react differently, we checked also for specificity in ant response to falling seeds as compared with seeds deposited directly on soil with the G likelihood test. Responsiveness (faster reaction) of each ant species to seeds was also checked. We tested the differences between the medians of times for each species with the Kruskal-Wallis one-way analysis of variance.

The points for each treatment were chosen from a table of random number pairs that were treated as x-y coordinates to be added at each previous point. In a previous study it was shown that retention times depend strongly on the precise moment of the day, following the rise in
temperature of the soil (Espadaler & Gómez 1996). The retention time is expected to be strongly dependent on ant densities, i.e., on the probability that workers foraging close to the falling area could detect the substrate-borne vibrations produced, but since the observations were done simultaneously, the distinct ant densities are not expected to affect mean scores for the two treatments. Data were collected from 6.30h to 10.45h (solar time) since thereafter the activity of ants is greatly reduced. We compared a subset (<30 minutes) of the above mentioned retention times — obtained in 1994 following the same protocol as the control treatment — with data from the present study to check for eventual differences between years. Any vibration caused by a falling seed or its limited movement when bouncing is expected to alert ants and reduce retention time (one-tailed hypothesis). We tested this with the Mann-Whitney U test. Frequency distributions of times were compared with a Kolmogorov-Smirnov two-sample nonparametric test.

**Attractivity of the elaisosome**

Seeds were deposited singly under the two following conditions: with the elaisosome intact or without the elaisosome. The time elapsed until an ant found — not necessarily retrieving — the seed was noted. A one-way ANOVA was performed on the normalized (log-transformed) data. All statistics are based on the book by Sokal & Rohlf (1995) and were run under Statistica 4.5 (Statsoft).

**RESULTS**

Data from both study days did not differ (Mann-Whitney U test; $z_{adj} = 0.03$; $p = 0.96$; two-tailed) and were subsequently considered together. For time retention values of less than 30 minutes, there was no difference between data from years 1994 and 1996 nor for retention times for noise and control treatments for 1996 data (Table 1). In addition, distribution of times for both treatments were not different (Kolmogorov-Smirnov test, D=0.16; $p>0.05$; Fig. 1). Mean retention time for 1996 was 6.2 minutes (s.e.=0.57) for both treatments (n=145). The two treatments did not affect the particular ant species that retrieved the seed (Table 2). The time distributions were similar for each species (Kruskal-Wallis $H_{(3,141)}$ =1.51, $p=0.67$); this suggests that the effect of a falling seed does not bias ant behaviour in the sense that it does not affect one species more than another.

The presence of the elaisosome does not affect the time before a seed is found by an ant (one-way ANOVA, $F_{1,108} = 0.0001$, $P = 0.98$). For scores <30 minutes, mean (s.d.; n) is 5.07 minutes (5.90; n=60) for seeds with elaisosome and 5.45 (6.07; n=50) for seeds without elaisosome. The
Table 1. Number of seeds of Euphorbia characias recovered by four ant species and time of response (minutes) under two treatments. Noise: seed falling from a height between 1.1 and 1.5 m; control: seed carefully deposited on top of soil. G = 2.54; p = 0.46, from log-likelihood G-test, for goodness of fit of noise values to control values. Data do not add up to 145 as in table 2 (1996) since in three cases the species could not be noted.

<table>
<thead>
<tr>
<th></th>
<th>Control</th>
<th>Noise</th>
<th>Time</th>
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</thead>
<tbody>
<tr>
<td>Pheidole</td>
<td>24</td>
<td>30</td>
<td>6.9</td>
</tr>
<tr>
<td>Tapinoma</td>
<td>25</td>
<td>27</td>
<td>5.9</td>
</tr>
<tr>
<td>Messor</td>
<td>4</td>
<td>3</td>
<td>4.7</td>
</tr>
<tr>
<td>Aphaenogaster</td>
<td>17</td>
<td>11</td>
<td>6.5</td>
</tr>
<tr>
<td>Totals</td>
<td>70</td>
<td>71</td>
<td></td>
</tr>
</tbody>
</table>

frequency of scores >30 minutes was: 8 for seeds with elaiosome, 6 for seeds without elaiosome.

DISCUSSION

Under the precise conditions of this study granivorous ants reacted in similar ways as omnivorous or nectarivorous species to falling seeds or seeds deposited on top of the soil. Ants do not seem to have special perceptual abilities concerning detection of hurled seeds. The time a seed remains on top of soil before being found and retrieved by an ant is not affected by the impact and/or lateral displacement when it falls or is ejected from the parent plant. This pattern contrasts with that observed by Pacini (1990) for hurled seeds of Mercurialis annua. Its seeds were collected by Messor structor usually in a few seconds. Elaiosome components of M. annua seem not to be responsible for this sharp response since its gross biochemical composition is similar to those from other species, Euphorbia spec. included (Lisci et al. 1996). Particular soils may have differing capacities in transmitting vibrations.

Both the sound and the movements are ephemeral. Sound or any

Table 2. Retention times (minutes) from seed depot on top of soil until an ant retrieves the seed. Data for two years were not different (Mann-Whitney U test; Zadj = 0.29; p = 0.77; two-tailed). Data for noise and control treatment were also similar (Mann-Whitney U test; Zadj = 1.56; p = 0.22; one tailed). For retention time distribution in 1996 see Fig. 1.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>s.e.</th>
<th>median</th>
<th>lower-upper %</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>control</td>
<td>7.08</td>
<td>0.86</td>
<td>3.71</td>
<td>1.43-11.96</td>
</tr>
<tr>
<td>1996</td>
<td>noise</td>
<td>5.31</td>
<td>0.71</td>
<td>3.20</td>
<td>1.15-6.60</td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>7.25</td>
<td>0.88</td>
<td>4.45</td>
<td>1.50-10.68</td>
</tr>
</tbody>
</table>
vibration produced by a falling seed could, in principle, alert ants that occurred near the falling point, but the seed remains still in a few seconds or instantly. Ants are sensitive to moving objects: activity of one species may be perceived by another species (Reznikova 1982; Savolainen 1991) and at Collserola we have shown that some species can detect other ants carrying a seed and rob them (Espadaler et al. 1996) but in the absence of volatile chemical attractants, the seed becomes an immobile object, one of the many that ants can find during foraging. The single instance in which sound or movement of the seed could affect retention time would be that rare event of a seed falling next to a foraging ant. Even in that case, the plant can not choose the identity of the ant, that can be of a true myrmecochorous species (*Tapinoma, Aphaenogaster, Pheidole*) or belong to a granivorous species (*Messor*) (Espadaler & Gómez 1996). There is but a single report (Slingsby & Bond 1981) of elaiosomes attracting ants from a distance; those authors mention seeds of *Minetes* and *Leucospermum* that were rapidly retrieved by ants from 2m away. Apart from this example we do not know of other instances in which elaiosomes have been shown to be attractive from some distance. This is in sharp contrast to the many volatile compounds that occur on the seeds of ant-garden epiphytes in western Amazonia (Davidson et al. 1990). In fact, the reverse is the usual situation: ants must touch the elaiosome or the seed to be aware of its presence and, eventually, transport them to the nest (Kjellsson 1985). This is not
unexpected since biochemical studies of elaiosome composition report no evidence for the volatile transmission of attractants (Marshall et al. 1979) or identify substances with rather high molecular weight (Hughes et al. 1994) and, hence, with low or no volatility at all under field conditions. Maybe this is why, all things being equal, elaiosomes are not attractive from a distance: it would not make sense to produce — at a cost — substances in the elaiosome that can attract ants, since they could also be predators of the seed. Elaiosomes are best interpreted as an adaptation to induce nongranivorous ants to transport the seeds to the nest.

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