SEED-ROBBING BETWEEN ANT SPECIES INTERVENES IN THE MYRMECOCHORY OF *EUPHORBIA CHARACIAS* (EUPHORBIACEAE)

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ABSTRACT

A case of interference competition in which some ant species (*Messor barbarus* and *Aphaenogaster senilis*) rob seeds of *Euphorbia characias* from other ants (especially *Tapinoma nigerrimum*) is reported. Seed robbing is here regarded as a possible natural impediment to myrmecochory as it may interfere with the seedling recruitment process of the myrmecochorous plant.

INTRODUCTION

Interference competition is a rather frequent phenomenon in ant communities (Hölldobler and Wilson, 1990) and may involve territorial guarding (Hölldobler and Lumsden, 1980), the use of chemical deterrents (Adams and Traniello, 1981), threat displays (Hölldobler, 1981), physical fighting (Hölldobler, 1979) and nest-plugging (Möglich and Alpert, 1979; Gordon, 1988). Interspecific prey robbing, as defined by Hölldobler (1986), is a spectacular form of competition in which the robber ant takes the food from the grasp of a foraging ant of another species. Though the success rate of prey robbing may be as high as 25.5% (Hölldobler, 1986), eventual positive or negative ecological and reproductive effects on both parties have not been evaluated. Intraspecific intercolonial prey robbing has been recently described (Breed, Abel, Bleuze, and Denton, 1990; Yamaguchi, 1995). Though not strictly similar, a case of indirect seed scavenging involving granivorous ants is reported by Lévieux (1979) in African dry savannas: *Brachyponera senaarensis* takes seeds from external middens of *Messor galla* and *Messor regalis*. This case could be regarded as an evolutionary step towards the robbing of individual ants.

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In this paper we report a case of direct interference competition, in which ants rob another ant species of the seeds of a myrmecochorous plant (*Euphorbia characias*). Myrmecochorous plants have seeds with an oily aril called an elaiosome. Ants that are attracted to the elaiosome feed on it and discard the seeds inside their nests or in nearby middens, where they may germinate. This results in the seeds being dispersed to sites that may offer better conditions for germination and growth (Beattie, 1985). Nothing is known of the relative importance of *Euphorbia* seeds in the diet of granivorous ants. The elaiosome is rich in lipids (Bresinsky, 1963) and may be an important source of nutrition for the growing larvae of robber species. Further work is needed to understand variation in the response of ants to the elaiosomes. Seed robbing may also have consequences for *E. characias*.

Methods

Observations were made during a long-term study on the dispersal ecology of west Mediterranean *Euphorbia* species, conducted in an herbaceous community of Inulo-Oryzopsietum miliaceae (Bolós, 1962) at the Collserola Park, an ecological preserve near Barcelona, NE Spain (2°6'E, 41°25'N; elevation: 315 m) during the summers of 1993 (July) and 1994 (June). The site is on an east-facing slope; the climate is Mediterranean, with 620 mm of annual rainfall. Mean monthly temperatures are highest in August (average 22.6°C) and lowest in January (7.1°C) (data from 1914–1991). The site is a clearing bordered by a mixed wood of *Pinus pinea*, *Pinus halepensis*, and *Quercus ilex* with a developed underwood of *Rhamnus alaternus*, *Rosa* sp., *Pistacia lentiscus*, *Hedera helix*, *Ruscus aculeatus*, and *Smilax aspera*. All observations were made in a field that has been abandoned for 13 years, with a slope of 15° and an area of 1800 m^2. The dehiscence period of *Euphorbia characias* at Collserola lasts for four weeks, and depending on the year, from mid May to the end of June. The plants scatter seeds singly throughout the day and the seeds do not release recruitment behavior by ants.

Seed retrieval was assessed from 8:30 a.m. to 19:30 p.m. as follows. A single seed was put at each corner of a square of 7 cm and the time elapsed between deposition and retrieval of the seed by an ant was recorded. The ant species initially finding the seed was

noted and followed when possible to the nest. Each sampling point was designated by changing randomly among six compass directions and with a random distance from one to six meters from the previous point. During seed retrieval some robbing by other ant species took place. Seed robbing can also occur during the manipulation time (MT) that occurs after an ant has found a seed for the first time and before it carries the seed away.We hypothesized that longer MT would result in more robbing. During separate trials and for each species, 40 manipulation times on individually offered seeds were measured with a stop watch.

RESULTS

A total of 285 seeds were offered individually. Four ant species retrieved seeds. *Tapinoma nigerrimum* (worker size: 2.5-5.1 mm; polymorphic) and *Pheidole pallidula* (size: 2.2–4.5 mm; dimorphic) were the two most abundant, retrieving 26.3% and 30.5% respectively. The nests of both species appear to act as safe-sites for *E. characias* seeds because seedlings appear there. *Aphaenogaster senilis* (size: 6.4–7.7 mm; monomorphic) took 23.8% of the seeds and deposits them outside of the nest in an external midden after elaiosome removal. *Messor barbarus* (size: 3-12 mm; polymorphic) took 19.3% of the seeds. This ant is granivorous and thus seeds are lost for plant recruitment. An analysis of *M. barbarus* middens from 9 nests yield 2 intact seeds and 185 empty seeds, proving that this ant consumes the seed as well as the elaiosome.

The percentage of seeds robbed did not differ between the two years of the study (Wilcoxon matched pairs signed ranks test, $z=1.6$; $p=0.1$). *Tapinoma nigerrimum* and *Pheidole pallidula* are the most frequent victims of seed robbing (Table 1). *Messor* ants are never robbed because they carry seeds high above the soil. Likewise, *A. senilis* holds the seeds in a similar position, above the level of the antennae of *Pheidole* or *Tapinoma*. In contrast, seeds transported by *Pheidole* or *Tapinoma* are readily detectable by *Messor* or *A. senilis*. Seed transport by *P. pallidula* is variable: sometimes it drags the seed, sometimes it carries the seed as in *Messor* or *A. senilis*. It is robbed both by *Messor* or *A. senilis* but defends the seed by leaving it and attacking the raider, which may allow other workers in the vicinity to rob the unprotected seed. *A. senilis* may even try to rob seeds when a *Pheidole* forager is near

Table 1. Seed robbing in ants retrieving myrmecochorous seeds of *Euphorbia characias* at Collserola, NE Spain. Indicated is the species initially getting the seed and the species finally taking the seed to the next. A. July 1993. B. June 1994. M: *Messor barbarus*; A: *Aphaenogaster senilis*. P: *Pheidole pallidula*. T: *Tapinoma nigerrimum*.

A		Final				
Initial	M	A	P	T	Total	% robbing
M	20	–	–	–	20	0
A	–	54	1	–	55	1.8
P	–	5	22	–	27	18.5
T	4	14	3	18	39	53.8
B		Final				
Initial	M	A	P	T	Total	% robbing
M	35	–	–	–	35	0
A	–	13	–	–	13	0
P	3	–	57	–	60	5
T	2	5	1	28	36	22.2

its nest entrance: the first try is usually fruitless, but in the second opportunity the movements of the robber ant are very precise, agile, and sometimes successful. If *Pheidole* continues its attack, *A. senilis* sets the seed aside, frees itself from the small *Pheidole*, and picks up the seed again.

Tapinoma always drags the seed. It has a small mandibular gap and usually has much difficulty carrying seeds. It often loses the seed but may find it again. It is frequently robbed by all of the other species. When a robbery is attempted, *Tapinoma* workers leave the seed and try to attack the intruder but its attack is frantic, making rapid, rather undirected turns. Encounters between individuals of different species seem to be haphazard and robbed species do nothing to avoid encounters with the robber species. Seed robbing consists entirely of encounters between two ants, the robber and the victim. Cooperative behavior, such as recruitment, does not occur in either of the participating ant species. Robbing may occur both during the manipulation process or during the transport

and either early in the morning or in the afternoon. This bimodal distribution of time of robbing reflects the daily bimodal activity rhythm of *Messor*, *Aphaenogaster*, *Pheidole*, and *Tapinoma*.

Manipulation time

The length of manipulation times differs between species (one-way ANOVA on log transformed data: $F(3,156)=3.9$; $p=0.009$) but the only statistically significant difference is between *Tapinoma* and *Pheidole* (post-hoc Scheffé test, $p=0.03$). All other combination pairs are not distinct. Manipulation time is not related to body size or to the frequency of being robbed.

Discussion

Many factors can affect the number and rates of robbing events. In 1994 the level of robbing (7.6%) was lower than in 1993 (19.1%). Combining data for both years reveals that 33.3% of seeds collected by *Tapinoma nigerrimum* are robbed. Of these robbed seeds, 25/29 were taken by *Aphaenogaster* or *Messor*, ants that substantially reduce the probability of seed survival. Because the attraction response to seeds is a generalized one released by key substances (Brew, O'Dowd, and Rae, 1989), it is difficult to imagine any strategy whereby the plant could target seed attractiveness towards ant species that promote seed survival by depositing seeds within the nest.

Robbing ants are an integral part of a guild of species very common in west Mediterranean open biotopes. The group of *Pheidole*, *Messor*, *Tapinoma*, and *Aphaenogaster* (s.str.) has been found elsewhere by Baroni Urbani, 1968 (Malta); Rodríguez and Fernández, 1983 (S. Spain); Cagniant, 1973 (Algeria), 1988 (Morocco); Casevitz-Weulersse, 1989 (Corsica). Zorrilla, Serrano, Casado, Acosta and Pineda, (1986) report this group of ants from therophytic pastures in central Spain with different degrees of disturbance. Seed robbing is very probably a widespread phenomenon.

Davidson and Morton (1981) suggest some Australian ant species may be parasites of the interaction between ants and chenopods. A more extreme case of disruption of myrmecochory involving the invasive Argentine ant and Proteaceae in Cape Fynbos

is reported by Bond and Slingsby (1984). At our site the level of disruption is apparently not so important as in the systems mentioned above. Moreover, since there is no reason to suspect that the relationship between disperser ants and robber ants is recent, plant populations are unlikely to be threatened by the toll imposed by robber ants. Myrmecochorous *Euphorbia characias* faces both beneficial and detrimental ants and it is a matter of chance which particular species finds its seeds. This case of seed robbing may be regarded as a possible natural impediment to myrmecochory.

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