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ORIGINAL PAPER

Are subordinate ants the best seed dispersers? Linking dominance hierarchies and seed dispersal ability in myrmecochory interactions

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Abstract True myrmecochory involves the dispersal of elaiosome-bearing seeds by ants. Between the guild of ants that are attracted to these seeds, only a few of them will act as effective dispersers, that is, transporting the seeds to suitable sites (the nests) for germination and plant establishment. Ant communities are known to be highly hierarchical, and subordinate ants quickly deliver resources to their nest rather than consuming it on-site, thereby avoiding encounters with more dominant species. As a result of a series of studies that were carried out during summer in semi-arid Northwest Argentina, we have found that the most important seed disperser of the myrmecochorous plant *Jatropha excisa* Griseb. (Euphorbiaceae), the ant *Pogonomyrmex cunicularius pencosensis* Forel, was the most subordinate species during interspecific interactions. The daily timing of release of the *J. excisa* seeds through ballistic dispersal increased their probability of being removed by the highly thermophilic *P. cunicularius pencosensis*. Foraging during the warmest hours of the day allowed *P. cunicularius pencosensis* ants to avoid the risk of interference competition with dominant species, which also behaved as elaiosome predators. As a conclusion, subordinance behaviour appears to be integral to successful myrmecochory, and also the timing of seed release plays a key role in shaping the dynamics of myrmecochorous interactions. Therefore, ant-dispersed plants should not only favour their discovery by subordinate ants, but also should present their seeds at those times of the day when the behaviourally dominant ants are less active.

Keywords Behavioural hierarchies · *Pogonomyrmex* · Myrmecochory · Seed dispersal · Thermophilia

Introduction

In ant communities, interference competition occurs when a species excludes the others from a limiting resource by using repellents or overt aggression (Wilson 1971; Fellers 1987; Hölldobler and Wilson 1990; Davidson 1998). A direct observation of interference competition is easy to observe in the field when a highly nutritive food resource such as canned tuna is placed on the ground. Among the several ant species attracted by the food, a hierarchy of dominance arises as a result from the competition for the bait control. The ant species behaving as dominant will outcompete the more subordinate species by means of stings, bits or chemical secretions, causing in some cases even their death but most generally their retreat from the bait (Fellers 1987; Savolainen and Vepsäläinen 1988).

Temporal segregation in foraging activity is a mechanism allowing coexistence between competing species and has been well documented in ants (e.g. Bernstein 1974; Fellers 1989; Vepsäläinen and Savolainen 1990; Albrecht and Gotelli 2001). In desert communities, it has been shown that, by means of their thermophilia, subordinate ant species have almost exclusive access to resources during the warmest part of the day, because dominant species delay their foraging activity until more moderate

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temperatures are available (Cerdá et al. 1997, 1998a, b; Retana and Cerdá 2000; Bestelmeyer 2000).

A behaviour feature reported for subordinate ant species is that they rapidly retrieve food to their nest after discovering a food source, thereby avoiding encounters with behaviourally dominant species (Fellers 1987). On the other hand, true myrmecochory, the dispersal of elaiosome-bearing seeds by ants, is successful when seeds are taken to the nest. After consuming the elaiosome (a lipid-rich appendage), seeds are discarded inside or near their nests, which represent particular microenvironments where germination and plant establishment should be favoured (Beattie 1985; Hanzawa et al. 1988). Therefore, deferring the elaiosome consumption until arriving to the nest should be a necessary condition for an effective dispersal.

The elaiosome acts as a reward for the dispersal process (Marshall et al. 1979; Lanza et al. 1992), and this reward is of a non-selective nature (Garrido et al. 2002). As a result, myrmecochorous seeds attract many ant species simultaneously, but in fact only a few of them, often in the order of one or two, will act as high-quality dispersers, transporting the seed and discarding it undamaged inside the nest (Giladi 2006; Ness et al. 2009; Manzaneda and Rey 2009). As a generality, the majority of the ant species will consume the elaiosome without transporting the seed, acting as elaiosome predators and without providing a dispersal service to the plant. Others will transport the seeds, but then drop the seed on the ground, eat the seed or transport it to unsuitable places for germination (e.g. deep nest chambers and ant nest mounds), therefore acting as low-quality dispersers. The high-quality disperser ants have also been described as keystone dispersers, as they play a disproportionate role in the dispersal process (Gove et al. 2007). Therefore, the question that arises is which plant traits will be favoured so that the high-quality disperser ants collect the seeds before the low-quality dispersers or the elaiosome predator ants do it.

In this study, we propose that, in desert environments, myrmecochorous plants will synchronize the release of their seeds with the peak of activity of their high-quality disperser ants. These high-quality disperser ants will be behaviourally subordinate species and will forage at the warmest temperatures of the day in order to avoid encounters with the dominant, heat-intolerant species. In turn, dominant species should act as elaiosome predators or low-quality disperser ants. Whereas many studies have shown a correlation at both seasonal and daily scales between the timing of seed release and the peak activity of seed disperser ants (e.g. Thompson 1981; Oberrath and Böhning-Gaese 2002; Turnbull and Culver 1983; Ohkawara et al. 1997), and some authors have suggested a relationship between behavioural subordinance and dispersal ability (Ohkawara et al. 1996; Giladi 2006; Gove et al. 2007), this is the first attempt to link empirically ant behavioural hierarchies with myrmecochory.

We focused our study on the myrmecochorous plant *Jatropha excisa* Griseb (Euphorbiaceae), a native shrub of semi-arid Northwest Argentina. In a previous study, we have demonstrated that the ant species *Pogonomyrmex cunicularius pencosensis* Forel (Myrmicinae) dominated the removal of the *J. excisa* elaiosome-bearing seeds in the study area (Aranda-Rickert and Fracchia 2011). Nest feeding with marked *J. excisa* seeds also revealed that after consuming their elaiosome in the brood chambers, seeds are left undamaged inside the nests at an appropriate depth for emergence (Aranda-Rickert and Fracchia 2011). Based on this, we set up the following hypothesis: (1) there is a negative relationship between the rank in the behavioural hierarchy and the removal ability of the ant species that are attracted to the *J. excisa* seeds, (2) there is a positive relationship between the rank in the behavioural hierarchy and the elaiosome predator ability of the ant species that are attracted to the *J. excisa* seeds. Additionally, we investigated whether there is some pattern of synchrony between the daily rhythm of *J. excisa* seed release and the daily rhythm of activity of the guild of ants attracted to their seeds.

Materials and methods

Study site

Field work was carried out at three undisturbed sites near Anillaco, La Rioja province, Northwest Argentina (28°54′S 66°39′W). Landscape features are foothills, valleys and bolson landforms, and vegetation consists of an open shrubland dominated by *Larrea cuneifolia* Cav. (Zygophyllaceae). Climate is semi-arid to arid, showing a marked seasonally and daily rhythm. Mean annual temperature is 16.6°C (average range, 37.2–4.9°C), and annual rainfall ranges from 145 to 380 mm, almost exclusively limited to the summer months (from December to March) (Anillaco Meteorological Station, data from 1999 to 2008). During the summer, ground insolation is high, and soil surface temperatures may reach more than 60°C (this study). Soils are typically low in organic matter and nutrients, particularly phosphorous and nitrogen (Abraham et al. 2009), and the watercourses are intermittent or ephemeral.

Myrmecochorous plant species

We centred our study on the myrmecochorous plant species *Jatropha excisa* Griseb. (Euphorbiaceae), an obligate seeding shrub endemic to Northwest Argentina and Bolivia (Lourteig and O'Donnell 1943). This species have a diplochorous dispersal system, shedding their seeds by explosive dispersal in a first step and being subsequently dispersed by ants in a second step (Aranda-Rickert and Fracchia 2010). Although the seeds of *J. excisa* have a considerably greater seed mass than other myrmecochorous seeds (mean ± SD = 60.7 ± 11.8 mg), previous experiments have shown that ants are readily attracted by their conspicuous elaiosome (mean mass ± SD = 2.32 ± 0.53 mg; Aranda-Rickert and Fracchia 2010).

Experimental design

The study was conducted at three sites located within the study region described above. Each site was at least 10 km from the nearest to it, covering a total area of 240 km^2. Sites were selected in order to maximize the homogeneity in terms of exposure to the sun, soil texture, percentage of ground cover, plant community composition, slope and elevation, all features that potentially influence ant community organization. Within each site, three replicate 100-m transects, placed at least 2 km from roads and separated by at least 100 m, were randomly established. Transects consisted of 10 points (10-m spacing), each point representing a sampling unit (30 points per site). All trials were conducted during January–February 2010, on days representative of this time of the year and coinciding with the seed release period of the natural populations of *J. excisa* as well with the peak ant foraging activity (Aranda-Rickert and Fracchia 2011).

Behavioural interactions and ant daily rhythm of activity

Ant daily rhythm of activity was assessed by tuna baiting. Baits were white cardboard cards (7 cm square) with a teaspoon (c. 3 g) of canned oil tuna. We used tuna in order to describe only those ant species that collect or are attracted to elaiosome-bearing seeds (e.g. Heithaus and Humes 2003; Ness and Morin 2008). Tuna baits were placed at each point of transects (30 points per site) and were observed at six consecutive periods within a day. Based on temperature periods among which different ant species could segregate their activity, baiting sessions were performed at early morning (08:00–09:00 h), morning (10:00–11:00 h), midday (12:00–13:00 h), early afternoon (15:00–16 00 h), afternoon (17:00–18:00 h) and late afternoon (19:00–20:00 h). During each census, the soil temperature adjacent to each bait was measured using a T-shaped digital thermometer inserted 1 cm into the soil. Before each hourly session, baits were replenished and moved approximately 2 m from their initial position to allow their independent discovering. During each session, 5 min after bait placement and every 15 min, two researchers recorded the ant species and the number of individuals per species feeding at each bait, along with any behavioural interaction between workers of different species. Species and interactions were recorded only if individuals were on the bait itself. Species occurrence was scored only once during each 60-min session, irrespective of how many times the species was recorded at the same bait. In total, our study was based on 90 baits and 2,700 observations (3 sites × 30 baits × 6 sessions × 5 observations). Ants observed in each bait station were transferred to 70% alcohol and identified using the methods described by Kusnezov (1978), Fernández (2003) and Cuezzo and Claver (2009).

Behavioural dominance relationships were based on the observed pairwise interactions between workers of different species at the baits, which were categorized as attacks, retreats or coexistence (modified from Fellers 1987). An attack occurred when an individual of one species bit, sting or use chemical spray to cause the individual of the other species to retreat from the bait. A retreat occurred when one species left the bait station because of the threat, attack or solely the presence of another species. Based on this, a species was characterized as behaviourally dominant when it attacks or elicits avoidance behaviour of another species. The dominance index for each species was calculated as the percentage of all the observed pairwise interactions in which that species behaved as dominant (Fellers 1987). For each observation at a bait station, only the first interaction observed between species during the first 20 s was scored.

Seed removal

Seed removal experiments were conducted within 1 week of the tuna baiting sessions. Fresh *J. excisa* seeds were obtained from mature capsules collected at the local populations, stored at 4–5°C in paper bags and used within 3 days for the trials. At each site, and along the three 100-m transects used for tuna baiting, we placed seed depots every 10 m, each consisting of a 7 cm × 5 cm white card anchored with nails to the ground (30 depots per site). Five fresh *J. excisa* seeds were placed on each seed depot. Experiments were conducted at the same six time intervals as for the tuna baiting experiments (5 seeds × 30 depots × 3 sites × 6 sessions = 2,700 seeds). Five minutes after the seeds were deposited, two researchers observed each depot station for 2 min at 15-min intervals for up to 60 min (i.e. 5 times). During each observation, the ant species and number of individuals per species present on the card were recorded, and every removal event (defined as the active transport of a seed from the card) was noted. After 60 min, we counted the number of seeds removed from each depot and the number of stations where at least one worker of a given species was consuming the elaiosome in situ. A seed was considered removed when it was not found within a ratio of 50 cm of the seed depot. As it was previously demonstrated that *J. excisa* seeds are removed only by ants, it was not necessary to use vertebrate exclusion cages (Aranda-Rickert and Fracchia 2010). All ant species observed interacting with the seeds were collected, preserved and identified to species. Additionally, during each census, the soil temperature adjacent to each seed depot was measured as described for the tuna baiting trials.

Timing of seed dispersal

At each of the three study sites, 10 vigorous *J. excisa* plants, separated by at least 5 m, were selected. Between 15 and 20 ripe capsules were marked on each plant, and the number of closed fruits was counted on each plant every hour from 08:00 to 20:00 h and at 08:00 h the following day. When a capsule dehisces, it splits longitudinally into three valves and the walls of each valve squeeze together to ballistically eject the seeds. Those capsules that were not found between two consecutive censuses were considered to have dispersed their seeds. During each census, the shade temperature beside one of the observed plants was measured. The rate of explosion was observed on three consecutive sunny dry days. The capsules that remained undispersed in the last census of any day were examined the next morning (08:00 h) to check whether any seeds had scattered during the night.

Data analysis

Ant species occurrence at baits was used as a measure of ant activity and was calculated as the proportion of baits ($N = 180$, 6 sessions × 30 baits) where at least one worker of each species was observed exploiting the food. Differences in the occurrence of each ant species among sites was calculated using a two-way ANOVA on arcsine-square-root-transformed data, with sites and species as factors. Ant species daily activity rhythm was calculated as the number of baits where the species occurred during each session, relative to the total number of occurrences across the six time intervals. Seed removal daily activity rhythm was calculated as the number of seeds removed during each session, relative to the total number of removals across the six time intervals. The rate of carpel opening was calculated as the number of carpels that opened out between two consecutives censuses relative to the number of carpels that opened out throughout the 24-h survey.

The behavioural dominance index for each species was estimated by pooling species interactions from all sites at all baiting sessions and was calculated as the percentage of all the observed pairwise interactions in which that species behaved as dominant. This index was calculated only for those species involved in more than five interactions.

The removal ability was estimated as the percentage of seed removal events observed for each species relative to the total number of removal events observed during all sessions. The elaiosome predator ability was estimated as the percentage of baits occupied by each species consuming the elaiosome in situ at the end of each 60-min session, relative to the total number of baits occupied by predator species during all sessions. The relationships between the removal ability and the elaiosome predator ability, and the dominance index of each species were analysed with nonparametric Spearman's correlations.

The effect of the session of the day on the daily rhythm of carpel dehiscence, the ant species daily activity rhythm and the seed removal daily activity rhythm were analysed by means of three separate analyses using generalized linear mixed models (GLMMs) assuming binomial error distributions and logit link. When the response variable was the dehiscence rhythm, the days ($n = 3$) and the sites ($n = 3$) were treated as random factors, with days nested within sites. When the response variable was the ant activity rhythm and the seed removal rhythm, transects ($n = 3$) and sites ($n = 3$) were treated as random factors, with transects nested within sites. We again employed GLMMs with binomial distribution and logit link to analyse the relationship between *P. cunicularius* and *Camponotus mus* daily rhythm of activity, and the daily rhythm of seed removal.

The GLMMs were fit using the Laplace approximation, and the model selection was based on the Akaike information criterion (AIC). The statistical analyses were performed using the 'R' program (R Development Core Team 2005) and the STATISTICA 7 software package (Statsoft, Tulsa, OK, USA).

Results

Ant daily rhythm of activity

Overall, 15 ant species were recorded foraging at tuna baits during the study (Table 1). The Formicinae *Camponotus mus* Roger and the Myrmicinae *P. cunicularius pencosensis* Forel were the most common ant species recorded at baits. Other frequent species were the Dolichoderinae *Forelius chalybaeus* Emery and *F. nigriventris* Forel, and the Myrmicinae *Pheidole bergi* Mayr.

Total species occurrence at baits differed among the different sessions of the day and showed the typical bimodal pattern of desert environments, with peaks in the morning and in the afternoon and a marked decrease at midday (Fig. 1). *Pogonomyrmex cunicularius pencosensis* was highly thermophilic, with no presence at baits at all during the early morning and the late afternoon sessions

Table 1 Occurrence of the ant species observed feeding at tuna baits during summer in Northwest Argentina

Species (Subfamily)	Occurrence (no. of occupied baits)			
	Site 1	Site 2	Site 3	Total
Camponotus blandus Smith F. (Formicinae)	0.03 (6)	0.06 (12)	0.07 (14)	0.059 (32)
Camponotus mus Roger (Formicinae)	0.52 (95)	0.43 (78)	0.46 (83)	0.47 (256)
Crematogaster quadriformis Roger (Myrmicinae)	0.06 (12)	0.05 (9)	0.05 (9)	0.055 (30)
Dorymyrmex ensifer Forel (Dolichoderinae)	0.01 (2)	0.005 (1)	0.05 (9)	0.022 (12)
Dorymyrmex exsanguis Forel (Dolichoderinae)	0.05 (10)	0.05 (10)	3 (0.016)	0.042 (23)
Dorymyrmex sp.1 (Dolichoderinae)	0.01 (2)	0.005 (1)	0.027 (5)	0.015 (8)
Dorymyrmex sp.2 (Dolichoderinae)	0.005 (1)	0	0.022 (4)	0.009 (5)
Forelius albiventris Forel (Dolichoderinae)	0.08 (15)	0.09 (17)	0.11 (20)	0.096 (52)
Forelius chalybaeus Emery (Dolichoderinae)	0.26 (48)	0.18 (33)	0.27 (49)	0.24 (130)
Forelius nigriventris Forel (Dolichoderinae)	0.11 (20)	0.08 (15)	0.16 (29)	0.118 (64)
Pheidole bergi Mayr (Myrmicinae)	0.14 (25)	0.12 (22)	0.08 (15)	0.11 (62)
Pheidole spininodis Mayr (Myrmicinae)	0.03 (6)	0.03 (6)	0.06 (12)	0.044 (24)
Pogonomyrmex cunicularius pencosensis Forel (Myrmicinae)	0.4 (72)	0.37 (68)	0.32 (58)	0.36 (198)
Pseudomyrmex denticollis Emery (Pseudomyrmecinae)	0.1 (18)	0.18 (33)	0.04 (8)	0.109 (59)
Solenopsis sp1 (Myrmicinae)	0.08 (15)	0.05 (9)	0.04 (8)	0.059 (32)

Occurrence is the proportion of baits occupied by each species along six consecutive sessions ($N = 180$ per site), from 08:00 to 20:00 h. Total occurrence is computed on pooled values for the three sites ($N = 540$)

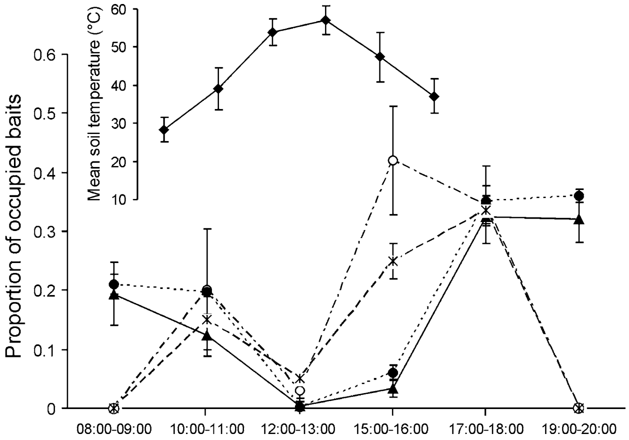

Fig. 1 Ant species daily activity rhythm during summer in semi-arid Northwest Argentina. Foraging activity was calculated as the proportion of baits occupied at each time interval session relative to the total number of baits occupied throughout the day. Data are given as means ± SE ($n = 3$ sites, $N = 90$ baits per time interval) and are shown for *Pogonomyrmex cunicularius pencosensis* (*empty circles*), *Camponotus mus* (*filled triangles*), *Forelius nigriventris* (*crosses*) and the other ant species combined (*Pheidole*, *Dorymyrmex*, *Crematogaster*, *Solenopsis, Pseudomyrmex* spp., *Forelius albiventris* and *F. chalybaeus*) (*filled circles*). The inserted graph shows the mean soil temperature adjacent to the bait stations (±SD, $n = 3$ sites, $N = 90$ baits per time interval) for the same time intervals

and a peak of activity during the afternoon sessions (GLMM, coeff. = 1.15, SE = 0.34, $z = 3.32$, $P < 0.001$). No significant differences were found between the early afternoon and the afternoon sessions ($P = 0.391$), whereas during midday occurrence was low but not null.

On the other hand, *Camponotus mus* showed a low degree of thermophilia, avoiding the warmest hours of the day. This species was registered during midday and early afternoon only at those baits under the shadow of a shrub. In contrast, they were significantly more active in the afternoon and late afternoon sessions (GLMM, coeff. = 0.87, SE = 0.26, $z = 3.42$, $P < 0.001$), with no significant differences between both sessions ($P = 0.65$).

The other ant species (*Pheidole*, *Dorymyrmex*, *Crematogaster*, *Solenopsis, Pseudomyrmex* spp., *Forelius albiventris* and *F. chalybaeus*) were significantly more active at moderate temperatures, during the early morning and morning sessions (GLMM, coeff. = 1.03, SE = 0.36, $z = 4.42$, $P < 0.001$), and again during the afternoon and late afternoon sessions (GLMM, coeff. = 2.43, SE = 0.45, $z = 5.22$, $P < 0.001$). *Forelius nigriventris* was the only ant species other than *P. cunicularius pencosensis* that was observed at baits during the early afternoon sessions.

In addition, the three GLMM analyses showed that neither the sites nor the nested factor transects had significant effects in the model ($P > 0.1$).

Behavioural dominance

From the 15 ant species recorded at tuna baits, we considered for the behavioural analysis only eight species (Table 2), whereas those involved in less than five interactions were excluded. Because sites had no significant effect on each species occurrence (two-way ANOVA test on arcsine-square-root-transformed data, $F = 0.22, df = 3, P = 0.79$),

Table 2 Behavioural dominance index for the ant species attracted to tuna baits during summer in Northwest Argentina

Ant species	No. of observed interactions	Dominance index	Min–max no. of workers per bait
Camponotus blandus	15	80	1–3
Camponotus mus	348	97.12	1–7
Forelius chalybaeus	126	66.6	5–50
Forelius nigriventris	57	64.91	4–32
Pheidole bergi	112	51.78	5–15
Pheidole spininodis	12	41.8	1–21
Pogonomyrmex cunicularius pencosensis	325	1.84	1–20
Pseudomyrmex denticollis	51	11.76	1–3

The dominance index is the percentage of interactions won by each ant species ($N = 1{,}046$ interactions)

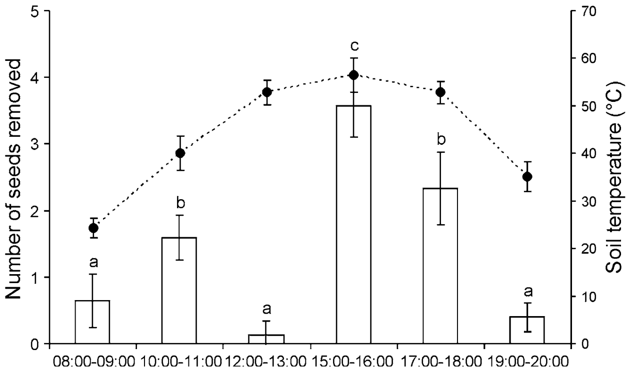

Fig. 2 Mean number of *J. excisa* seeds removed by ants across six time intervals during summer in Northwest Argentina. *Bars* represent means ± SE from $N = 5$ seeds per depot, and values are pooled from three sites ($N = 90$ seed depots per time interval). *Different letters* indicate significant differences ($P < 0.05$). The mean soil temperature adjacent to the seed depots (±SD, $n = 3$ sites, $N = 90$ baits per time interval) is given in the secondary *y* axis

the behavioural interaction data were pooled for the three sites. Overall, a total of 1,101 interactions involving the eight species were observed. Interactions in the form of aggression or avoidance were the most frequent (95%), whereas neutral interactions (coexistence) made up 5% of the records. The most common form of aggressive behaviour was physical attack in the form of biting. In the case of the attack of small ants with mass recruitment such as *F. chalybaeus* against large ants like *P. cunicularius pencosensis*, these ants climbed over the body of the other species making quick bites mainly on the antennae and legs.

Table 2 summarizes the outcome of the observed interactions for the ant species considered in the analysis. *Pogonomyrmex cunicularius pencosensis* was the most subordinate species, followed by *Pseudomyrmex denticollis*. The most dominant ant species was *C. mus*, followed by *C. blandus*. Both are large ants (up to 13 mm), which caused the other species to retreat from baits by means of biting. *Forelius chalybaeus*, *F. nigriventris* and *P. bergi* showed intermediate dominance indexes. In five occasions, *C. mus* ants caused the death of several *F. chalybaeus* individuals while attacking baits that were first monopolized by this last species.

Seed removal

The number of seeds removed per depot was significantly affected by the session of the day (Fig. 2). More seeds were removed during the early afternoon session (GLMM, coeff. = 2.82, EE = 0.17, $z = 16.18$, $P < 0.001$), whereas lowest values were registered during the early morning, midday and late afternoon sessions, with no significant differences between them ($P > 0.5$). Morning sessions showed intermediate values, with no significant differences with the afternoon sessions ($P = 0.22$). Neither the sites nor the nested factor transects had significant effects ($P = 0.17$ and $P = 0.12$, respectively).

Pogonomyrmex cunicularius pencosensis ants removed the majority of the offered seeds (75.517% from a total of 617 dispersal events observed across all the time intervals). These removal events were mostly registered during the afternoon sessions (51.91% during the early afternoon and 32.78% during the afternoon), whereas during the morning the remaining 13.48% of the dispersal events were observed. On the other hand, *P. bergi* removed 21.43% of the offered seeds and *Ph. spininodis* an additional 3.06%. Both *Pheidole* species removed the seeds mostly during the early morning and morning sessions (63.73%) and, in a minor proportion, during the afternoon and late afternoon sessions (33.33%).

After the 60-min sessions, a total of 330 seed depots from 540 (61.1%) were occupied by species that predated the elaiosomes in situ without transporting the seeds. Pooling the data for all six sessions, the species more frequently observed consuming the elaiosome was *C. mus* (26.9% of 330), followed by *Forelius nigriventris* (22.02%), *F. chalybaeus* (19.64%) and *C. blandus* (17.26%). During midday and early afternoon, the only species observed predating the elaiosomes was *F. nigriventris.*

Timing of fruit dehiscence

The timing of daily dehiscence of *J. excisa* was observed on a total of 515 fruits at the three study sites. The session of the day significantly affected the proportion of capsules that opened throughout the day (Fig. 3). Most capsules (81.34%)

opened between 10:00 and 15:00 h (GLMM, coeff. = 1.11, SE = 0.25, $z = 4.36$, $P < 0.0001$), with no significant differences between the sessions within this time interval ($P > 0.05$). Later in the afternoon, the rate decreased progressively and approached zero during the night. Neither the sites nor the factor days had significant effects in the model ($P = 0.55$ and $P = 0.28$, respectively).

Relationship between dominance rank and removal ability

The dominance index of each species was not significantly correlated with their removal ability (Spearman's correlation, $r_s = -0.65$, $P = 0.078$, $n = 8$), but a significant and positive relationship was found between the dominance index and the elaiosome predator ability of the analysed species ($r_s = 0.83$, $P = 0.01$, $n = 8$; Fig. 4).

The GLMM result analysing the effect of daily activity rhythm of the most important seed remover, *P. cunicularius pencosensis*, and the most important elaiosome predator, *C. mus*, on the daily rhythm of seed removal showed that seed removal was significantly and positively correlated with *P. cunicularius* foraging activity (coeff. = 8.26, EE = 0.48, z = 17.05, $P < 0.001$; Fig. 5a). In contrast, seed removal was negatively correlated with *C. mus* daily activity rhythm (coeff. = −2.62, SE = 0.65, $z = -6.14$, $P < 0.01$; Fig. 5b), with a significant interaction term between both effects (coeff. = −9.28, EE = 2.13, $z = -4.35$, $P < 0.001$).

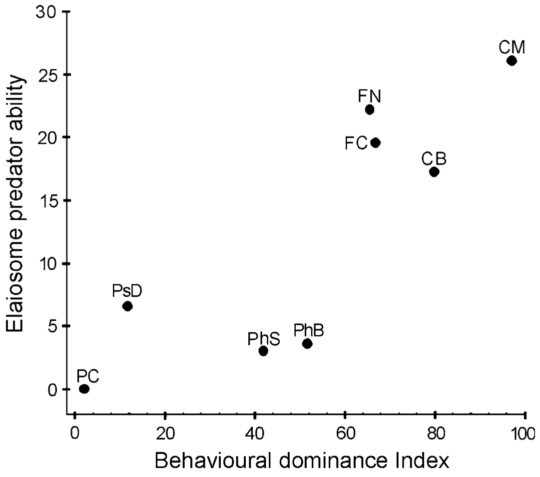

Fig. 4 Relationship between the behavioural dominance index and elaiosome predator ability for eight ant species in Northwest Argentina. The elaiosome predator ability is the percentage of seed baits occupied by each species consuming the elaiosome in situ ($N = 540$). Data are pooled from six sessions and three sites. PC, *Pogonomyrmex cunicularius pencosensis*; PB, *Pheidole bergi*; PS, *Ph. spininodis*; CM, *Camponotus mus*; CB, *C. blandus*; FC, *Forelius chalybaeus*; FN, *F. nigriventris*; PD, *Pseudomyrmex denticollis*

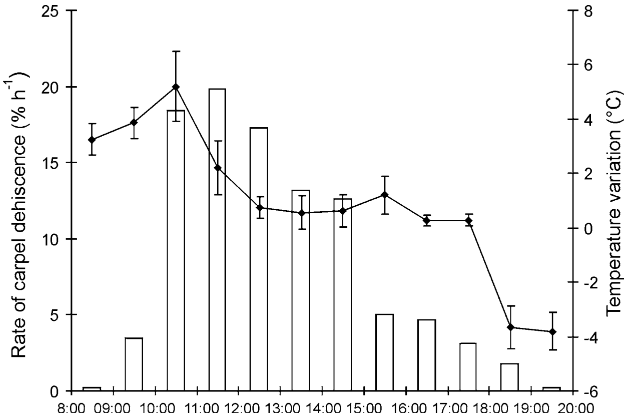

Fig. 3 Daily rate of carpel dehiscence of *Jatropha excisa* fruits during summer in Northwest Argentina. *Bars* represent the cumulative percentages ($N = 515$ fruits) of the fruits that opened at each time interval across three consecutive days. The *line* in the secondary *y* axis shows the average ambient temperature variation (±SD, $N = 9$) measured between two consecutive time intervals

Discussion

The outcomes of interspecific interactions are often conditioned on the abiotic and biotic contexts of the interaction and on the identities and behaviours of the participating species (Cushman and Beattie 1991; Bronstein 1994; Giladi 2006). It has been suggested that for myrmecochory, the identity of the ant partner should play a significant role in the ultimate fitness gained by the dispersed plant and that this type of mutualism should be described not as a diffuse mutualism but as an unevenly diffuse one, in which one or two species play a disproportionately important role in the dispersal process (Gove et al. 2007). These ant species, which have been referred as high-quality dispersers and keystone dispersers, share a number of physical and behavioural features that, altogether, determine that the dispersed seed should end undamaged and in an appropriate site for its germination and establishment as a plant (Rico-Gray and Oliveira 2007). The Australian *Rhytidoponera violaceae* Forel (Gove et al. 2007), the North American *Aphaenogaster rudis* Enzmann (Ness et al. 2009) and, in a recent study, *P. cunicularius pencosensis* in Northwest Argentina (Aranda-Rickert and Fracchia 2011) have all been characterized, at least at a local scale, as keystone seed dispersers of myrmecochorous plants.

A number of structures and mechanisms have been described for myrmecochorous plants that may enhance the probability of their seeds being removed by high-quality disperser ants (reviewed by Giladi 2006). Between them, shedding the seeds synchronously with the peak of activity of their main seed disperser has been demonstrated in a number of studies, both at seasonal (Thompson 1981; Ohkawara et al. 1997; Oberrath and Böhning-Gaese 2002; Guitián and Garrido 2006) and at daily scales (Turnbull

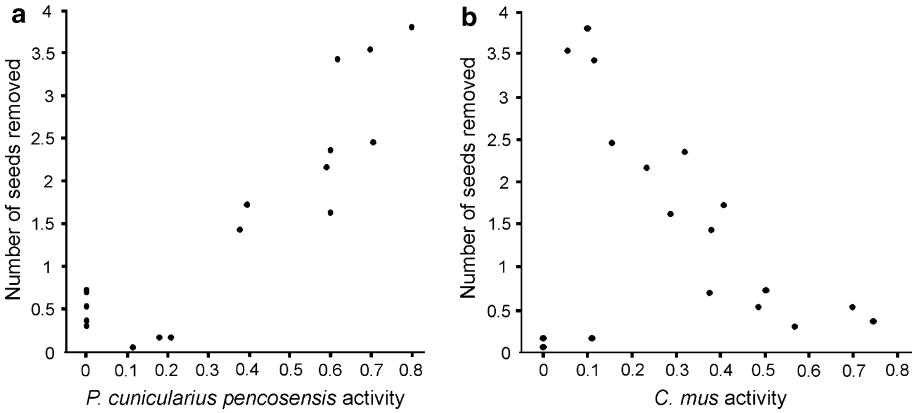

Fig. 5 Relationship between **a** *P. cunicularius pencosensis* activity and **b** *C. mus* activity and the removal of *J. excisa* seeds. *Each point* represents the mean number of seeds removed from each depot (5 seeds per depot, $N = 30$ depots) and the mean proportion of tuna baits occupied by each ant species ($N = 30$ baits) for each time interval and each site ($n = 18$)

and Culver 1983; Espadaler and Gómez 1996; Boulay et al. 2007). In our study, we have found that the peak of dehiscence of the *J. excisa* capsules was not synchronous with the peak of their main seed disperser ant foraging activity, but instead preceded it. Therefore, when *P. cunicularius pencosensis* ants have their peak of activity, seeds are already scattered on the ground and have a high probability to be first found and subsequently transported by a *P. cunicularius pencosensis* ant. This is mainly due to three important factors regarding the ecology of this ant species. First of all, *P. cunicularius pencosensis* ants are highly thermophilic, being active at those times of the day when soil temperatures reach maxima as high as 61°C (pers. obs.). Therefore, before the other ant species begin their foraging activity after their midday hiatus, *P. cunicularius pencosensis* ants have already been searching the ground for potential food. Second, the solitary mode of foraging of this ant species allows them to efficiently explore the environment and to transport individually the food items to their nests (Aranda-Rickert and Fracchia 2011). Third, their subordinate behaviour determines that once a seed is found, it should be immediately transported to the nest, in order to avoid encounters with dominant ants.

The *J. excisa* seeds that were experimentally placed on the ground were removed almost exclusively by *P. cunicularius pencosensis* ants. Seed removal increased with the foraging activity of this ant species and peaked during the early afternoon, coinciding with the peak of activity of *P. cunicularius pencosensis*. By contrast, the main elaiosome predator *C. mus*, as well as the other *Pheidole* spp. that also removed the *J. excisa* seeds, foraged mainly when the rate of carpel dehiscence was low (during the early morning) or progressively decreasing (during the afternoon and late afternoon).

Pogonomyrmex cunicularius pencosensis was the most subordinate ant within the behavioural hierarchy of the analysed species. This ant species typically abandoned the baits when confronted with other ant species and also exhibited an opportunistic robbing behaviour: when a bait was being monopolized by other species, the ant rapidly took a piece of food while avoiding the other species attack and then returned with the prey to the nest. When characterizing the ant communities of North America, Andersen (1997) has also classified the *Pogonomyrmex* genus of that region as thermophilic (hot-climate specialists) and behavioural subordinates.

As the temperature cooled down towards the end of the afternoon, the elaiosome predator *C. mus* exploited the majority of the baits in small groups of maximal 5 workers. Because of their extreme aggressiveness, the ant species of this genus occupied the top of the dominance hierarchy in our study. In Northeast Argentina, the species of *Camponotus* have also been reported to be highly competitive at baits (Calcaterra et al. 2008), whereas in Australia (Andersen 1995) and North America (Andersen 1997), it has been described as a behaviourally subordinate genus.

The *Forelius* species of this study also scaled high in the dominance hierarchy. They are small-sized ants that recruit massively to forage and also behaved as elaiosome predators. *Forelius nigriventris* was the only ant species other than *P. cunicularius pencosensis* that was observed at baits during the early afternoon and has also been characterized as thermophilic by Bestelmeyer (2000). Generalized myrmicinae species such as *Pheidole* are reported to be sub-dominant to dolichoderines in Australia (Andersen 1995), but competitively dominant in North America (Andersen 1997). In our study, they were intermediate in their competition abilities and climatic tolerances and exploited in groups only those baits located near their nests. They behaved as seed dispersers, transporting the *J. excisa* seeds cooperatively mainly during the early morning and late afternoon.

The heat tolerance of subordinate species can be attributed to a greater thermal tolerance associated with a physiological specialization (Fellers 1989; Gehring and Wehner 1995; Cros et al. 1997) or to a ecological specialization, where subordinate and dominant species may have similar thermal tolerance but subordinate species are forced to forage at a wider range of temperatures to get access to resources (Savolainen and Vepsäläinen 1988; Cerdá et al. 1997). Kusnezov (1963) has suggested that *P. cunicularius* radiated from ancestors in mesic habitats, such that stress tolerance may have evolved in response to competitive interactions with behaviourally dominant ants in relatively mesic environments. This adaptation may have favoured them to secondarily invade the arid zones. The use of high environmental temperatures may also provide additional resources in the form of heat-stressed preys, giving that *P. cunicularius pencosensis* are mainly scavengers, with a diet that comprises predominantly dead arthropods (Aranda-Rickert A., unpublished data).

The lack of a significant correlation between the removal ability of each ant species and their rank in the dominance hierarchy may be explained by the fact that in our study, many ants which ranked intermediate in the dominance hierarchy behaved as seed cheaters, that is, their removal ability equalled zero. Therefore, we cannot state that the more subordinate an ant species is, the more the seeds that are removed, but instead we can conclude that best seed remover in our study was also the most behavioural subordinate species. The high-quality seed disperser genus *Rhytidoponera* of Australia and its North American ecologically equivalent *Aphaenogaster*, as well as the *Myrmica* seed disperser species of Europe, have been reported to be behaviourally subordinate species (Fellers 1987; Andersen 1997; Vepsäläinen and Savolainen 1990). Giladi (2006) has suggested that subordinate ants may have been under selection pressure to minimize the risk of being 'robbed' by dominant species. Deferring the elaiosome consumption until arrival to the nest should be advantageous to the plant, as guarantees that ants are rewarded for their dispersal service only after it was done.

A main topic in the study of plant–animal mutualisms is to determine whether structures and mechanisms that enhance visits by the most effective mutualists derive from selective pressures exerted by animals or constitute pre-adaptations favouring the evolution of mutualisms (Thompson 1981, 1994; Herrera 1995; Irwin et al. 2004; Giladi 2006). Regarding the daily correspondence between seed shedding and disperser abundance or foraging activity, abiotic factors acting independently on both plants and animals may explain the observed temporal correspondence. As the daily activity rhythm of *P. cunicularius* is explained by physiological and competitive causes, the daily rhythm of dehiscence of the *J. excisa* fruits can be explained by physical causes: the rapid increase in the environmental temperature during the morning makes the capsules to dry out, therefore expelling the seeds due to a hygroscopic mechanism (Giliberto et al. 1980; Boulay et al. 2007). Nevertheless, being in the right place and at the right moment has important consequences for the outcome of the ant–plant interaction described here and may constitute the initial step for myrmechochorous-associated traits to evolve. Given the lack of studies about the influence of ant hierarchies on ant-mediated seed dispersal, further studies are needed to verify whether the subordinance behaviour is a crucial trait for an ant species to act as an effective disperser. The results presented here contribute to the current search for a generalization of those traits that characterize the high-quality and keystone seed disperser ant species at a global scale.

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