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Seed predation by ants in south-eastern Spain (Desierto de Tabernas, Almería)

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Abstract

Seed predation by ants was studied in the Tabernas Desert (Province of Almería, south-eastern Spain). Eight different species of harvester ants were found collecting seeds in single or foraging trails. Six of them feed mainly or exclusively on seeds. The most important predators are polyphagous *Messor* ants collecting all available seed types from the soil surface as well as directly from the mother plant. Predation of seeds was confirmed for 41 plant species. Their seed masses vary between 0.08 – 95.9 mg. Resource partitioning according to seed size was not observed, indicating that coexistence of ant species may be facilitated by different foraging strategies. To estimate the influence of seed predation on the vegetation structure, the number of collecting runs per colony per day and composition of food items brought in were determined for *Messor bouvieri* and *M. timidus* in a *Stipa tenacissima*-dominated grassland. Collecting-activity correlates strongly with soil temperature. The major part of their diet consists of seeds of *Helianthemum almeriense* and *Launaea lanifera*. Both *Messor* species are very similar with respect to worker size range, size of collected seeds, and foraging strategy, which results in a high degree of dietary overlap.

Key words: *Messor,* Pre-dispersal predation, Seed-harvesting ants, Semiarid environment, South-eastern Spain.

Resumen

Depredación de semillas por hormigas en el sureste de España (Desierto de Tabernas, Almería).

Se han encontrado ocho especies de hormigas recolectoras en solitario o mediante rastros de aprovisionamiento. Seis de ellas se alimentan mayoritaria o exclusivamente de semillas. Los más importantes depredadores pertenecen al polífago género *Messor*, que recogen todo tipo de diásporas disponibles en el suelo e incluso directamente de la planta madre. La depredación de semillas se ha confirmado para 41 especies de plantas vasculares, variando el peso de las semillas de 0,08 a 95,9 mg. Dado que no existe reparto de recursos de acuerdo con los tamaños de las semillas, la coexistencia de especies puede estar facilitada por diferentes estrategias de recolección. Para estimar la influencia de la depredación de semillas sobre la estructura de la vegetación, se ha determinado, en un matorral dominado por *Stipa tenacissima*, el numero de recoleciones por colonia y día y la composición de la comida transportada para dos especies, *Messor bouvieri* y *M. timidus*. La actividad de recolección esta correlacionada con la temperatura del suelo. La mayor parte de sus dietas consiste en diásporas de *Helianthemum almeriense* y *Launaea lanifera*. Ambas especies de *Messor* se comportan de forma muy similar con respecto al tiempo de trabajo, tamaño de las semillas recolectadas y estrategia de aprovisionamiento, lo que da lugar un alto grado de solapamiento en sus dietas.

Palabras clave: *Messor*, Depredación predispersiva, Recolección de semillas, Hormigas, Ambiente semiárido, Sudeste de España.

Introduction

In semiarid and arid regions, the survival and distribution of plants can be strongly influenced by predators. A striking element of desert-like landscapes are harvester ants collecting diaspores (dispersal units, hereafter called seeds) as a high-quality and nutrient-rich food source suitable for storage. Most of these species belong to Myrmicinae (Hölldobler & Wilson 1990). Typically, they collect amounts of seeds that exceed their current requirement at the time of high seed availability and store them within their nest. Here, seed germination and/or disintegration are prevented by mushrooms and bacteria through the application of a metapleural glandular secretion (Schildknecht & Koob 1971, Celli & Maccagnani 1994). By this foraging strategy, periods of low seed production can easily be bridged. Splitting of seeds is often carried out by a morphologically suitable caste of worker ants (Delage-Darchen 1974, Hölldobler & Wilson 1990). Parts not significant as a food resource are transported to a waste pile located next to the nest entry.

According to Andersen (1989), Crist & MacMahon (1992), and Brown & Human (1997), granivorous ants have important effects on the composition and structure of semi-desert plant communities. Their seasonal activity pattern has a strong correlation to seed availability (Briese & Macauley 1980, Steinberger et al. 1992) that is highest shortly before the drought period in thermomediterranean landscapes (Hensen 1999a). To ensure that a high proportion of seeds remains vital until the following season, species were forced to evolve mechanisms to avoid heavy losses of seeds due to predation (Gutterman 1994).

In the Tabernas Desert (Province Almería), seed-harvesting ants have been observed to destroy a large proportion of seeds of various species (Hensen 1999b, 1999c, Hensen & Zuther 1999). The aim of the present paper is to examine the following questions: 1. Which species of harvester ants occur in the Tabernas Desert? 2. Which types of seeds are collected? 3. What pattern of collecting activity they follow? 4. What is the food composition during the period of seed dispersal?. In answering these questions, a firm basis for further research is created with respect to the foraging ecology of seed-harvesting ants and the adaptive value of certain seed characteristics of semi-desert plant species in south-eastern Spain.

Material and methods

The present study was carried out in the Tabernas Desert, situated approximately 25 km north of the city of Almería, Andalucía, south-eastern Spain (37º05'N, 2º25'W, 300 m a. s. l.). Marly substrates are the main geological basis of soil formation. The climate in the area is semi-arid, with a mean annual temperature of 17.3 ºC and a mean annual rainfall of 243 mm (Peinado et al. 1992: 40). There is a pronounced dry season from May to September and a large variation in both the pattern and the total amounts of rainfall from year to year (which ranged from 41 to 365 mm between 1960 and 1990). From April to June 1999, harvester ants together with their food items were collected in various parts of the study area. In addition, several nests were dug up to expose their seed content. Nomenclature of species refers to Collingwood (1978) for ants, and to Castroviejo et al. (1989-1997), Tutin et al. (1968-80, 1993) and Valdés et al. (1987) for plants and seeds. Determination of seed mass is based on 100 air-dried seeds.

Within a *Stipa tenacissima*-dominated grassland, the colony distribution, number of collecting runs per colony per day and composition of food items brought in were determined for *Messor bouvieri* and *M. timidus* (size of area 10.674 m^2; total number of *Messor* colonies 19). To determine the number of collect runs, workers of two colonies of each *Messor* species were counted returning into their nest every hour for a three minute period at 6 occasions between 30.04./1.05. and 16./17.6.1999 from 4 PM until 3 PM the following day. Air temperature in the shade as well as soil surface temperature 10 cm from the nest entry were measured hourly, and the total number of active colonies was determined. Composition of food items was analysed once a week between 27.04. and 15.06.1999 for three colonies respectively. For each of them, 100 collecting ants returning on a foraging trail to their nest were randomly cought with an aspirator and put back after removal of their food. Percentage of dietary overlap D between *Messor bouvieri* and *M. timidus* was calculated according to Schoener (1970) as: $D = 100\,(1 - 0.5 \cdot \Sigma\,|p_{Mbo,i} - p_{Mti,\,i}|)$, with $p_{Mbo,i}$ = percentage of the i^{th} food particle of *Messor bouvieri*, $p_{Mti,\,i}$ = percentage of the i^{th} food particle of *M. timidus*.

Results

Eight different species of harvester ants were identified in the Tabernas Desert (Table 1). Except for the omnivorous *Pheidole*

Species	Size (body-length, mm)	Organisation of foraging (Single, Trail)	Variability of size (worker ants)	Size of colonies	Maximum size of seed (mass in mg)	Foraging type
Messor barbarus	4.1 - 12.65	S, T	polymorphous	< 12000 [1,2]	95.9 *Retama sphaerocarpa*	granivorous
M. bouvieri	4.0 - 8.15	S, T	polymorphous	< 12000 [1]	95.9 *Retama sphaerocarpa*	granivorous
M. timidus	4.1 - 10. 4	S, T	polymorphous	< 12000 [1]	95.9 *Retama sphaerocarpa*	granivorous
Goniomma blanci	3.3 - 3.5	S	monomorphous	< 1000 [3]	2.2 *Euzomodendron bourgaeanum*	granivorous
G. compressisquama	3.4 - 3.4	S	monomorphous	< 1000 [3]	2.2 *Euzomodendron bourgaeanum*	granivorous
Oxyopomyrmex saulcyi[3]	no data, < *G. blanci*	S	monomorphous	?	?	granivorous
Pheidole pallidula	1.2 - 4.9 [4]	S, T	dimorphous	600 – 6000 [5]	0.7 *Helianthemum almeriense*	omnivorous
Tetramorium semilaeve	2.0 -3.2 [4]	S, T	monomorphous	< 1000 [1]	0.7 *Helianthemum almeriense*	omnivorous

Table 1. Characteristics of harvester ants in the Tabernas Desert. Notes: [1] estimation, [2] according to Cerdan (1989) up to 21000 in south-eastern France, [3] personal communication of Prof. X. Espadaler (University of Barcelona), [4] according to Retana et al. (1992), [5] according to Detrain (1990). Organisation of foraging: «Single»: Foraging ants collect alone, without recruitment of nest companions. «Trail»: Foraging ants recruit nest companions to places of high food density, resulting in foraging trails. Maximum size of seed: the heaviest seed for which entry into the nest was observed directly or verified by finding them within.
Tabla 1. Características de las hormigas recolectoras en el Desierto de Tabernas.

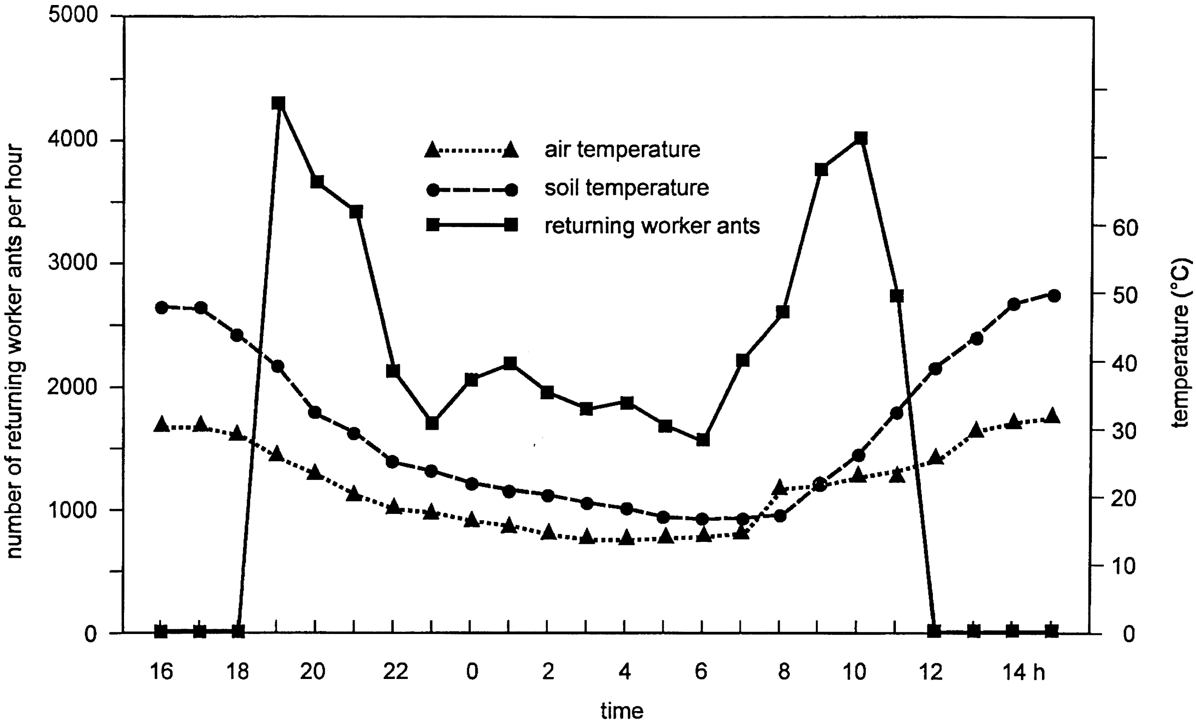

Figure 1. Collecting activity of a *Messor bouvieri* colony on 10./11.5.1999.
Figura 1. Actividad recolectora de la colonia de *Messor bouvieri.*

pallidula and *Tetramorium semilaeve*, all ant species collect almost exclusively seeds as food. The largest and most striking colonies are built up by the three *Messor* species of which *Messor timidus* is endemic to the Tabernas Desert (Espalader 1996). Their polymorphous workers differ strongly in size (Table 1) and are able to carry the heaviest seeds (up to 95.9 mg; Table 1). Depending on seed density, they collect single or in foraging trails reaching lengths up to 55 m (Schöning 2000). In contrast, both *Goniomma blanci* and *G. compressisquama*, as well as *Oxyopomyrmex saulcyi,* are organized in very small colonies that are difficult to observe. Their worker ants collect primarily smaller seeds.

Table 2 contains data on seeds for which direct entry into the nest was observed or which were found within the nest. In quantity and quality, the polyphageous *Messor* ants are the most important predators collecting all available seed types. The smallest seeds brought in were those of *Thymus hyemalis* (0.08 mg); the heaviest, those of *Retama sphaerocarpa* (see

Family	Species	Fruit-setting[2]	Mass of dispersal unit (mg)			Type of dispersal unit brought into the nest	Collected by	Pre-dispersal predation by
			Mean (SD)	MIN - MAX	N			
Apiaceae	*Thapsia villosa*	V - X				fruit	Mbo, Mti	
Apocynaceae	*Nerium oleander*	I - III	3.50 (1.02)	1.17 - 5.28	100	seed	Mbo	
Asteraceae	*Artemisia barrelieri*	I - III				capitulum	Mbo	Mbo, Mti
	A. herba-alba	I - III	0.1[1]			capitulum	Mbo	Mbo, Mti
	Atractylis cancellata	V - VI	2.1[1]			achene	Mbo, Mti	
	Calendula arvensis	V - VI		1.9 - 5.2[1]		achene	Mbo, Mti	
	Centaurea aspera	V - VI	2.22 (0.56)	1.02 - 3.64	100	achene	Mbo, Mti, Tse	Mbo
	C. melitensis	V - VI	1.31 (0.21)	0.92 - 1.90	100	achene	Mbo	
	Launaea arborescens	IV - VI	1.34 (0.19)	0.72 - 1.83	100	achene	Mbo, Mti	
	L. lanifera	V - VI	0.80 (0.22)	0.36 - 1.52	100	capitulum, achene	Mbo, Mti	Mbo, Mti
	Reichardia tingitana	V - VI		0.2 - 0.4[1]		achene	Mbo, Mti	
Brassicaceae	*Carrichtera annua*	IV - VI	0.8[1]			seed	Mbo. Mti, G	Mti
	Diplotaxis harra	IV - VI	0.1[1]			siliqua, seed	Mbo, Mti	Mbo, Mti
	D. virgata	IV - VI	0.1[1]			siliqua, seed	Mbo, Mti	Mbo, Mti
	Euzomodendron bourgaeanum	V - VI	2.2 (0.4)	1.2 - 3.1	100	siliqua, seed	Mbo, Mti, G	Mbo, Mti
	Lobularia maritima	V - VI	0.2[1]			siliqua	Mbo, Mti	
Chenopodiaceae	*Salsola genistoides*	VIII - XII[1]	3.4[1]			fruit incl. tepals	Mbo	
Cistaceae	*Cistus libanotis*	III – V				seed	Mbo	
	Helianthemum almeriense	IV - VI	0.68 (0.11)	0.48 - 0.98	100	fruit, seed	Mbo, Mti, G, Ph, Tse	Mba, Mbo, Mti
	H. salicifolium	V	0.1[1]			fruit, seed	Mbo, Mti, G	Mbo, Mti
Dipsacaceae	*Scabiosa monspeliensis*	V - VI	6.8[1]			fruit	Mbo, Mti	
Euphorbiaceae	*Euphorbia peplus*	IV - VI				seed	Mba	
Fabaceae	*Anthyllis cytisoides*	V - VIII[1]	2.69 (0.53)	1.12 - 3.94	100	pod, seed	Mba, Mbo, Mti	Mbo, Mti
	Hippocrepis ciliata	IV - VII	10.8[1]			pod	Mti	Mbo, Mti
	Medicago littoralis	V - VI				pod	Mbo	
	Retama shaerocarpa	VI - X	95.88 (10.32)	75.56 - 122.40	100	seed	Mba, Mbo	
Lamiaceae	*Thymus hyemalis*	IV - VI	0.08[1]			fruit, nutlet	Mba, Mbo	Mbo, Mti
Plantaginaceae	*Plantago albicans*	V - VII	1.6[1]			infructescence, seed	Mbo, Mti	Mbo, Mti
	P. ovata	V - VI	0.99 (0.12)	0.73 - 1.24	100	infructescence, seed	Mbo, Mti, G	Mbo, Mti
	P. coronopus	V - VI				infructescence, seed	Mbo	Mbo, Mti
Plumbaginaceae	*Limonium cossonianum*	V - VII	2.7[1]			seed	Mbo	Mbo
Poaceae	*Aegilops geniculata*	V - VII	81.6[1]			infructescence	Mba	Mba
	Avena barbata	V - VI	5.4[1]			caryopsis encl. by glumes	Mba, Mbo, Mti	
	Bromus rubens	V - VI	3.0[1]			caryopsis encl. by glumes	Mba	Mba
	Lygeum spartum	V - VI	62.44 (14.31)	37.91 - 85.46	20	caryopsis encl. by glumes	Mba	
	Stipa capensis	V - VI	4.87 (1.13)	2.18 - 7.79	100	caryopsis encl. by glumes	Mba, Mbo, Mti	Mba, Mbo, Mti
	S. parviflora	IV - VI	1.93 (0.30)	1.22 - 2.85	100	caryopsis encl. by glumes	Mba, Mbo, Mti	Mbo
	S. tenacissima	IV - VI	9.03 (1.32)	6.08 - 12.82	100	caryopsis encl. by glumes	Mba, Mbo, Mti	Mba, Mbo, Mti
Resedaceae	*Reseda lanceolata*	V - VII				seed	Mti	Mti
Solanaceae	*Lycium intricatum*	V - VI				seed	Mbo, Mti	Mbo, Mti
Thymelaeaceae	*Thymelaea hirsuta*	I - IV[1]				seed	Mba, Mbo	Mba, Mbo

Table 2. Survey of seeds collected by harvester ants in the Tabernas Desert. Notes: [1] data of Hensen 1999b. [2] data of Valdés et al. (1987). G = *Goniomma* spp., Mba = *Messor barbarus*, Mbo = *M. bouvieri*, Mti = *M. timidus*, Ph = *Pheidole pallidula*, Tse = *Tetramorium semilaeve*.

Tabla 2. Observaciones sobre las semillas recolectadas por hormigas en el Desierto de Tabernas.

Date	Percentage of active colonies	
	Messor bouvieri	***Messor timidus***
30.4. /1.5.1999	100	100
10./11.5.1999	100	100
20./21.5.1999	91	100
30./31.5.1999	91	100
9./10.6.1999	73	13
16./17.6.1999	9	13

Table 3. Percentage of active colonies in the sample area (N = 11 for *Messor bouvieri* and N = 8 for *M. timidus*).
Tabla 3. Porcentaje de colonias activas en el área muestreada.

		Messor bouvieri	***Messor timidus***
Mean percentage of loaded collectors (SD)		57.0 (13.2)	61.5 (18.4)
Mean percentage of collectors loaded with food items (SD)		49.6 ± 14.0	57.7 ± 20.6
Food item (%)			
Helianthemum almeriense	fruit	7.57	10.39
	seed	47.36	42.02
Thymus hyemalis	fruit	10.61	07.56
	seed	2.52	0.86
Launaea lanifera		24.70	17.01
Launaea arborescens		0	0.59
Stipa tenacissima		3.93	12.57
Stipa capensis		0.56	0.42
Anthyllis cytisoides		0	4.14
Other seeds		0.93	1.85
Dead arthropods		1.82	2.59
Σ		100.00	100.00

Table 4. Percentage of collected ants (N = 3100) carrying food items (seeds, fruits, and dead arthropods; N = 1835) and percentage of food composition (data for *Messor bouvieri* and *M. timidus*).
Tabla 4. Porcentaje de hormigas recolectadas (N=3100) transportando diferentes alimentos (semillas, frutos, artrópodos muertos; N = 1835) y porcentaje de la composición alimentaria (Datos correspondientes a *Messor bouvieri* y *M. timidus.*

above). *Messor* species are harvester ants in the true sense of the word: they collect not only seeds from the soil surface (post-dispersal seed predation) but also from the plant (pre-dispersal seed predation; see Table 2). Plants affected by the latter behaviour are several, widely distributed species such as *Stipa tenacissima, Aegilops geniculata, Anthyllis cytisoides, Euzomodendron bourgaeanum,* and *Helianthemum almeriense*. Among the four last-mentioned species, whole fruits are cut off regardless of whether they are already ripe or not.

Messor colonies do not necessarily collect daily. As shown in Table 3, the number of active colonies of *Messor bouvieri* and *M. timidus* sank drastically in June although the temperatures did not increase. The average number of collecting runs per day calculated from activities at 30.4./1.5., 10./11.5., 20./21.5. and 30./31.5. was 40.980 and 16.310 for *Messor bouvieri* and 23.690 and 23.670 for *M. timidus*. Collecting activity starts in the evening, when the temperature of the soil surface has dropped below 40 °C (Fig. 1). Activity is highest shortly after collection begins. During the night, a steady level of activity is kept until a further peak is reached in the morning, just after sunrise. After a few hours, increasing soil temperatures force the seed collectors to break off their work. Highest and lowest soil temperatures measured during seed collection were 41.5 and 13.8 °C for *Messor bouvieri* (air temperatures 11.0 - 29.0°C) and 42.1 and 12.0 °C for *M. timidus* (air 11.0 - 27.0°C).

As shown in Table 4, only 50 % of the collectors return to their nest loaded with food items (seeds, fruits and dead arthropods). Between 30.04. and 17.06., the major part of the diet of both *Messor* species consists of seeds of *Helianthemum* *almeriense* followed by *Launaea lanifera* and *Stipa tenacissima*. In addition, different plant particles were frequently brought in, presumably not serving as food, such as leaves, petals, and parts of infrutescences like capsule walls, glumes, or awns. The degree of dietary overlap between *Messor bouvieri* and *M. timidus* calculated according to Schoener (1970) is 82.16 %.

Discussion

Among the eight species of harvester ants occuring in the Tabernas Desert, six feed mainly or exclusively on seeds. The three *Messor* species are the most important as predators because the amount of seeds collected by them is by far larger than that brought in by the other species. However, also smaller ants such as *Goniomma* ssp., *Pheidole pallidula,* or *Tetramorium semilaeve* may be important with respect to the reproductive success of plant species since their small workers are probably much better at finding and removing seeds fallen into small soil cracks or between rocks.

Although a large variety of different seed types is consumed by ant species in Tabernas Desert, resource partitioning according to seed size has not been observed, in contrast to the results found by Davidson (1977) in the south-western part of the USA. The smallest seeds of *Thymus hyemalis* are collected not only by *Goniomma*, but also by *Messor timidus* and *M. bouvieri*. On the other hand, *Goniomma* species also feed on *Helianthemum almeriense* that makes up more than half of all the forage items of the *Messor* species studied. However, according to Davidson (1977), coexistence of species with broadly overlapping diets may be facilitated by different foraging strategies. *Goniomma* collects seeds occurring in low density, while *Messor* species recruit foraging trails and harvest seeds mainly from areas with higher seed density. Fighting between *Messor* and *Goniomma* was never observed even when a foraging trail passed by very close to the nest entrance of a *Goniomma* colony. In contrast, inter- and intraspecific competition for the same food resources were observed between *Messor* species. The result of a Nearest neighbour´s distance test carried out by Schöning (2000) for the same study site indicates a very regular distribution of their colonies. The overdispersed distribution of *Messor* species in the Tabernas Desert can be explained by their mutual avoidance: as a rule one of two colonies meeting each other changes direction of collecting activity without fighting, when they are of equal size. However, it was observed twice that an encounter of worker ants of a large *Messor* colony and those of a clearly smaller one resulted in a violent attack ending in the destruction of the small colony.

As the high degree of dietary overlap between *Messor bouvieri* and *M. timidus* reveals, these species are very similar with respect to worker size, size of collected seeds, and foraging strategy. According to the results of preference studies carried out by Schöning (2000), *Messor* species can be regarded as generalistic granivores with preferences. This result is in agreement with several other research papers (Gordon 1980, Hahn & Maschwitz 1985, Hobbs 1985, Neumayer 1994, Detrain & Pasteels 2000). Possible traits enhancing the attractiveness of a seed might be energy content, handling time, seed hardness and/or presence of an elaiosome (MacMahon et al. 2000). Nevertheless, as shown by Nielsen & Baroni-Urbani (1990) or Schöning (2000), causes of seed preferences are extremely difficult to justify. Whether substances on the seed surface could be responsible for the selective collection of certain seed types, as suggested by Nielsen & Baroni-Urbani (1990), remains to be proved.

Species that disperse their seeds shortly before the drought period should have developed mechanisms to avoid heavy seed losses due to predation. According to Hensen (1999c), *Euzomodendron bourgaeanum* (Brassicaceae) develops myxophorous seeds that, after being moistened and desiccated, adhere strongly to the soil crust. It was proved that myxospermy effectively prevents secondary dispersal by wind or rain as well as seed predation by ants (Gutterman & Shem-Tov 1997). The fixation of seeds to the ground as a means of preventing removal also is exhibited in the caryopsis of *Lygeum spartum* and *Stipa tenacissima* (Hensen 1999b). In the cases in which soil covers the seeds, they are even more protected from predation, since ants do not collect seeds buried more than 1.5 cm under the surface (Bernstein 1974, Schöning 2000). However, *Euzomodendron bourgaeanum* and *Stipa tenacissima* belong to species that are frequently subjected to pre-dispersal seed predation. This type of seed collecting is described by several authors (e.g. Levieux & Diomande 1978, Hahn & Machwitz 1985, Gutterman 1993, Neumayer 1994).

Whether seed predation by ants has or has not an impact on the population structure of long-lived perennials is still discussed (Andersen 1989, Haase et al. 1995). Briese (1982) estimates that in the semi-arid salt bush vegetation of New South Wales (Australia) approximately 18 % of the entire seed production was destroyed. In scrublands of Wyoming (USA), *Pogonomyrmex occidentalis* consumed 9.1 % of seeds in the first and 25.6 % in the second study year (Crist & MacMahon 1992). Comparable data are provided by Tevis (1958) for Colorado Desert (10 %), Cerdan (1989) for south-eastern France (6 %), and Whitford (1978) for New Mexico (10 %). However, in comparison with the high number of other factors important for the reproductive success of a plant species, such as rate of precipitation, competition, damage through predation by herbivores and/or pathogens, the role of harvester ants appears negligibly small. Nevertheless, due to selective collection of favoured seeds, ants may certainly play an important role on the plant population structure. In the Sonara Desert (Arizona, USA), density of all plants increases 1.35-fold - with those of *Filago californica* (Asteraceae) reaching a 1.9-fold increase - during a 4-year period of harvester ant exclusion (Inouye et al. 1980). Crist & MacMahon (1992) proved that, for a favoured *Poa* species and for *Alyssum* *desertorum* (Brassicaceae), in the first year of study 66 % and 72.6 %, in the second year 44.9 % and 100 % of the total seed production was destroyed. Andersen (1987, 1989) found that in New South Wales (Australia), 58 % of the seed production of *Casuarina pusilla* (Casuarinaceae), 93 % of *Eucalyptus baxteri* (Myrtaceae), 90 % of *Leptospermum juniperum* (Myrtaceae), and 90 % of *L. myrsinoides* (Myrtaceae) were removed by different ant species. Thus, further research on the impact of harvester ants on the species composition of plant communities, on the population structure of key species and on the adaptive value of certain seed characteristics is a fascinating challenge.

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