

Seed and fruit selection by harvester ants, *Messor barbarus*, in Mediterranean grassland and scrubland

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Summary

1. We analyse diet and propagule selection by the harvester ant *Messor barbarus* (L.) in Mediterranean grassland and scrubland in central Spain.
2. Diet was estimated by the identification of worker-transported prey in 34 colonies per system type, and compared with seed and fruit availability in the foraging areas. Propagules were characterized by six morphological traits: total weight; weight of seed content; the three main dimensions; and shape.
3. The effect of propagule attributes on selectivity was analysed after transforming data into phylogenetically independent contrasts. Propagules from a small number of species dominate the diet of *M. barbarus* in the study area, in terms of both frequency and contribution in seed weight. In grassland, prey selection depends on $\ln(\text{prey length})$ and $\ln(\text{prey weight})$ ($R^2 = 0.57$). In scrubland, $\ln(\text{prey length})$ explains 64% of selection. Long and heavy propagules are preferred.
4. This pattern of selection can be a mere effect of a time-saving foraging strategy, as apparent preference for long propagules can be expected even if workers forage in a non-selective way.
5. *Messor* ants are likely to play a role in the plant composition of Mediterranean grassland and scrubland, limiting the abundance of long propagules and thus indirectly favouring small-seeded species without dispersal appendages.

Key-words: diet, foraging strategy, morphological traits, phylogenetically independent contrasts, seed size

Functional Ecology (2005) **19**, 273–283
doi: 10.1111/j.1365-2435.2005.00956.x

Introduction

Messor harvester ants are the main seed predators in therophyte grassland and certain types of scrubland of the Mediterranean Basin (López, Acosta & Serrano 1993; Cerdá & Retana 1994; Hensen 2002; Azcárate & Peco 2003). Both types of system show a high proportion of annual species (Peco 1989), which makes them particularly sensitive to ant–seed interactions. Foraging by ants can constitute a severe source of seed mortality for many species, limiting their recruitment odds (Andrew 1986; Louda 1989). In some cases, however, ants behave as vectors of dyszoochory (accidental seed dispersal), abandoning viable seeds on trails and refuse piles (Retana, Picó & Rodrigo 2004), where levels of plant competition and soil properties are altered by ant activity (Dean & Yeaton 1993a, 1993b).

The relevance of interactions between *Messor* ants and plants depends primarily on rates of seed or fruit removal. Previous studies show that harvester ants tend

to concentrate their diet on a relatively small number of propagule species (Crist & Wiens 1994; Andersen, Azcárate & Cowie 2000; Wilby & Shachak 2000; Willott, Compton & Incoll 2000), which reveals the existence of traits that favour collection by ants. Prey-selection criteria can vary to some extent (Fewell & Harrison 1991; Crist & MacMahon 1992; Reyes-López & Fernández-Haeger 2002a, 2002b). However, certain morphological traits such as weight (Baroni-Urbani & Nielsen 1990; Baroni-Urbani 1992; Milton & Dean 1993; Detrain & Pasteels 2000); size (Rissing 1981; Campbell 1982; Crist & MacMahon 1992; Willott *et al.* 2000); shape (Pulliam & Brand 1975); or the possession of awns and other appendages (Schöning *et al.* 2004) explain a part of prey selection in harvester ants. Other non-morphological traits, such as nutritional or calorific content (Kelrick *et al.* 1986), chemical composition (Pizo & Oliveira 2000) and viability (Andrew 1986; Crist *et al.* 1992), can also influence preference by ants.

Seed predation can promote evolutionary changes on the design and reproductive strategies of plants (Harper, Lovell & Moore 1970; Louda 1989). Some authors have suggested that certain propagule

morphologies can be favoured in communities where seed predation by ants is intense (Detrain & Pasteels 2000; Willott *et al.* 2000; Schöning *et al.* 2004). Likewise, plants can develop ant-attractive propagules in communities where myrmecochory or dyszoochory are important (Hughes & Westoby 1992). As *Messor* harvester ants are abundant in Mediterranean grassland and scrubland, it is plausible that plants composing these communities show traits or mechanisms capable of reducing seed harvesting, or at least seed consumption.

There are few data on seed selection by *Messor barbarus* (L.) in Mediterranean grassland. Detrain *et al.* (2000) analysed one single colony of *M. barbarus* in south-eastern France. According to these authors, ants collect seeds from a small number of species, and apparently prefer weighed ones (>0.4 mg). However, prey selection can vary between colonies (Traniello & Beshers 1991), and seed or fruit weight can be correlated with other traits not included in the study (Sánchez *et al.* 2002). There are no published studies on Mediterranean scrubland, although in semiarid scrubland of the Iberian Peninsula Willott *et al.* (2000) found a strong preference by *Messor bouvieri* for large seeds. Some research into seed selection by *Messor* spp. has also been conducted under laboratory conditions or using artificial seeds (Baroni-Urbani & Nielsen 1990; Baroni-Urbani 1992; Reyes-López & Fernández-Haeger 2002a, 2002b) and manipulating propagules from a single species (Schöning *et al.* 2004).

The aim of this work is to analyse diet and propagule selection by *M. barbarus* in Mediterranean grassland and scrubland under natural conditions. The study addresses two specific questions: (1) which propagule types comprise the diet of *M. barbarus* in Mediterranean grassland and scrubland?; (2) are propagule attributes good predictors of selection by harvester ants?

Methods

STUDY SITE

Fieldwork was conducted in the Moncalvillo-Pedrezuela study site (2000 ha; 40°38' N, 3°70' E; 900 m height; 20 km north of Madrid). Climate is continentalized mediterranean, with a severe drought period in summer, 550 mm mean annual rainfall, and a mean annual temperature of around 13 °C. Soils are shallow, on siliceous substrata (mainly pre-Ordovician gneiss), and vegetation is dominated by two types of clearly differentiated system: grassland and scrubland. Grasslands are the product of extensive livestock grazing over the past few centuries, and are dominated by therophyte species. Scrubland areas are located on abandoned grassland and dry farming croplands, and are dominated by *Lavandula stoechas* subsp. *pedunculata*. For a more detailed description of the site, see Azcárate & Peco (2003).

Messor barbarus is the main harvester ant in both types of system (Azcárate & Peco 2003). This species is very common in dry grassland and open scrubland

of the western Mediterranean and northern Africa. Colonies make conspicuous trunk trails for food searching, collection and transport (López *et al.* 1993; Reyes-López & Fernández-Haeger 2001). *Messor bouvieri* is also an important harvester ant in the scrubland of the area. There are other seed-eating species in the study site belonging to the genera *Messor*, *Aphaenogaster*, *Oxyopomyrmex*, *Goniomma*, *Tetramorium* and *Pheidole*, although their abundance and harvesting capacity is much lower than those of *M. barbarus*, the only exception being *M. bouvieri*, which is common in the scrubland areas (Azcárate *et al.* 2003).

DIET

The diet of *M. barbarus* was estimated by the identification of worker-transported prey close to the nest entrance (Davidson 1980; Hahn & Maschwitz 1985; Gordon 1993; Milton & Dean 1993; Cerdá & Retana 1994; Detrain *et al.* 2000; Wilby & Shachak 2000; Willott *et al.* 2000). Sampling took place between March and November 1997. We took 34 observations per system type, each from one independent colony. Minimum distance between sampled colonies was 20 m. In each observation, we took the first 41 prey items brought to the nest hole by the ants, which required a gathering time of 2–3 min. Previous data about *M. barbarus* recorded in the study site show that summer (June–August) comprises 60% of the annual harvesting activity; spring (March–May), 30%; and autumn (September–November), 10% (Azcárate 2003), so sampling was distributed according to the relative contribution of each season. In spring we recorded 12 observations in grassland and 11 in scrubland; in summer, 19 and 20, respectively; and in autumn, three in both system types.

Prey was classified into five categories: plant propagules, other vegetal fragments, animal fragments, lichen fragments and mineral fragments. Differences in diet composition between system types were analysed comparing the arc-sin-transformed frequencies of each group following a *t*-test approach. We performed one test per prey group, and then a sequential Bonferroni correction for multiple tests (Rice 1989).

Only propagules were identified to specific level. We also distinguished between 'seeds' (seeds or single-seeded fruits in their simplest form, following Bekker *et al.* 1998) and 'fruits' (more complex or multiseeded propagules).

PROPAGULE AVAILABILITY

For every diet observation, we identified the main foraging area and set a circular 6 m diameter plot, where we placed 10 sampling points at random. *Messor barbarus* foragers are able to dig up shallow prey, and also to cut mature propagules from vegetation. Hence, in order to measure propagule availability, we extracted a 3 mm wide × 4 cm diameter cylindrical soil core per sampling point, along with the seed/fruit content of

the standing herbaceous vegetation of the same area. The 10 subsamples belonging to the same plot were pooled for the laboratory analysis.

Prior to the evaluation of the propagule content, we dispersed the samples using a solution of 20 g sodium hexametaphosphate $[(\text{NaPO}_3)_6]$ and 10 g sodium bicarbonate (NaHCO_3) for 1 l water. Samples were kept in contact with dispersing solution for 2 h at a ratio of 100 ml for 7 g soil. They were then passed through a series of three sieves (2, 1 and 0.5 mm wide). After a preliminary analysis of diet data, we concluded that ants never collect prey <0.5 mm wide, thus the material crossing the third sieve was refused. Finally the three fractions resulting from the sieving process were scanned under a binocular microscope. In most cases seeds and fruits were identified at the specific level, with the aid of reference collections made with specimens from the study site. Those propagules showing any doubt about their viability (empty or broken ones) were rejected.

This procedure was adequate to estimate the availability of seeds produced by herbaceous vegetation, but did not include predispersed seeds of woody species. Therefore in scrubland plots we also counted the total number of predispersed *Halimium* capsules and *Lavandula* infructescences per plot. The availability of *Lavandula* fruits (calyces +1–4 mericarps) was estimated by collecting 30 infructescences per plot. Data from the two techniques were pooled and transformed into average densities of each propagule type per dm^2 . As we were unaware of the origin of prey carried by foragers, we did not distinguish between predispersed and dispersed items in the propagule availability data set.

MORPHOLOGICAL TRAITS OF PROPAGULES

We selected the following morphological traits to describe each propagule type: total weight; weight of seed content; the three main dimensions (dim1, length; dim2, width; dim3, thickness); and shape (the variance of the three main dimensions, first divided by length; Thompson, Band & Hodgson 1993). In the case of seeds, we used the mean values published by Azcárate *et al.* (2002) and Sánchez *et al.* (2002). For fruits, we collected 30 units of each propagule type, then estimated the mean value of each morphological trait following the same procedure as in Azcárate *et al.* (2002). To assess the mean weight of the seed content, we first estimated the mean number of seeds per fruit, then multiplied this value by the mean weight of a single seed. The values assigned to each propagule type are shown in Appendix 1.

PROPAGULE SELECTION

We evaluated selection of each propagule type by comparing its contribution in weight in the diet and availability data sets. The use of weight rather than frequency is a closer approximation of the actual

importance of each prey type as a food resource. Other authors have also employed weight to evaluate prey preference in harvester ants (Kelrick *et al.* 1986; Reyes-López & Fernández-Haeger 2002a).

For each propagule type, i , we calculated the following selectivity index, S_i :

$$S_i = Nr_i/N_i$$

where Nr_i = number of observations in which the relative contribution in weight of propagule i is higher in diet than in availability; and N_i = total number of observations with information for the propagule i (present in diet and/or availability data sets). We calculated selectivity indices only when $N_i \geq 10$. The minimum value of the index ($S_i = 0$) means that the propagule i always occurs in diet in a proportion lower than in availability, or that it was found only in availability samples. In contrast, the maximum value ($S_i = 1$) reflects that, in all cases in which the propagule i is present in the diet, its relative contribution in weight is higher than in the correspondent availability samples. The limit between positive and negative selection is at $S = 0.5$. The existence of some propagule types detected only in the diet data set impeded the use of some well known selectivity indices (Chesson 1983; Milton *et al.* 1993; Detrain *et al.* 2000).

The effect of propagule attributes on selectivity index was analysed by fitting multiple regression models. The selection indices, and all propagule traits except shape, were log-transformed to achieve normality of residuals. As individual species cannot be regarded as independent data points (Felsenstein 1985; Harvey *et al.* 1995; Harvey 1996; Martins & Hansen 1996), we obtained phylogenetically independent contrasts (PICs), following Felsenstein (1985). Accurate phylogeny information was not available, so we used current taxonomy to infer phylogeny (Appendix 2), as suggested by Martins & Hansen (1996).

In the analysis we included only those propagule types occurring in diet or availability data sets at least in 10 observations. In species showing more than one propagule type, we selected one at random.

Results

DIET

More than 91% of prey collected by *M. barbarus* in grassland are fruits or seeds (Fig. 1). We found 43 different propagule types, corresponding to 35 plant species (Appendix 3). In scrubland, plant propagules were also the main group of prey, although the frequency was significantly lower than in scrubland (77.7%, $t_{66} = 4.4$; $P < 0.001$; Fig. 1). In this type of system, ant diet included 51 different types belonging to 40 plant species (Appendix 3). Ants also collected a considerable amount of other plant fragments, particularly in scrubland (18.2% vs 6.1% in grassland; $t_{66} = 3.5$; $P < 0.001$; Fig. 1);

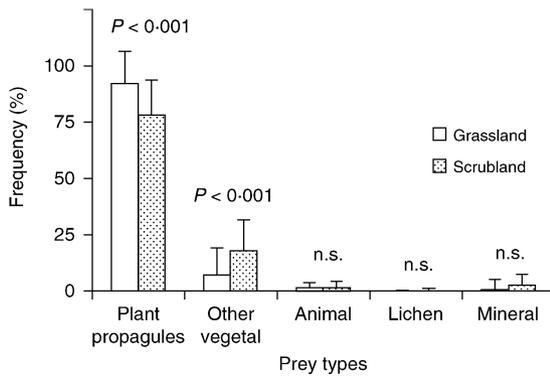


Fig. 1. Diet of *Messor barbarus* in grassland and scrubland. Mean frequency of the five groups of prey types considered for the study. Bars, standard deviations; $N = 34$ for both system types. Results of comparison t -test between grassland and scrubland are shown on top of bars. n.s., $P < 0.05$.

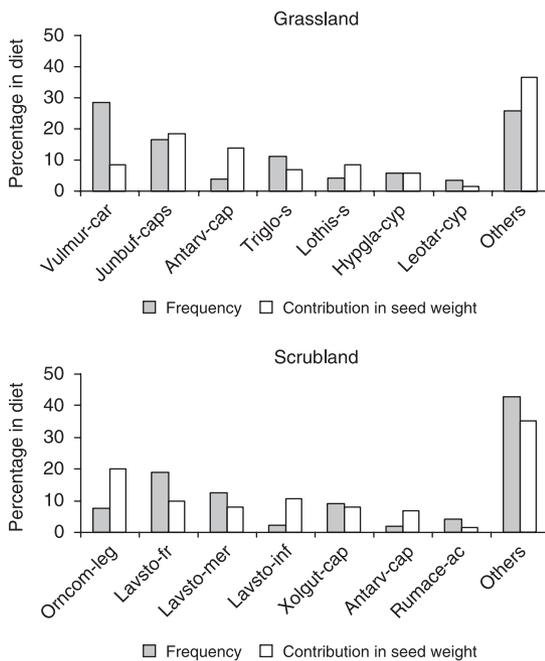


Fig. 2. Diet of *Messor barbarus* in grassland and scrubland. Mean frequency and contribution in seed weight of the main propagules collected by ants. Antarv, *Anthemis arvensis*; Hypgla, *Hypochoeris glabra*; Junbuf, *Juncus bufonius*; Lavsto, *Lavandula stoechas*; Leotar, *Leontodon taraxacoides*; Lothis, *Lotus hispidus*; Orncom, *Ornithopus compressus*; Rumace, *Rumex acetosella*; Triglo, *Trifolium glomeratum*; Vulmur, *Vulpia muralis*; Xolgut, *Xolantha guttata*. ac, Achene; cap, capitulum; caps, capsule; car, caryopsis; cyp, cypsela; f, fruit; inf, infrutescence; leg, legume; mer, mericarp; s, seed. Percentages refer to the plant propagule group.

a few animal remains (insects and excrement; >1% in both system types); some mineral particles in scrubland (2.4%); and, more rarely, lichen fragments.

Fig. 2 shows the main seeds and fruits of the propagule subgroup. In grassland the two most frequent prey types are the caryopsis (plus lemma and palea) of *Vulpia muralis* (28.7%) and the capsule (plus tepals) of *Juncus bufonius* (16.8%). In scrubland the commonest prey species is *L. stoechas*, which shows three pro-

pagule types: infrutescences (2.2%), fruits (19.1%), and mericarps (12.5%). Legumes of *Ornithopus compressus* are also frequent in the diet of scrubland ants (12.9%). The relative importance of each propagule type varies when considering its contribution in seed weight. From this point of view, the main prey in grassland is *J. bufonius* capsules (18.6%); *Anthemis arvensis* heads (14.0%); *V. muralis* caryopsis (8.5%); and *Lotus hispidus* seeds (8.5%). In scrubland, *O. compressus* contributes 24.1% of the total seed weight (legumes 20.1%, mericarps 4%). The three propagule types of *L. stoechas* together reach 28.4% (infrutescences 10.7%, fruits 9.8%, mericarps 7.9%). Appendix 3 shows data for all the propagules found in the study.

PROPAGULE SELECTION

Availability sampling found 79 propagule types in grassland and 71 in scrubland. We obtained selectivity indices for only 18 types in grassland and 22 in scrubland (Table 1), as the other types occurred in fewer than 10 observations of diet/availability (Appendix 3).

In grasslands the preferred propagule types were *J. bufonius* capsules, *Leontodon taraxacoides* cypselas and *V. muralis* caryopses. Most types present low or even null selectivity indices. After log-transformation and assessment of PICs, the normal distribution fitted the variable ($K-S d = 0.21$; $P > 0.20$). The existence of non-dichotomous nodes in the phylogenetic structure (Appendix 2) reduced the number of available contrasts to 14. All Pearson's correlation coefficients between $\ln(S + 1)$ and morphological variables were positive, and significant ($P < 0.05$) for $\ln(\text{weight})$ ($r_{12} = 0.61$); $\ln(\text{length})$ ($r_{12} = 0.60$); and $\ln(\text{dim3})$ ($r_{12} = 0.56$). The best regression model ($R^2 = 0.57$; $F_{2,11} = 7.27$; $P = 0.01$) for $\ln(S + 1)$ included two morphological variables: $\ln(\text{weight})$ ($\beta = 0.094$; $t_{12} = 2.29$; $P = 0.042$) and $\ln(\text{length})$ ($\beta = 0.098$; $t_{12} = 2.26$; $P = 0.045$).

In scrubland, the higher selection indices were shown by *O. compressus* legumes and *L. stoechas* calices (Table 1). We obtained 19 PICs from the 22 available propagule types. As in grassland, $\ln(\text{weight})$ and $\ln(\text{length})$ positively correlate with $\ln(S + 1)$ ($r_{17} = 0.53$ and $r_{17} = 0.80$, respectively). Fig. 3 shows a scatter plot for the best regression model ($R^2 = 0.64$; $F_{1,17} = 29.93$; $P < 0.001$) found for $\ln(S + 1)$, which included $\ln(\text{length})$ as a single dependent variable ($\beta = 0.114$; $t_{17} = 5.471$; $P < 0.001$).

Discussion

DIET

Seeds and fruits are the basis of the diet of *M. barbarus* in central Spain, which coincides with other observations for this genus (Hahn & Maschwitz 1985; Cerdá *et al.* 1994; Detrain *et al.* 2000). However, in scrubland ants collected a lower proportion of seed material, and took a relatively high amount of other plant fragments, which very often consisted of leaves and small branches

Table 1. Selection indices shown by propagule types present in at least 10 observations of diet/availability

Species	Propagule type	Grassland	Scrubland
<i>Agrostis castellana</i>	Caryopsis + l/p	–	0.00
<i>Anthemis arvensis</i>	Cypsella	0.23	0.00
<i>Anthoxanthum aristatum</i>	Caryopsis + l/p + fl	–	0.18
<i>Aphanes microcarpa</i>	Achene	0.00	–
<i>Asterolinon linum-stellatum</i>	Seed	–	0.00
<i>Cerastium</i> spp.	Seed	0.00	–
<i>Coronilla repanda</i> ssp. <i>dura</i>	Mericarp	–	0.13
<i>Halimium umbellatum</i>	Capsule	–	0.18
<i>Hypochoeris glabra</i>	Cypsella	0.40	0.09
<i>Juncus bufonius</i>	Capsule + tepals	0.86	–
<i>Lavandula</i> st. ssp. <i>pedunculata</i>	Mericarps + calyx	–	0.54
<i>Leontodon taraxacoides</i>	Cypsella	0.55	0.23
<i>Lotus hispidus</i>	Seed	0.48	–
<i>Moenchia erecta</i>	Capsule + calyx	0.00	–
<i>Montia fontana</i>	Seed	0.07	0.00
<i>Myosotis</i> spp.	Mericarp	–	0.00
<i>Ornithopus compressus</i>	Legume	–	0.93
<i>Poa annua</i>	Caryopsis + l/p	0.00	–
<i>Poa bulbosa</i>	Caryopsis + l/p	0.00	0.09
<i>Rumex acetosella</i> ssp. <i>angiocarpus</i>	Achene	–	0.31
<i>Scirpus setaceus</i>	Achene	0.00	–
<i>Silene scabriflora</i>	Seed	–	0.00
<i>Spergula arvensis</i>	Seed	0.00	0.00
<i>Spergula pentandra</i>	Seed	0.00	0.00
<i>Tolpis barbata</i>	Cypsella	0.20	–
<i>Trifolium arvense</i>	Seed	–	0.25
<i>Trifolium campestre</i>	Seed	0.17	0.21
<i>Trifolium glomeratum</i>	Seed	0.04	–
<i>Vulpia ciliata</i>	Caryopsis + l/p	–	0.17
<i>Vulpia muralis</i>	Caryopsis + l/p	0.74	0.39
<i>Xolantha guttata</i>	Capsule	–	0.30

l/p, lemma and palea.

belonging to *Lavandula* and *Halimium*. We lack data to explain this finding, which probably requires research on the chemical composition of the collected fragments, and more information on their use by the ants. Differences in seed availability between system types may also be involved. As in most studies of harvester ants (Hahn *et al.* 1985; Hobbs 1985; Cerdá *et al.* 1994;

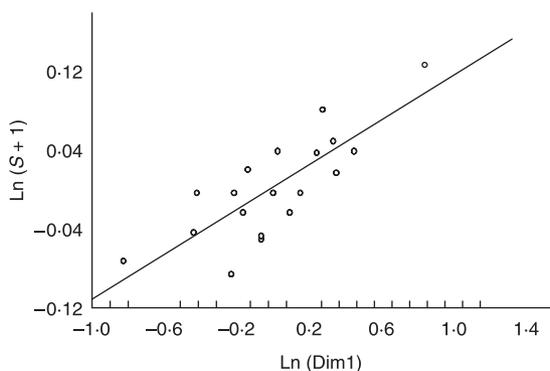


Fig. 3. Scrubland, propagule selection by *M. barbarus*. Phylogenetically independent contrasts in $\ln(\text{Dim}1)$ against contrasts in $\ln(S+1)$. S, Selectivity index. Dim1 given in mm. $N = 19$ contrasts.

Vorster, Hewitt & van der Westhuizen 1994; Detrain *et al.* 2000), we found a small proportion of animal fragments in the diet, which are normally interpreted as a complementary protein source. The sporadic collection of soil particles could be explained by the presence of resin exudates on them (Fernández-Escudero & Tinaut 1993).

Most propagules collected by *M. barbarus* belong to a small number of species, in agreement with previous research into harvester ants (Crist & Wiens 1994; Andersen *et al.* 2000; Detrain *et al.* 2000; Wilby & Shachak 2000; Willott *et al.* 2000). In each system type, only two plant species comprise around half of the propagules taken by ants. However, some of the most frequent types (e.g. *V. muralis* caryopsis) show relatively small contributions when analysed in terms of weight of seed content. In other words, in at least some cases ants apparently focus their foraging effort on lowly profitable prey.

PREY SELECTION

Our results reveal a clear association between prey selection and prey length in both system types. The model estimated for grassland includes a second variable, prey weight, a trait that has been related to ant preference in previous research (Baroni-Urbani 1992; Detrain *et al.* 2000).

Selection for heavy prey cannot be justified on the basis of energy yield, as the variable 'weight of seed content', more closely related to the propagule calorific value, does not correlate with selectivity in either of the two system types. In fact, heavy propagules normally coincide with those possessing appendages for seed dispersal, which are later refused by ants and discharged into the chaff piles. Outstanding examples are caryopsis of *V. muralis*, fruits of *L. stoechas*, legumes of *O. compressus*, or capsules of *J. bufonius*. In the latter case we observed that some capsules transported by ants were actually empty of seeds.

In harvester ants, the balance between energy costs and benefits of resource collection appears to be positive, even for very small prey (Fewell 1988; Baroni-Urbani & Nielsen 1990). In this case the foraging strategy would reduce time costs rather than enhance the energy benefit per prey (Morehead & Feener 1998; Reyes-López & Fernández-Haeger 2001). Shorter trip times should increase the amount of prey carried into the nest, and reduce exposure to predators and desiccation risk. In fact, preference for long propagules can be explained as a mere effect of a time-saving foraging strategy. Regardless of their calorific content, long propagules are more easily detectable, and tend to be buried more slowly, than short ones (Peart 1984; Thompson *et al.* 1993), which makes them more accessible to ants. If so, an apparent preference for long propagules is expected even if workers forage in a non-selective way. Propagule enlargement can be a consequence of the possession of awns, pappus or other dispersal appendages. The

acquisition of this type of prey suggests an increase in processing time inside the nest, although this type of task is likely to be less limited by environmental conditions or predation risk.

EFFECTS OF *M. BARBARUS* ON VEGETATION

Detrain *et al.* (2000) and Willott *et al.* (2000) have suggested that *Messor* ants could favour small-seeded species in communities where they are abundant. According to our data, risk of predation by *M. barbarus* in Mediterranean grassland and scrubland is higher for long propagules, and this can indirectly promote the occurrence of small-seeded species without dispersal appendages. Previous research shows that this type of species is over-represented in Mediterranean grasslands (Azcárate *et al.* 2002).

However, we lack evidence in favour of a hypothetical shortening of propagules in response to *M. barbarus* activity. Production of small seeds has been related to endozoochory (Malo & Suárez 1995) or mediterranean climate conditions (Azcárate *et al.* 2002), and can also be a simple consequence of allometric or phylogenetic constraints (Herrera 1992; Kang & Primack 1999; Guerrero-Campo & Fitter 2001). In addition, we lack detailed information on the phenotypic variability of each species; inheritance of seed attributes; or strength of the above-mentioned factors as selective pressures, making a discussion that is consistent in evolutionary terms difficult.

Still, *M. barbarus* ants are likely to play a role in the plant composition of Mediterranean grassland and scrubland. Both types of community have been modelled by human management (Joffre, Rambal & Ratter 1999), and thus can be considered young systems whose plant species composition has recently been selected from the regional flora. In this context, it seems plausible that *M. barbarus* activity limits the abundance of long propagules in Mediterranean grassland and scrubland, and thus indirectly favours small-seeded species without dispersal appendages.

Although most large-seeded species in Mediterranean grasslands are scarce (Azcárate *et al.* 2002), there are some remarkable exceptions. For instance, long-seeded species such as *V. muralis* and *L. taraxacoides* are widespread in Mediterranean grasslands, despite the fact that their propagules are consistently selected by *M. barbarus*. Research into the fate of these seeds is necessary, as it should not be assumed that all prey brought into nests by *Messor* ants are consumed (Retana *et al.* 2004). Mutualistic interactions such as dyszoochory could contribute to the success of certain long-seeded species in communities where *Messor* ants are abundant.

In scrubland, the risk of seed predation is more heterogeneous, favouring the existence of refuge habitats that are safe from the action of harvester ants (Azcárate *et al.* 2003). This could explain the high occurrence of largely predated species, such as *O. compressus* and *L. stoechas*. For the latter species, evidence also

suggests the existence of ant–plant mutualistic interactions (unpublished data). The effects of other harvester ants, such as *M. bouvieri* (Azcárate *et al.* 2003), whose selection criteria have not been studied, may overlap with those of *M. barbarus*, making the final vegetation patterns more complex in scrubland than in grassland.

In summary, propagule morphological traits (length and total weight) are involved in selection by *M. barbarus* ants in both Mediterranean grassland and scrubland. While the evolutionary consequences of this behaviour are difficult to derive, it is likely that ants affect plant species composition in these system types by limiting the abundance of long propagules. More research is needed in order to corroborate these predictions, and to answer some questions that remain open. From the ants' point of view, our data are consistent with a hypothetical relationship between collection and detectability, although the behavioural interpretation of the selection criteria is still incomplete. From the plants' side, we need to understand the mechanisms that allow the success of certain long-seeded species in habitats where their propagules are collected in quantity by ants. In this sense, the effects of collateral ant–plant mutualistic interactions should not be discarded.

Acknowledgements

We are grateful to C. Levassor for her help in the field work. The study was supported by the Spanish Ministry of Science and Technology (projects AMB 990382 and REN 2003-01562), the Spanish Ministry of Education and Culture (FPI scholarships to F.M.A. and A.M.S), and the Madrid Regional Government (FPI scholarship to L.A.).

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Received 16 September 2004; revised 2 December 2004;
accepted 6 December 2004

Appendix 1

Table A1. Morphological traits of the propagule types used to estimate regression models

Species	Propagule type	No. seeds	Total weight (mg)	Seed content (mg)	Dim1 (mm)	Dim2 (mm)	Dim3 (mm)	Shape
<i>Agrostis castellana</i>	Caryopsis + l/p	1	0.38	0.26	2.30	0.96	0.96	0.11
<i>Anthemis arvensis</i>	Cypsella	1	0.72	0.72	1.97	1.01	1.01	0.08
<i>Anthoxanthum aristatum</i>	Spikelet	1	0.26	0.23	6.78	3.97	0.86	0.19
<i>Aphanes microcarpa</i>	Achene	1	0.19	0.19	0.73	0.50	0.25	0.11
<i>Asterolinon linum-stellatum</i>	Seed	1	0.29	0.29	1.05	0.86	0.43	0.09
<i>Cerastium</i> sp.	Seed	1	0.05	0.05	0.57	0.50	0.16	0.15
<i>Coronilla repanda</i> ssp. <i>dura</i>	Mericalp	1	1.10	0.60	3.60	1.05	1.05	0.17
<i>Halimium umbellatum</i> ssp. <i>viscosum</i>	Capsule	6	16.67	8.57	5.87	4.07	4.07	0.03
<i>Hypochoeris glabra</i>	Cypsella	1	0.78	0.78	9.10	3.61	3.61	0.12
<i>Juncus bufonius</i>	Capsule + tepals	16	1.20	0.46	5.75	2.20	2.20	0.13
<i>Lavandula stoechas</i> ssp. <i>pedunculata</i>	Calyx + mericalps	0.75	1.40	0.68	6.50	3.00	3.00	0.10
<i>Leontodon taraxacoides</i> ssp. <i>longirostris</i>	Cypsella	1	0.24	0.24	10.32	3.44	3.44	0.15
<i>Lotus hispidus</i>	Seed	1	1.60	1.60	0.85	0.81	0.50	0.05
<i>Moenchia erecta</i>	Capsule + calyx	5	0.45	0.21	5.25	3.40	3.40	0.04
<i>Montia fontana</i>	Seed	1	0.08	0.08	0.89	0.89	0.45	0.08
<i>Myosotis</i> spp.	Mericalp	1	0.13	0.13	1.06	0.69	0.63	0.06
<i>Ornithopus compressus</i>	Legume	6	32.31	14.81	22.11	2.21	1.20	0.23
<i>Poa annua</i>	Caryopsis + l/p	1	0.21	0.15	3.10	1.10	1.00	0.15
<i>Poa bulbosa</i>	Caryopsis + l/p	1	0.13	0.08	2.51	0.79	0.79	0.16
<i>Rumex acetosella</i> ssp. <i>angiocarpus</i>	Achene	1	0.36	0.36	1.24	0.88	0.88	0.03
<i>Scirpus setaceus</i>	Achene	1	0.05	0.05	0.90	0.59	0.59	0.04
<i>Silene scabriflora</i>	Seed	1	0.32	0.32	0.70	0.63	0.53	0.02
<i>Spergula arvensis</i>	Seed	1	0.16	0.16	0.87	0.87	0.65	0.02
<i>Spergula pentandra</i>	Seed	1	0.14	0.14	1.98	1.98	0.30	0.24
<i>Tolpis barbata</i>	Cypsella	1	0.10	0.10	3.36	1.44	1.44	0.11
<i>Trifolium arvense</i>	Seed	1	0.29	0.29	0.98	0.73	0.73	0.02
<i>Trifolium campestre</i>	Seed	1	0.25	0.25	1.27	0.83	0.42	0.11
<i>Trifolium glomeratum</i>	Seed	1	0.45	0.45	1.54	1.28	1.28	0.01
<i>Vulpia ciliata</i>	Caryopsis + l/p	1	0.19	0.12	11.23	0.51	0.34	0.31
<i>Vulpia muralis</i>	Caryopsis + l/p	1	0.19	0.10	20.65	0.54	0.81	0.31
<i>Xolantha guttata</i>	Capsule	30	1.90	1.32	3.60	2.80	2.80	0.02

l/p, Lemma and palea; No. seeds, average number of seeds per propagule type.

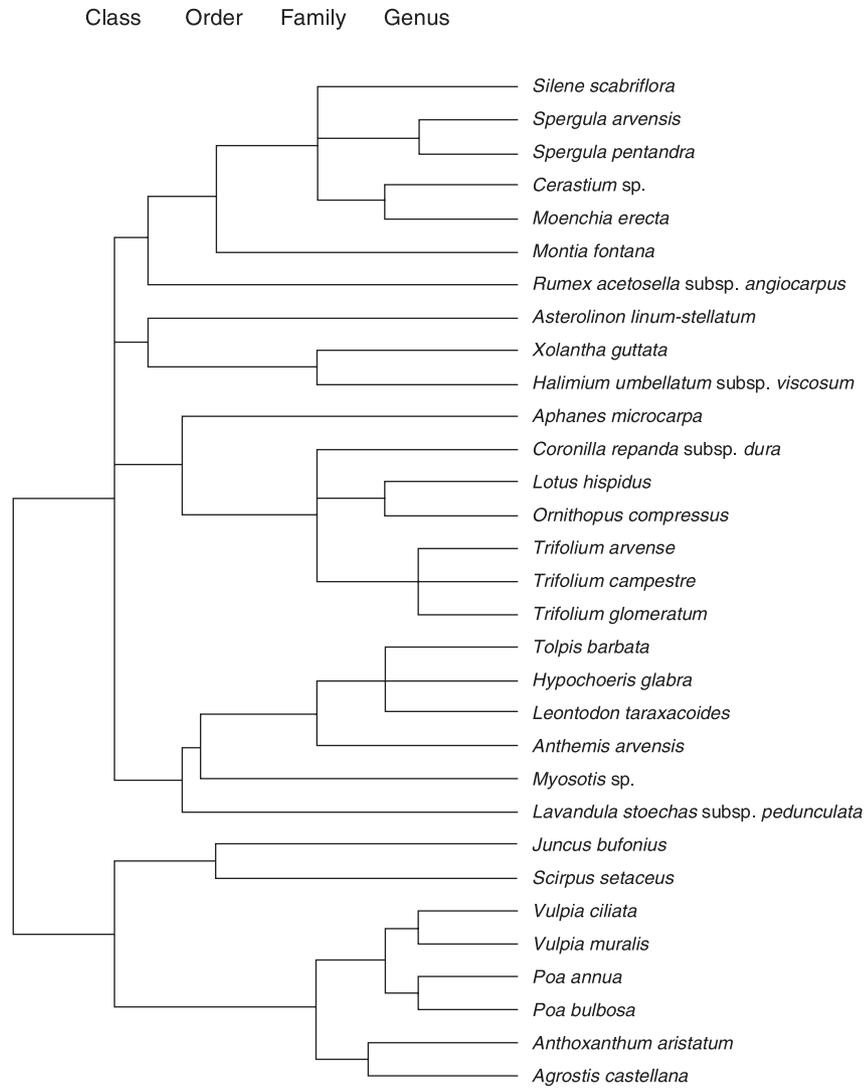


Fig. A1. Taxonomic structure followed to infer the phylogeny of the species included in the analyses. See Azcárate *et al.* (2002) for references used to compose the taxonomic tree.

Appendix 3

Table A2. Propagule types recorded in the samplings of diet and availability

Species	Propagule type	Diet						Availability		Diet and/or availability	
		Mean frequency (%)		Contribution in seed weight (%)		No. occurrences (n = 34)		No. occurrences (n = 34)		No. occurrences (n = 34)	
		Grass	Scrub	Grass	Scrub	Grass	Scrub	Grass	Scrub	Grass	Scrub
<i>Agrostis castellana</i>	Caryopsis	–	4.23	–	2.17	–	5	2	7	2	11
	Caryopsis + l/p	–	–	–	–	–	–	6	14	6	14
<i>Aira caryophylla</i>	Caryopsis + l/p	–	–	–	–	–	–	3	5	3	5
<i>Alyssum granatense</i>	Silicula	–	0.05	–	0.03	–	1	–	–	–	1
<i>Andryala integrifolia</i>	Cypsela	0.06	–	0.00	–	1	–	5	9	5	9
	Capitulum	–	0.14	–	0.48	–	1	–	2	–	3
<i>Anthemis arvensis</i>	Cypsela	0.88	–	0.63	–	4	–	15	13	18	13
	Capitulum	4.05	1.92	14.02	6.71	4	5	–	–	4	5
<i>Anthoxanthum aristatum</i>	Spikelet	0.41	2.91	0.13	1.02	2	6	3	16	5	17
<i>Aphanes microcarpa</i>	Achene	–	–	–	–	–	–	31	6	31	6
<i>Arrhenatherum album</i>	Caryopsis + l/p	–	1.19	–	1.84	–	1	–	5	–	6
<i>Asterolinon linum-stellatum</i>	Seed	–	–	–	–	–	–	1	15	1	15
<i>Bromus hordeaceus</i>	Caryopsis + l/p	–	–	–	–	–	–	–	2	–	2
<i>Bromus tectorum</i>	Caryopsis + l/p	–	0.20	–	0.24	–	1	1	–	1	1
<i>Capsella bursa-pastoris</i>	Seed	0.93	–	0.16	–	1	–	2	–	3	–
	Silicula	0.53	–	0.90	–	1	–	3	–	4	–
<i>Carduus tenuiflorus</i>	Cypsela	–	–	–	–	–	–	1	–	1	–
<i>Carex divisa</i>	Utriculus	–	–	–	–	–	–	8	–	8	–
<i>Cerastium ramosissimum</i>	Capsule + calyx	1.63	–	1.58	–	1	–	–	–	1	–
<i>Cerastium semidecandrum</i>	Capsule + calyx	0.23	–	0.18	–	1	–	–	–	1	–
<i>Cerastium</i> sp.	Seed	–	–	–	–	–	–	19	9	19	9
	Capsule + calyx	0.08	–	0.03	–	1	–	7	–	8	–
<i>Coincya monensis</i>	Seed	–	–	–	–	–	–	–	9	–	9
ssp. <i>orophila</i>											
<i>Coronilla repanda</i>	Mericalp	–	0.93	–	0.64	–	2	–	16	–	16
ssp. <i>dura</i>											
<i>Corynephorus canescens</i>	Spikelet	–	–	–	–	–	–	–	3	–	3
<i>Corynephorus fasciculatus</i>	Caryopsis + l/p	–	–	–	–	–	–	–	4	–	4
<i>Crepis capillaris</i>	Capitulum	–	–	–	–	–	–	1	–	1	–
<i>Cynodon dactylon</i>	Caryopsis + l/p	–	–	–	–	–	–	–	2	–	2
<i>Cytisus scoparius</i>	Seed	–	1.88	–	3.09	–	5	–	1	–	5
<i>Echium vulgare</i>	Mericalp	–	–	–	–	–	–	–	2	–	2
<i>Erodium cicutarium</i>	Mericalp	0.46	0.11	0.52	0.07	3	1	5	–	7	1
<i>Erophila verna</i>	Silicula	0.13	–	0.37	–	1	–	4	–	4	–
<i>Euphorbia exigua</i>	Seed	–	–	–	–	–	–	8	1	8	1
<i>Festuca rothmaleri</i>	Caryopsis + l/p	–	0.05	–	0.10	–	1	3	4	3	4
<i>Galium parisiense</i>	Mericalp	–	–	–	–	–	–	5	1	5	1
<i>Halimium umbellatum</i>	Seed	–	1.40	–	2.67	–	1	2	3	2	3
ssp. <i>viscosum</i>	Capsule	–	0.91	–	2.36	–	4	–	11	–	11
<i>Holcus setiglumis</i>	Spikelet	–	–	–	–	–	–	1	5	1	5
<i>Hymenocarpus lotoides</i>	Seed	–	0.06	–	0.01	–	1	3	–	3	1
	Mericalp	–	0.31	–	0.06	–	2	–	–	–	2
<i>Hypochoeris glabra</i>	Cypsela	5.88	1.39	5.60	0.53	10	3	14	23	17	22
	Capitulum	–	–	–	–	–	–	1	–	1	–
<i>Jasione montana</i>	Capsule	–	2.36	–	0.15	–	1	–	2	–	3
<i>Juncus acutiflorus</i>	Capsule + tepals	–	–	–	–	–	–	3	3	3	3
<i>Juncus bufonius</i>	Capsule + tepals	16.73	–	18.58	–	18	–	15	–	21	–
<i>Juncus capitatus</i>	Capsule + tepals	–	–	–	–	–	–	2	–	2	–
<i>Lamium amplexicaule</i>	Mericalp	–	–	–	–	–	–	1	2	1	2
<i>Lavandula stoechas</i>	Mericalp	–	12.53	–	7.97	–	14	1	30	1	29
ssp. <i>pedunculata</i>	Calyx + mericarps	–	19.09	–	9.80	–	17	–	19	–	26
	Infrutescence	–	2.24	–	10.68	–	8	–	–	–	8
<i>Leontodon taraxacoides</i>	Cypsela	3.50	0.63	1.41	0.20	9	5	7	12	15	13
ssp. <i>longirostris</i>	Capitulum	–	0.40	–	1.48	–	1	1	–	1	1
<i>Logfia minima</i>	Capitulum	–	–	–	–	–	–	3	–	3	–
<i>Lotus hispidus</i>	Seed	4.32	1.77	8.53	2.48	6	2	7	1	11	3
	Legume	0.20	–	1.77	–	1	–	–	–	1	–
<i>Lupinus hispanicus</i>	Seed	–	0.28	–	1.24	–	1	1	–	1	1
<i>Melica ciliata</i>	Caryopsis + l/p	–	0.09	–	0.01	–	1	–	–	–	1
<i>Merendera pyrenaica</i>	Seed	–	–	–	–	–	–	3	–	3	–
<i>Mibora minima</i>	Spikelet	–	0.11	–	0.01	–	1	–	1	–	1
<i>Micropyrum tenellum</i>	Caryopsis + l/p	–	–	–	–	–	–	–	9	–	9
<i>Moenchia erecta</i>	Capsule + calyx	0.05	0.16	0.00	0.04	1	1	14	2	14	2
<i>Molineriella laevis</i>	Caryopsis + l/p	–	0.26	–	0.01	–	1	–	–	–	1
<i>Montia fontana</i>	Seed	1.61	0.04	0.27	0.00	5	1	28	14	28	14

Table A2. Continued.

Species	Propagule type	Diet				Availability				Diet and/or availability	
		Mean frequency (%)		Contribution in seed weight (%)		No. occurrences (n = 34)		No. occurrences (n = 34)		No. occurrences (n = 34)	
		Grass	Scrub	Grass	Scrub	Grass	Scrub	Grass	Scrub	Grass	Scrub
<i>Myosotis</i> sp.	Mericaarp	–	–	–	–	–	–	6	11	6	11
<i>Ornithopus compressus</i>	Mericaarp	0.11	1.29	0.45	4.01	1	2	5	16	5	16
	Legume	0.06	7.72	1.49	20.08	1	13	–	2	1	14
<i>Ornithopus perpusillus</i>	Mericaarp	–	–	–	–	–	–	–	3	–	3
<i>Parentucellia latifolia</i>	Capsule	–	–	–	–	–	–	2	–	2	–
<i>Petrorrhagia nanteuillii</i>	Seed	–	3.19	–	1.19	–	3	–	4	–	4
	Capsule	–	0.21	–	0.41	–	2	–	3	–	3
<i>Plantago lagopus</i>	Capsule	0.10	–	0.04	–	1	–	3	–	4	–
	Head	0.24	–	1.86	–	1	–	–	–	1	–
<i>Plantago lanceolata</i>	Seed	–	–	–	–	–	–	2	5	2	5
	Capsule	–	1.32	–	1.49	–	4	2	4	2	7
<i>Poa annua</i>	Caryopsis + l/p	–	–	–	–	–	–	16	1	16	1
	Spikelet	1.87	–	3.26	–	2	–	–	–	2	–
<i>Poa bulbosa</i>	Caryopsis + l/p	–	0.04	–	0.00	–	1	12	10	12	11
	Spikelet	1.56	–	1.64	–	2	–	1	–	3	–
<i>Polycarpon tetraphyllum</i>	Seed	–	–	–	–	–	–	1	–	1	–
<i>Rumex acetosella</i>											
ssp. <i>angiocarpus</i>	Achene	–	4.23	–	1.49	–	4	8	10	8	13
<i>Sagina apetala</i>	Capsule	–	–	–	–	–	–	1	–	1	–
<i>Sanguisorba minor</i>	Achene	–	–	–	–	–	–	2	–	2	–
<i>Scilla autumnalis</i>	Seed	0.64	–	1.14	–	1	–	–	–	1	–
	Capsule	0.36	–	1.11	–	1	–	–	–	1	–
<i>Scirpus setaceus</i>	Achene	–	–	–	–	–	–	20	2	20	2
<i>Scleranthus delortii</i>	Achene	0.23	–	0.10	–	1	–	3	4	3	4
<i>Senecio jacobaea</i>	Capitulum	0.24	–	2.12	–	1	–	1	–	2	–
<i>Silene gallica</i>	Seed	–	–	–	–	–	–	–	4	–	4
	Capsule + calyx	–	0.30	–	0.44	–	2	–	–	–	2
<i>Silene scabriflora</i>	Seed	–	–	–	–	–	–	1	11	1	11
	Capsule	–	–	–	–	–	–	–	2	–	2
<i>Spergula arvensis</i>	Seed	–	–	–	–	–	–	26	15	26	15
	Capsule	–	–	–	–	–	–	2	–	2	–
<i>Spergula pentandra</i>	Seed	–	–	–	–	–	–	21	20	21	20
<i>Spergularia purpurea</i>	Capsule	–	–	–	–	–	–	3	–	3	–
<i>Teesdalia coronopifolia</i>	Silicula	0.23	0.10	0.28	0.01	1	1	–	–	1	1
<i>Thapsia villosa</i>	Mericaarp	–	0.10	–	0.08	–	1	–	2	–	3
<i>Tolpis barbata</i>	Cypsela	0.30	–	0.03	–	3	–	12	9	15	9
<i>Trifolium arvense</i>	Seed	–	0.43	–	0.10	–	3	–	11	–	12
	Achene + calyx	0.99	–	0.90	–	2	–	2	4	4	4
<i>Trifolium campestre</i> s.l.	Seed	2.24	3.77	1.46	0.78	6	9	28	23	30	24
<i>Trifolium campestre</i>	Achene + calyx	2.16	0.83	0.93	0.17	4	5	2	8	6	12
	Head	0.40	0.29	2.28	1.41	1	3	1	–	2	3
<i>Trifolium dubium</i>	Achene + calyx	–	–	–	–	–	–	15	11	15	11
	Head	–	0.13	–	0.87	–	1	–	–	–	1
<i>Trifolium glomeratum</i> s.l.	Seed	11.18	–	6.96	–	16	–	34	3	34	3
<i>Trifolium glomeratum</i>	Achene + calyx	1.82	–	1.10	–	4	–	9	–	11	–
	Head	–	–	–	–	–	–	2	–	2	–
<i>Trifolium striatum</i>	Seed	–	0.21	–	0.04	–	1	4	4	4	5
	Achene + calyx	0.16	0.58	0.46	0.55	2	3	2	7	4	9
<i>Trifolium strictum</i>	Seed	–	–	–	–	–	–	1	–	1	–
<i>Trifolium subterraneum</i>	Seed	0.11	–	1.15	–	1	–	4	–	5	–
<i>Veronica arvensis</i>	Seed	–	–	–	–	–	–	–	–	1	–
<i>Veronica verna</i>	Seed	–	–	–	–	–	–	–	1	–	1
	Capsule	0.82	–	1.58	–	2	–	2	–	3	–
<i>Vulpia ciliata</i>	Caryopsis + l/p	–	1.14	–	0.07	–	5	2	11	2	12
<i>Vulpia muralis</i>	Caryopsis	–	–	–	–	–	–	6	9	6	9
	Caryopsis + l/p	28.60	3.93	8.55	0.46	22	9	25	16	26	18
	Spikelet	0.26	0.14	0.32	0.06	2	1	–	–	2	1
<i>Xolantha guttata</i>	Capsule	0.31	9.15	0.85	7.86	4	20	7	17	9	23
Unknown		3.31	3.27	5.27	2.32	11	14	12	14	–	–
No. propagule types		43	51	43	51	43	51	79	71	90	86
		74		74		74		103		120	
No. species		33	40	33	40	33	40	64	59	72	67
		54		54		54		80		90	

l/p, Lemma and palea.

Nomenclature follows Castroviejo (1986–2003), except taxa yet to be covered, which follow Tutin *et al.* 1964–80).