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ORIGINAL PAPER

Effect of substrate roughness on load selection in the seed-harvester ant *Messor barbarus* L. (Hymenoptera, Formicidae)

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Abstract We investigated the effect of substrate roughness on load selection in the seed-harvester ant *Messor barbarus*. Ants were forced to travel either on sand or on gravel to reach a seed patch containing seed fragments of different weights. We hypothesized that foragers travelling on a rough substrate could either increase their load as a result of the increased distance travelled (due to a more sinuous path and an increase in the vertical component of the path) or decrease their load because of the anticipated difficulty of moving with a heavy load on a rough surface. Our results were consistent with neither of these hypotheses: Load selection by ants did not depend on the roughness of the substrate encountered during their outbound trip. The main effect of substrate roughness was to slow down the progression of the ants and increase their probability of dropping or transferring heavy seeds on their way back to the nest, thus resulting in an overall reduction of the rate of seed return to the nest.

Keywords Ant · Foraging · Load transport · *Messor barbarus* · Substrate roughness

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Introduction

Central-place foraging animals are faced with particular energetic constraints because the energetic gain of the food they retrieve depends on the energy they have spent during both their unladen outbound trip and their laden inbound trip. This leads to particular predictions concerning the way they should select food in order to maximize their net rate of energy intake (Orians and Pearson 1979; Stephens and Krebs 1986). One of these predictions, derived from the marginal value theorem (Charnov 1976), states that they should be more selective in their choice of food and, in the case of single-prey loader, should choose food items with greater energetic contents as distance from the central place to the food increases (Orians and Pearson 1979; Stephens and Krebs 1986). This can occur not only when the straight line distance of the food from the central place increases, but also when the actual distance covered by an animal increases because of a higher tortuosity of its path due to moving through a structurally complex environment (Crist and Wiens 1994; Wiens et al. 1995; Ross et al. 2005).

Substrate roughness is one element that can contribute to the structural complexity of an environment. In central-place foraging animals, it is bound to have important consequences on the net rate of food return, either by decreasing the locomotory rate (Fewell 1988; Powell and Franks 2005) and/or by increasing the difficulty in transporting a heavy food load. The importance of this factor is attested by the fact that many central-place foraging animals, e.g. rodents (Jamon 1994) and humans (Bates 1950; Helbing et al. 1997), move within their home range along heavily worn paths that offer an even and plain surface on which to walk and that facilitate load transport. This phenomenon is common in ants forming big colonies. In the leaf-cutting ant *Atta cephalotes* for example, moving on physical trails allows ants to increase their locomotory rate by a four to tenfold factor compared to moving on uncleared ground (Rockwood and Hubbell 1987). In this paper, we report the results of laboratory experiments in which we tested the effect of substrate roughness on load selection in the seed-harvesting ant *Messor barbarus* L. 1767. We hypothesized that a rough substrate could have direct and indirect effects on the loads transported by ants. Whilst direct effects act on the process of load selection by individual ants, indirect effects act on the subsequent transport of the loads.

A rough substrate can have two direct and opposite effects on load selection. If ants base their choice solely on the distance covered during their outbound trip, then, according to optimal foraging theory (Stephens and Krebs 1986; Reyes-Lopez 1987), they should choose heavier loads after travelling on a rough substrate. In addition, the loads chosen should increase as the distance from the nest increases. If, on the other hand, ants base their choice solely on the anticipated difficulty of moving with a heavy load on an uneven, irregular surface, they should choose smaller loads, whatever the distance of the seed patch. Note that the word anticipation does not imply a complex cognitive operation. Ants have been shown to be able to integrate the horizontal component of their path (Wohlgemuth et al. 2001) and they could simply base their load choice on the amount of time it takes them to travel a unit length of the horizontal component of their path. Finally, if ants take into account both the distance covered during their outbound trip and the difficulty of moving with a heavy load on a rough substrate, the loads chosen should be smaller after walking on a rough substrate, but should also increase with the distance of the seed patch from the nest. In order to dissociate the effect of increased distance covered due to walking on a rough substrate from the effect of the increased difficulty of walking with a load on an uneven surface, we tested the ants with seed patches placed at three different distances from their nest (1, 3 or 6 m) and on two different substrates differing in roughness (sand and gravel).

In addition to having direct effects on load selection, a rough substrate could also have an indirect effect by acting as a sieve on the load carried by ants: Whilst progressing on a rough substrate, ants transporting heavy loads could have a higher probability of dropping their load than ants transporting lighter loads. This effect is addressed by comparing the load carried by ants picked up just after leaving the seed patch to those carried by ants picked up at some distance from the seed patch.

Materials and methods

Species studied and rearing conditions

We used five colonies of *M. barbarus* collected in the south of France (Saint-Hyppolite, Aude) in autumn 2006 and spring 2008 and 2010. This species is characterized by a high degree of worker polymorphism (body mass ranges from 1.3 to 31.5 mg in our study). It plays an important role as a seed predator in Mediterranean grassland environments (Cerdan 1989; López et al. 1993; Detrain and Tasse 2000; Detrain et al. 2000; Azcárate and Peco 2003, 2007; Azcárate et al. 2005). *M. barbarus* foragers also contribute to seed dispersion through dyszoochory, i.e. the accidental dropping of seeds on the way to the nest or the mistaken rejection of intact seeds on refuse piles (Wolff and Debussche 1999; Azcárate and Peco 2007). Seed collection is mainly achieved through the use of trunk trails that connect the nest entrances to temporary seed patches (Detrain et al. 2000). The five colonies were reared in the laboratory under controlled temperature (25±1.5°C) and photoperiod (12:12 L/D) conditions. They were used as a stock to constitute five standardized experimental groups without queen or brood and containing about 1,000 workers. The number of workers in each experimental group was kept constant throughout the experiments by taking ants from the stock colonies to compensate for loss and death. The ants of each experimental group were housed in a plastic box of 17.0-cm diameter which was connected to a rectangular plastic box (25.5×18.5 cm) that was used as a foraging area. The walls of the foraging area were coated with Fluon® to prevent ants from escaping. Ants were continuously deprived of seeds except during the experiments. Each experimental group was starved for 6 days before the day of the experiments. After being tested, ants were given access to food (a mixed diet of vitamin-enriched food (Bhatkar and Whitcomb 1970) and maggots, but not seeds) only for 24 h.

Experimental setup

The experimental setup consisted of a foraging arena (100.0×60.0 cm) which was connected to the foraging area of the experimental groups by a cardboard bridge (length× width, 38.5×2.0 cm). The foraging arena was partitioned by six PVC vertical walls (length×height, 90.0×8.0 cm) to create a 10-cm-wide corridor that could be extended to a maximal length of 6 m (Fig. 1). All walls were coated with Fluon® to prevent ants from escaping.

To study the effect of substrate roughness on seed selection, the floor of the arena was covered by either a fine or a coarse substrate (a layer of sand or gravel, respectively). We used white marble calibrated granules for the two substrates (OMG,

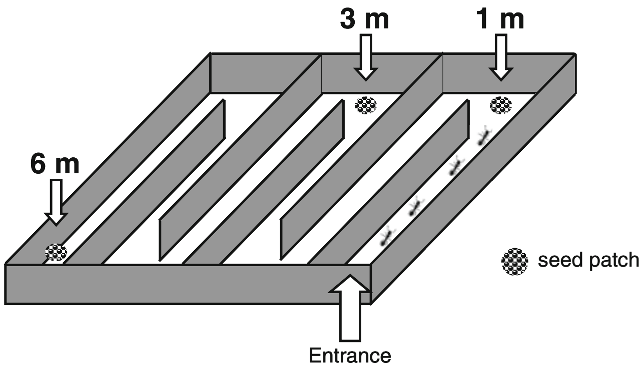

Fig. 1 Experimental setup. Ants had access to a foraging arena by a cardboard bridge and, depending on the experiment, could find a seed patch at 1, 3 or 6 m from the arena entrance. The floor of the arena was covered either by sand (granule size, 1.25–2.50 mm) or gravel (granule size, 8.00–16.80 mm)

Onyx et Marbres Granulés, France). The size range of the granules was 1.25–2.50 mm for the sand and 8.00–16.80 mm for the gravel. The granules were glued as a single layer on 10-cm-wide PVC plates that were laid on the floor of the arena during the experiments. To study the effect of distance on seed selection, the seed patch was placed at 1, 3 or 6 m from the foraging arena entrance. Ants could not go beyond this distance as the corridor was closed just after the location where the seeds were deposited.

Experimental procedure

For a given substrate (sand or gravel), an experimental session consisted of testing the same experimental group within the same day at three different distances (1, 3 and 6 m, chosen in a random order). In order for the ants to get familiarized with the setup, foraging workers were given access to the whole foraging arena for 12 h before the start of the experiment. The arena did not contain food during this period. All ants were removed from the arena half an hour before the beginning of the experimental session.

We used oat (*Avena sativa*) seeds to test the influence of distance and substrate roughness on load selection. To create seeds of different sizes, a small quantity of seeds was crushed in a mixer and the seed fragments obtained were sorted into four weight categories: 0.4–5.0, 5.0–10.0, 10.0–15.0 and >15.0 mg. We discarded seed fragments weighing <0.4 mg because in their natural environment, *M. barbarus* foragers rarely collect seeds of this weight (Detrain and Pasteels 2000). The range of seed weights offered to the ants in our experiment was 1.25–35.27 mg. This corresponds to two thirds of the range of the weights of the seeds harvested by *M. barbarus* in a Mediterranean grassland environment (Detrain and Pasteels 2000). Twenty seed fragments of each size category were offered to the ants within a patch. The seeds collected by ants during an experiment were not replaced. To offer a non-slippery surface to the ants, the 80 seed fragments were arranged randomly on a piece of abrasive paper (7.0×5.0 cm). Ants were given access to the setup as soon as the seeds were placed in the arena.

In order to study simultaneously the ant locomotory and seed manipulation behaviour, the experimental setup was filmed by two cameras. The first camera (GANZ® ZC-Y11P3), equipped with a macro-lens, recorded the events occurring on the seed patch. The second camera (SONY® DCR-VX2000E) filmed the last 50 cm of the corridor before the seed patch. The fields of both cameras overlapped on the seed patch. The two cameras allowed us to follow each ant on their way to the seed patch (when unladen), whilst on the seed patch and whilst returning from the patch (when laden with a seed fragment).

The first series of experiments was designed to evaluate both the difficulties of ants in walking on a rough substrate with or without a load and the effect of substrate roughness on load choice. Returning ants and their loads were picked up with forceps after they had travelled 40 cm from the seed patch. They were immediately placed in numbered individual vials, and their fresh wet mass, along with the weight of the seed they carried, were subsequently measured with a precision balance (±0.1mg). An experiment stopped after 20 loaded workers had been captured. All ants were then removed from the foraging area, and after a minimal interval of 30 min, we proceeded with another experiment. In order to eliminate any chemical cues that ants could have deposited during the experiments, the PVC plates on which the substrate was glued was washed with soapy water at the end of the experimental session. The number of ants tested in this first series of experiments varied between experimental sessions: 294 ants were tested on sand (90 at 1 m, 99 at 3 m and 105 at 6 m) and 249 ants on gravel (81 at 1 m, 80 at 3 m and 88 at 6 m). Of those 543 ants tested, 159 belonged to the first colony, 206 to the second and 178 to the third colony.

In a second series of experiments, returning ants and their loads were picked up, not at 40 cm from the seed patch as in the first series of experiments but just after leaving the patch. We ran this second series of experiments to test a potential sieve-like effect of a rough substrate. If this effect exists, any difference in load values observed in the first series of experiment between the smooth and the rough substrates would be due to a sieve-like action of the substrate, not to an actual choice of the ants. In this second series of experiments, 241 ants were tested on sand (107 at 1 m, 66 at 3 m and 68 at 6 m) and 239 ants on gravel (125 at 1 m, 53 at 3 m and 61 at 6 m). Of those 480 ants tested, 19 belonged to the first colony, 38 to the second, 40 to the third colony, and 363 and 20 to the additional fourth and fifth colonies, respectively.

Data collection

Assessment of distance covered and difficulty of transport

To assess the difficulty of walking on a rough substrate with and without a load, the outbound and inbound travel times of the workers in the first series of experiments were measured on a 30-cm section of the corridor leading to the seed patch. This 30-cm section ended at 10 cm from the seed patch. For each ant collected, we measured the time required to cross this 30-cm section when unladen (before reaching the seed patch) and when laden (after picking a seed fragment on the seed patch).

We used the inbound travel time as a proxy of the distance covered by the ants to reach the seed patch. An increase in either or both the horizontal and vertical components of the ants' path on a rough substrate should yield a higher travel time. The travel time could be further increased if ants reduce their speed whilst walking on a rough substrate.

Load selection

The number of seed fragments contacted by each ant, as well as the sum of the handling time of each seed fragment contacted, i.e. the total time the ant spent manipulating the seed fragments, were measured in the first series of experiments only. These two variables were used to compute the mean seed handling time for each ant. A seed fragment was considered as contacted when a worker began to manipulate it with its mandibles; seed fragment manipulation was considered as having stopped when the ants' mandibles were no longer in contact with the seed. We assumed that if ants are choosier in making their selection, i.e. use more selection criteria, this should be reflected by a longer mean seed handling time: According to the hypothesis stated above, this parameter should thus increase with both the patch distance and the roughness of the substrate.

For each ant in both series of experiments, we measured the weight of the seed fragment chosen, either after being transported on the first 40-cm length of the corridor after patch departure in the first series of experiments or directly after leaving the seed patch in the second series of experiments. The weight of the ants was also measured. This allowed us to express the weight of the seed fragments in unit of body mass, i.e. as the ratio ((ant body mass+seed mass)/ant body mass; see Bartholomew et al. 1988), hitherto called load ratio in the rest of the paper.

Statistical analyses

To investigate the effect of substrate roughness, distance of the seed patch and ant body mass on the variables we measured, we used linear mixed effect models (GLMM, see Pinheiro and Bates 2000). For outbound travel time, mean seed handling time and load ratio, we started with a full model that included colony as a random effect factor, substrate roughness (two modalities: sand or gravel), distance and ant body mass as fixed effect factors, as well as all interaction terms between these three factors. The full model used for the inbound travel time was similar to that used for the outbound travel time, except that it also included load ratio as an additional fixed effect factor.

For each dependent variable, we obtained a minimal model by a stepwise backward elimination procedure, i.e. by successively removing from the model the non-significant terms and by comparing the nested models with a maximum likelihood (ML) method (Pinheiro and Bates 2000). Following Pinheiro and Bates' (2000) recommendation, the minimal models were estimated using a restricted ML method.

All analyses were performed and graphs generated with the statistical software R 2.8.1 (R Development Core Team 2008, http://www.r-project.org) and the R-package nlme: Linear and Nonlinear Mixed Effects Models, version 3.1-90 (http://www.r-project.org). In all analyses, distance was coded as a continuous variable, not as a categorical variable. The independent continuous variable load ratio and ant body mass were centred on their mean to facilitate the interpretation of the model coefficients. To comply as much as possible with the assumption of normality and homoscedasticity, the data were $\log_{10}$-transformed. All data in the text are given as mean $\pm CI_{0.95}$

Results

The minimal model for the outbound travel time of the ants included all fixed effect factors as significant. Larger workers travelled significantly more rapidly than smaller workers ($F_{1,537}$=38.36, P<0.001; Fig. 2a), and ants travelled significantly more rapidly on sand than on gravel ($F_{1,537}$=112.67, P<0.001; 31.06±2.76 and 41.83±3.16 s for sand and gravel, respectively; Fig. 2a). Moreover, ants that collected seeds at 1 m were significantly slower than ants that collected seeds at 3 or 6 m ($F_{1,537}$=5.52, P=0.02; 40.20±4.37, 32.57±2.52 and 35.46±3.83 s for 1, 3 and 6 m, respectively). This can probably be explained by the fact that the density of ants around the seed patch was more important when this latter was at 1 m from the nest than it was at either 3 or 6 m. As a result of higher density, the number of contacts between ants is increased and their travel speed is therefore decreased.

The minimal model for the inbound travel time of the ants includes ant body mass, load ratio, substrate roughness, as well as the interaction between ant body mass and substrate as

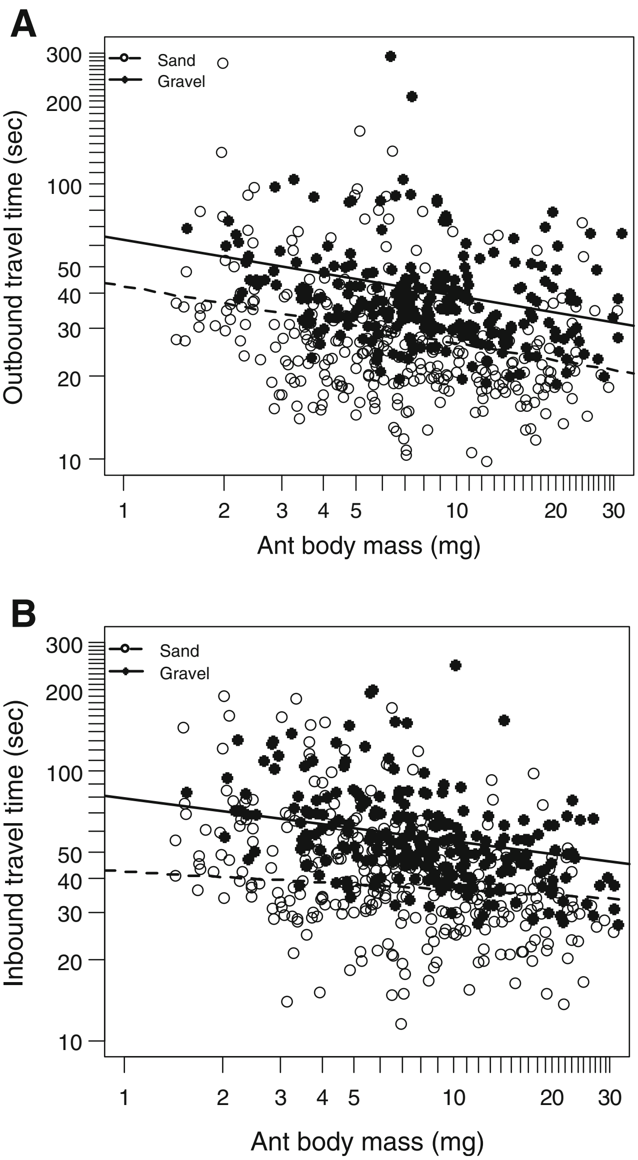

Fig. 2 Relationship between outbound travel time and ant body mass for unladen ants walking on gravel and on sand (y=1.63–0.20x and y=1.80–0.20x for sand and gravel, respectively) (**a**) and inbound travel time and ant body mass for laden ants walking on gravel and on sand (y=1.63–0.07x and y=1.90–0.16x for sand and gravel, respectively) (**b**). Travel time was measured on a 30-cm section of trail preceding the seed patch. (N=294 and N=249 for sand and gravel, respectively)

significant fixed effect factors. The factor distance and the interaction between ant body mass and load ratio were included in the model, but were not significant ($F_{1,534}$=0.09, P=0.770 and $F_{1,534}$=2.42, P=0.120, respectively; travel time, 50.85±4.19, 56.49±4.91, 51.93±4.00 s for 1, 3 and 6 m, respectively). The duration of the inbound trip decreased significantly with increased ant body mass ($F_{1,534}$=122.16, P<0.001; Fig. 2b) and increased significantly with substrate roughness ($F_{1,535}$=154.180 P<0.001; 46.52±3.30 and 60.85±3.71 s for sand and gravel, respectively; Fig. 2b) and load ratio ($F_{1,534}$=218.46, P<0.001). There was also a significant interaction between ant body mass and substrate ($F_{1,534}$=3.96, P=0.047): The effect of substrate roughness on inbound travel time was more pronounced for small than for big ants.

The minimal model for mean seed handling time retains only the effect of seed patch distance as significant effect ($F_{1,539}$=13.85, P<0.001): Mean seed handling time was significantly lower when the seed patch was at 1 or 3 m than when it was at 6 m from the nest (9.52±1.21, 10.03±1.11 and 11.71±1.08 s for 1, 3 and 6 m, respectively; Fig. 3).

Ant body mass was included in the minimal model explaining load ratio in both the first series of experiments, where ants were collected after having travelled 40 cm from the seed patch, and the second series of experiments, where ants were collected just after leaving the seed patch. In both cases, load ratio decreased with increasing body mass ($F_{1,537}$=186.71, P<0.001 and $F_{1,474}$=284.47, P< 0.001 for the first and second series of experiments, respectively) so that large ants carried relatively lighter loads. Distance was included neither in the minimal model explaining load ratio in the first series of experiments nor in that explaining load ratio in the second series of experiments (load ratio=2.68±0.21, 2.88±0.23, 2.58±0.19 and 2.86±0.22, 3.03±0.29, 2.77±0.29 for seed patch placed at 1, 3 and 6 m from the nest and for the first and second series of experiments, respectively). Finally, the effect of substrate roughness was retained in the minimal model of the first series of experiments, but not in that of the second series of experiments. Ants travelling on sand and picked up at 40 cm from the seed patch

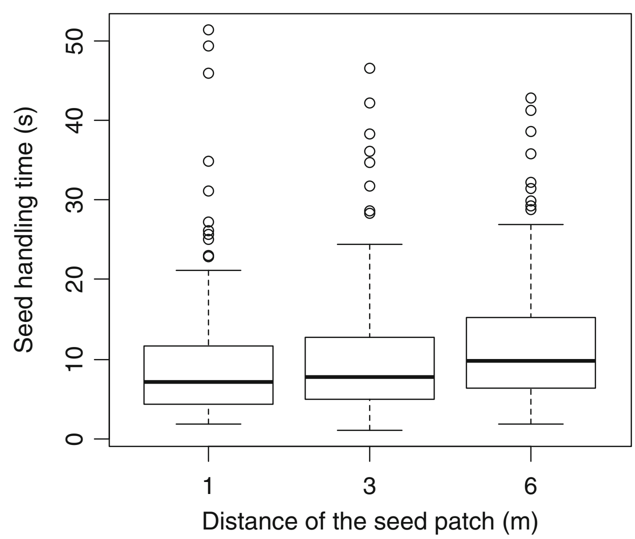

Fig. 3 Seed handling time as a function of the distance of the seed patch. The *bold line* within the *boxes* represents the median, the lower and upper boundaries of the boxes represent, respectively, the 25th and 75th percentiles, whilst the *whiskers* extend to the smallest and largest values within 1.5 box lengths (N=171, 179, and 193 for 1, 3 and 6 m, respectively)

transported on average significantly heavier seed fragments relative to their weight than those travelling on gravel ($F_{1,537}$=8.44, P=0.004; 2.96±0.19 and 2.41±0.13 for sand and gravel, respectively). There was also a significant interaction between ant body mass and substrate roughness ($F_{1,537}$=7.11, P=0.008; Fig. 4a), showing that the effect of substrate roughness on load ratio was more pronounced for small than for big ants. On the other hand, substrate roughness had no significant effect on the load ratio of ants picked up just after leaving the seed patch ($F_{1,472}$=0.32, P=0.569, values given from the ultimate model of the backward elimination procedure which still included this effect; Fig. 4b). The discrepancy between the results obtained with ants collected just after leaving the seed patch (Fig. 4b) and those collected at 40 cm from the seed patch (Fig. 4a) can probably be explained by a higher probability of heavy seed abandonment for ants walking on a rough substrate.

Discussion

Our work shows that seed-harvesting ants experience real difficulties when walking on an uneven surface. Whether loaded or not, ants walking on a rough substrate were significantly slower than ants walking on a smooth substrate. In addition, ants walking on a rough substrate more often abandoned heavy seed fragments on their way back to the nest. Indeed, regardless of body size, the travel time of unladen workers was 48% longer on gravel than on sand. This is concordant with the results found in other species of ants showing a decrease in locomotory rate with increasing complexity of the habitat structure, whether this complexity is due to a denser low vegetation cover (*Pogonomyrmex occidentalis*: Fewell 1987, 1988; Crist and MacMahon 1991; Crist and Wiens 1994; *Rhytidoponera aurata*: Nielsen 2001) or to the coarseness of the substrate (*Eciton burchellii*: Powell and Franks 2005; *Lasius niger*: Bernadou and Fourcassié 2008). In the same way as for unloaded ants, the travel time of loaded ants was also significantly impacted by substrate roughness and was between 13% and 51% (depending on ant weight, see Fig. 2b) longer on gravel compared to sand. A reduction in speed in foraging ants transporting external loads has been reported in several ant genera (*Atta*: Lighton et al. 1987; Burd 2000; Rudolph and Loudon 1986; Röschard and Roces 2002; Dussutour et al. 2009; *Pogonomyrmex*: Lighton et al. 1993; Weier and Feener 1995; Morehead and Feener 1998; *Rhytidoponera*: Nielsen 2001; *Eciton*: Bartholomew et al. 1988; *Dorymyrmex*: Torres-Contreras and Vasquez 2004). In *M. barbarus*, laden workers probably move more slowly because their centre of mass is shifted by the seed fragment they carry (see also in leaf-cutting ants: Moll et al. 2010). Consequently, they may have to reduce their stride length in order to preserve their balance and maneuverability (Zollikofer 1994). Also, small ants may have more difficulties than big ants in walking with a load on a rough substrate since the reduction in speed of ants walking on gravel was greater for small than

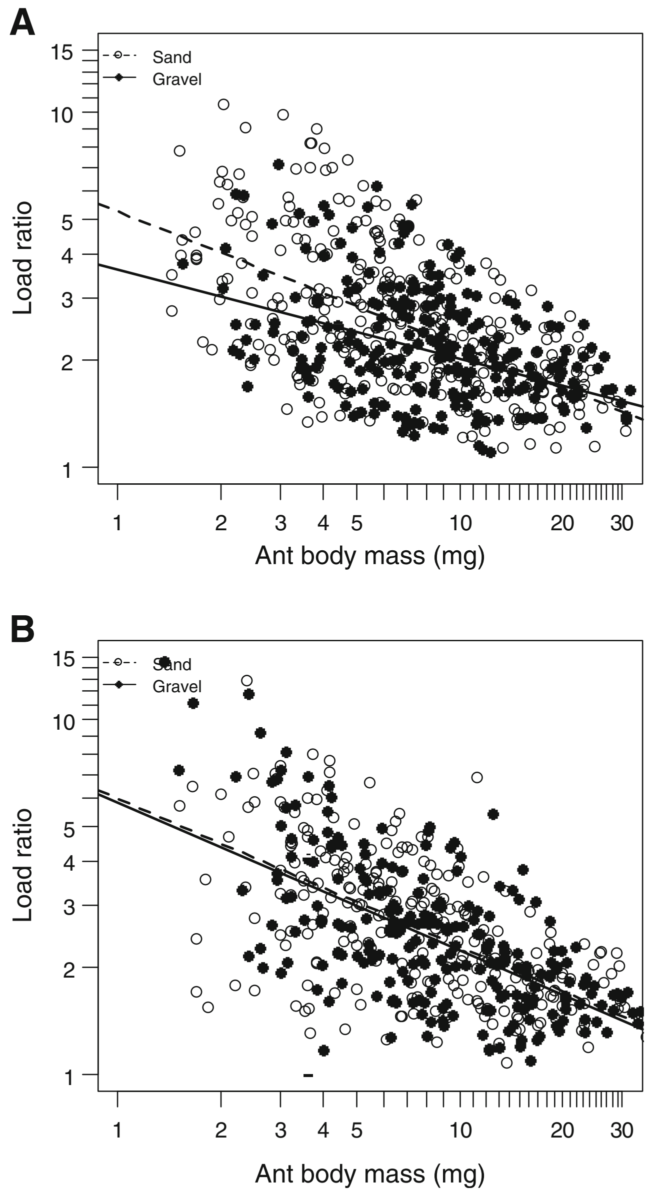

Fig. 4 Relationship between load ratio and ant body mass computed from the mass of the seed carried by ants in the first series of experiments, when ants were picked on their way back to the nest, at 40 cm from the seed patch (y=0.72−0.38x and y=0.57−0.27x for sand and gravel, respectively; N=294 and N=249 for sand and gravel, respectively) (**a**) and load ratio and ant body mass, computed from the mass of the seed carried by ants in the second series of experiments, just after they have made their choice on the seed patch (y=0.78−0.41x for both sand and gravel; N=241 and N=239 for sand and gravel, respectively) (**b**). The load ratio is defined as the ratio of the ant body mass plus seed mass divided by the ant body mass

for large ants (interaction ant body mass × substrate roughness). However, this is probably due to the fact that because of the limited size of the seed fragments offered, small ants could select seed fragments representing a much higher load ratio than large ants (maximum load ratio allowed considering the smallest and largest ant and the heaviest seed fragment collected: 49.45 for small ants and 2.65 for large ants). This is confirmed by the fact that the interaction between ant body mass and substrate roughness was no longer included in the model when only minor and media workers (ant body mass ≤10 mg) were considered in the analysis.

Our first hypothesis concerning the effect of substrate roughness on seed selection was that, concordant with the prediction of optimal foraging theory, ants should choose heavier seed fragments after travelling on a rough substrate because of the higher distance covered. Our results allow us to reject this hypothesis: Independent of the distance of the seed patch, ants picked up at the seed patch, directly after making their choice, did not choose heavier seed fragments when they had travelled on a rough substrate during their inbound trip (Fig. 4b). Moreover, independent of substrate roughness, there was also no effect of seed patch distance on load ratio, neither in the first series of experiments nor in the second series. This shows that contrary to the prediction of optimal foraging theory, the process of load selection was not affected by the distance of the seed patch. Previous tests on the effect of distance on seed selection in seed-harvesting ants have led to conflicting results, with some results being in agreement with the prediction of optimal foraging theory (Crist and MacMahon 1992; Davidson 1978; Detrain et al. 2000) and others not (Taylor 1977; Rissing and Pollock 1984; Holder Bailey and Polis 1987; Baroni Urbani and Nielsen 1990; Morehead and Feener 1998; Wetterer 1991; Ferster and Traniello 1995; Willott et al. 2000). The two main reasons that have been proposed in the literature to explain the absence of distance effect can also apply in our study. First, the energetic cost of running in seed-harvesting ants is very small compared with the energetic content of the seeds they collect (Rissing and Pollock 1984; Fewell 1988; Weier and Feener 1995; Morehead and Feener 1998). Second, central-place foraging models generally assume that the loads carried by animals are small compared with their own body mass and therefore have a negligible effect on their inbound travel time (Orians and Pearson 1979; Schoener 1979). However, this certainly does not apply to animals such as ants that can carry loads several times their own weight (up to ten times in our study). Of course, one cannot exclude that the distances tested in our experiment were not high enough to reveal an effect on seed choice. Detrain et al. (2000), for example, were able to show in field experiments that seed selectivity in *M. barbarus* increases significantly for trunk trails ranging in length from a few metres to up to than more than 20 m.

Although ants did not adjust their load ratio according to the distance from the nest, the mean handling time was lower at seed patches at 1 and 3 m than at 6 m from the nest. Given that the cumulative seed handling time increased linearly with the number of fragments contacted (for the 73% of the ants that contacted less than three seed fragments before making their choice; $F_{1,392}=132.16$, $P<0.001$), the ants apparently spent as much time inspecting seed fragments they rejected as those they eventually chose. If seed handling time were related to a selection process through a satisficing procedure whereby an ant considers each seed in turn for several criteria (Franks et al. 2003), one would have expected a longer handling time for the seed fragment eventually chosen than for the seed fragments rejected. An increase in the mean handling time per seed with the distance from the nest thus means either that ants added more criteria to their choice or that they spent more time evaluating each criterion, e.g. the weight of the seeds (for size matching and not for load adjustment since there was no significant effect of seed patch distance on load ratio), their odour (Warburg 2000; Youngsteadt et al. 2008) or their "transportability", i.e. the ease with which they can be seized or handled. The fact that the composition of the seed patch presented at different distances from the nest was the same suggests that ants, independent of the variance in seed properties, could be systematically more cautious in their choice with increasing distance from their nest.

Our second hypothesis concerning the effect of substrate roughness on load selection was that ants could anticipate from their outbound trip the difficulty of moving on a rough substrate with a heavy load and therefore select lighter seed fragments at their arrival on the seed patch. Our results do not suggest that this is the case, however. Substrate roughness had no effect on load selection; ants apparently do not monitor the substrate during their outbound journey and cannot anticipate difficulties in transporting heavy loads and adjust for this on their inbound journey. The load ratio of ants picked up directly after making their choice in the second series of experiments was not significantly different for ants that had travelled on sand or on gravel (Fig. 4b). Nevertheless, the results obtained in the first series of experiments, in which loaded ants were collected at 40 cm from the seed patch, show that substrate roughness does have an effect on seed retrieval. The fact that the load ratio of ants travelling on gravel was on average lower than that of ants travelling on sand (Fig. 4a) suggests that whilst progressing on a rough substrate, ants transporting heavy loads have a higher probability of abandoning the seed they carry. The seed could be simply dropped on the ground or, as often occurred on natural foraging trails (Reyes and Fernández Haeger 1999; Reyes-López and Fernández-Haeger 2001), transferred to a nestmate. That the inferred effect of substrate roughness on seed abandonment was more pronounced for small than for large ants could again be explained by the fact that small ants transported on average much heavier seed fragments than large ants relative to their weight. This effect was no longer included in the model when only minor and media workers (ant body mass ≤10 mg) were considered in the analysis; the effect of substrate roughness, however, remained significant ($F_{1,359}$=12.54, P<0.001).

The results of our experiments show that substrate roughness can substantially decrease the rate of seed return to the nest in seed-harvester ants because of two concomitant effects. First, laden ants walking on a rough substrate walk much more slowly than those walking on a smooth substrate. Second, seeds carried on a rough substrate have a higher probability of being dropped or transferred than those carried on a smooth substrate. Both effects contribute to slowing down the progression of the seed to the nest. These effects can be relaxed if ants invest part of their time and energy in building physical trunk trails, which is often the case in seed-harvester ants (Gordon 2010), in *M. barbarus* in particular (Lopez et al. 1993). Although one can assume that the seeds dropped or transferred by small ants are eventually transported by larger ants and reach the nest, it is likely that the heaviest seeds dropped by large ants on a rough substrate, i.e. those with high energetic contents, will never make it to the nest. One can thus hypothesize that seed dispersion by dyszoochory will be more important in environments characterized by a rough substrate than in those characterized by a smooth substrate.

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Ethical standards The experiments comply with the current laws of the country in which they were performed.

Conflict of interest The authors declare that they have no conflict of interest.

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