



## RESEARCH ARTICLE

# Decision making by young queens of the harvester ant *Messor semirufus* while searching for a suitable nesting site

M. Motro<sup>1</sup> · U. Motro<sup>2</sup> · D. Cohen<sup>3</sup>Received: 6 February 2016 / Revised: 6 August 2016 / Accepted: 23 August 2016  
© International Union for the Study of Social Insects (IUSSI) 2016

**Abstract** Field observations on the behavior of young queens of the harvester ant *Messor semirufus*, reveal a considerable variance among individuals in the time span between landing after nuptial flight, and the start of nest digging. During that interval, which can last from a few minutes to almost 2 h, the queens wander around while being exposed to many dangers, especially to the risk of predation. Furthermore, queens were observed digging in places where other queens have just passed through and declined to dig. We hypothesized that *M. semirufus* queens are performing a sequential sampling of the environment, to deduce its quality distribution, before making the decision to dig. To test this hypothesis, we conducted laboratory experiments to examine the influence of two factors, soil hardness and queen density, on digging decisions. The results indicate that these factors indeed affect the walking and searching time until digging. Furthermore, it turns out that the young queens are able to perceive and react to changes, either an improvement or a deterioration, in soil hardness and in queen density: their digging decision is stimulated by an improvement, and impeded by a deterioration in these factors, relative to initial condition.

**Keywords** Colony founding · Decision making · Formicidae · *Messor semirufus* · Nuptial flight · Searching behavior

## Introduction

A well-known problem in decision theory is the secretary problem, where by sequentially sampling a sequence of unknown items the decision maker has to decide when to optimally stop the sampling process (for a review on this problem and its various variants see Freeman 1983). This is largely relevant in optimal food foraging, where in a patchy environment foragers have to decide where or when to accept the current patch, based on their past experience and without full knowledge of the possible quality of future encountered patches (Stephens and Krebs 1986). A similar situation is faced when an individual is searching for a suitable mate (Real 1990), for a shelter or for a nesting place. The basic assumption in these sequential selection models is that continued sampling is costly—either by being time consuming, or by increasing the risk of predation, starvation or dehydration, or by the impossibility of recalling past better possibilities (Ward 1987; Luttbeg 1996, 2002; Baker and Rao 2004; Stamps et al. 2005; Stamps and Davis 2006).

Decision making by sequentially sampling the environment is quite common. As was first pointed out by Oaten (1977), the rewards can provide a forager with information about its environment. Thus, the resources collected by the forager, which primarily serve as energy supplies, can also provide it with some information as to the quality and the distribution of these resources, and consequently affect its subsequent movements. There are numerous such examples among the Hymenoptera—the movements between flowers

✉ M. Motro  
motro@dyellin.ac.il

<sup>1</sup> David Yellin Academic College of Education, 91035 Jerusalem, Israel

<sup>2</sup> Department of Ecology, Evolution and Behavior, Department of Statistics, and The Federmann Center for the Study of Rationality, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel

<sup>3</sup> Department of Ecology, Evolution and Behavior, and The Federmann Center for the Study of Rationality, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel

by bumblebees (Pyke 1978) and honeybees (Waddington 1980), the different 'major' flower types of individual bumblebees in a patchy environment (Kearse et al. 2013), or the patch leaving decision rules in the parasitoid wasps *Cotesia rubecula* (Tenhumberg et al. 2001) and *Leptomastix dactylopii* (Pierre et al. 2003). Thus, in a heterogeneous environment we can expect similar individuals to make different decisions as a result of their different history.

A majority of ant species disperse through some form of mating flight in which winged males and females depart their mother colonies and found new colonies some distance away (Hölldobler and Wilson 1990). In Israel, nuptial flight in *Messor semirufus* usually takes place on warm days following the first heavy rains at the beginning of the winter. When the young alates emerge from the nest, they are guarded by hundreds of workers that swarm around the nest entrances. Not many predators can reach the alates at this stage (although we observed predation by the wasp *Vespula germanica*). After takeoff, while in the air, the young reproductives are vulnerable to bird predation. When the queens land, they are usually still attached to their mate (or mates). After separating from their mate, the queens may take off to the air once again, or may shed their wings and wander around in search of a place to dig their nest. The time period of the wandering phase is very risky. During that time, the young queens are exposed to desiccation and overheating, but principally to predation. In the Australian meat ant *Iridomyrmex purpureus*, for example, many young queens are being preyed upon while searching over the ground for a nesting site (Hölldobler and Carlin 1985), and Greaves and Hughes (1974) report losses of 80 % or higher during that period from ground-feeding birds alone. In spite of these risks, the young queens of *M. semirufus* tend to wander and search around before they start to dig their nest.

During their nuptial flight, the reproductive alates of *M. semirufus* fly in a diffused manner, and do not swarm as a cloud in the air, nor congregate on the ground [as some other ant species do, e.g., *Myrmica rubra* (Donisthorpe 1915), *Myrmecia sanguinea* (Wheeler 1916), *Formica obscuripes* (Talbot 1972), and *Pogonomyrmex rugosus* (Hölldobler 1976)]. Thus, aggregation avoidance can be ruled out as the main cause to this ground wandering period.

After landing from her nuptial flight, the young queen of *M. semirufus* has to search on the ground for a suitable nesting site. This primarily includes the appropriate type of soil, since exaggerated excavation efforts can lead to higher rates of queen's mortality [Camargo et al. (2011) for *Atta sexdens rubropilosa*] and carbohydrates loss [Silva et al. (2015) for *Atta sexdens rubropilosa*]. Johnson (1992)

reports differing preferences to soil texture between founding queens of two ecologically similar species of harvester ants (*Pogonomyrmex rugosus* and *Messor pergandei*). In *M. semirufus*, colony founding is claustral and mostly haplometrotic, meaning that the inseminated young queen seals herself off in a chamber and rears the first brood in isolation. These young queens are able to go through nuptial flight, then search for a suitable place for the new nest, dig the nest, lay eggs and nurse the first brood, altogether without any external supply of food. The queens lay their first eggs only 2 months after their nuptial flight, and the first workers emerge more than 3 months later, in the spring, when seeds are abundant. Thus, the young queen stays alone in her burrow during the entire winter, so choosing the right place and the right depth of digging can be crucial for her survival.

There are contrasting results about the relative cost of the searching and digging phase in different ant species. Measurements taken on the leaf-cutting ant *Atta sexdens rubropilosa* indicate that a nest founding queen loses almost 55 % of her body's crude protein content (Silva et al. 2014) and almost 40 % of her body's soluble carbohydrates (Silva et al. 2015) during the nuptial flight and nest digging. Therefore, a queen has to manage her limited energy supply in an efficient way, so that she has enough resources left to reach the stage when her young daughters emerge and provide for the nest. Any extra or unnecessary effort may jeopardize her entire reproductive success. In contrast, the excavation of complete founding chambers in *Solenopsis invicta* incurred no measurable cost on the subsequent reproductive output of queens (Tschinkel 1993, 1998).

A suitable site is characterized not only by the physical features of the soil, but also by the distance to established colonies of the same species—e.g., in *Messor semirufus* (Kawecki 1992), in *Lasius niger* (Sommer and Hölldobler 1995) and in *Temnothorax albipennis* (Franks et al. 2007)—probably to avoid exploitative competition and active destruction of the new nest by workers of established colonies.

The expected duration of the search represents a balance between the prospects of finding a better digging site, and the risk of predation. Thus, we expect a longer walking and searching period in a less homogenous environment, and if the risk of predation is reduced. Perhaps the phenomenon of synchronized nuptial flights, which certainly enhances outbreeding (Craig and Crozier 1979; Pamilo and Varvio-Aho 1979; Pearson 1983; Ward 1983) and the avoidance of interbreeding with congeneric species (Kannowski 1959; Hölldobler 1976), also reduces predation risk by saturation of local predators, as has

already been suggested for synchronized activities of other animals (e.g., Estes 1966).

In spite of the heavy risk during the searching period, our field observations revealed that young queens of *M. semirufus* spend a considerable time walking on the ground, before they start digging their nest. This period of walking and active searching varies among different individuals, and can last from less than 5 min to almost 2 h. While such a risky delay could be the result of encountering unfavorable digging conditions, we were quite puzzled by the fact that at the same place, some queens found it suitable and decided to dig their nest, whereas other queens which have been there just before decided that these same conditions are unfavorable, and wandered away without digging.

In the present paper we describe the searching process of young queens of the harvester ant *M. semirufus* for a suitable nesting site within the environment into which they have landed after their nuptial flight (the microhabitat selection phase). Our observations and experiments demonstrate that these young queens are sequentially sampling the environment before taking their digging decision.

We first conducted field observations, which exhibit the variability in the time spent between landing and digging by young queens of *M. semirufus*. Our observations led to the hypothesis that queens actually sample the environment before they decide where and when to dig their nest, and the variance in their actions may be due to their different experience. We then tested this sampling and learning hypothesis with more detailed lab experiments.

If young queens of *M. semirufus* actually perform sequential sampling in order to evaluate the quality distribution of the environment before they decide to dig their nest, we expect them to react not only to the absolute digging conditions, but also to changes in these conditions. Therefore, an improvement in digging conditions should enhance digging, whereas deterioration should hinder digging. In a series of laboratory experiments, we examined the influence of two factors, soil hardness and queen density, on the queens' decision whether or not to start digging, and then examined how changes in these factors affect their decision.

## Field observations

### Aim

To follow the searching behavior of young queens in the field, in order to understand their decision making with respect to nest digging.

## Methods

The study area is located in the Judean Mountains around Jerusalem (Israel). The soil is terra rossa over hard limestones, and the plant community is a Mediterranean scrub, with low bushes and small trees.

Altogether, 45 young queens were tracked in the field immediately after landing. The location of each queen, and the soil hardness at each location (which was determined by the depth of penetration of a 4.5 mm thick nail, under the pressure of a 700 g weight) were recorded every 5 min. Encounters with conspecific ants or with other organisms were recorded continuously.

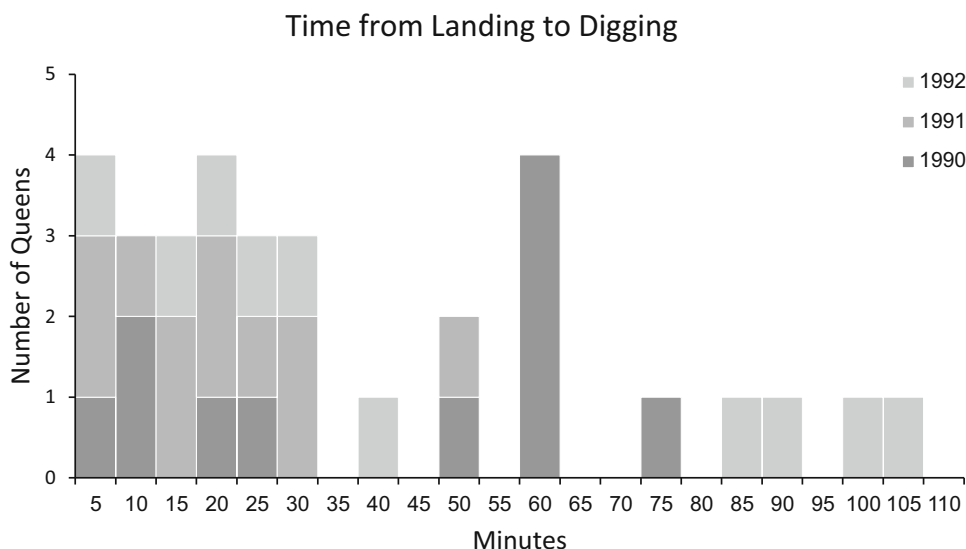
Of the 45 tracked queens, four took off and flew again after separating from their mates. Four queens were preyed upon (two by spiders, one by *Cataglyphis* ants, and one by a blackbird). Our presence probably deterred some predators, mainly birds and lizards. Five other queens landed in territories of conspecific colonies, and were caught and killed by their workers. Only 32 were seen digging. Generally, queens stop and try to dig several times during their walk, but in most cases these trials are very short, and subsequently the queens cease digging and move on. We thus considered a nest founding to occur only if the queen was observed digging at the same spot for more than 20 min. When two wandering queens encounter each other, they usually retreat, and move quickly away in different directions. When a wandering queen comes across a digging site of another queen, most of the times she is chased away by the resident queen.

## Results

When hard soil is encountered, the queen tends to move greater distances. For 14 queens we had enough data to calculate the correlation coefficient between the soil hardness at each (except the last) location, and the linear distance (the displacement) to the next location. Twelve of these correlation coefficients were positive, and only two were negative. The pooled correlation coefficient was 0.4645, with a standard error of 0.0831, indicating a positive correlation ( $p < 0.001$ , using a Chi square test) between the soil hardness at a location, and the linear distance to the next location.

The time interval between landing and digging varied considerably. Four queens started digging within the first 5 min, while three wandered around more than an hour and a half before digging (Fig. 1). On several occasions, queens were observed digging at places which were not chosen by previous queens. Such a variable response can result from lack of prior information: if the queens cannot have complete information about the distribution of the different digging conditions in the area into which they have landed, we can expect to observe different digging decisions being made under the same digging conditions.

**Fig. 1** The distribution among 32 queens of the time interval between landing and the start of digging



### Laboratory experiments

In a series of laboratory experiments we examined the influence of two factors, soil hardness and queen density, on the queens' decision whether or not to start digging, and then examined how changes in these factors affect their decision.

### Methods

In 1991 and 1992, young queens were collected in areas around Jerusalem, immediately after landing from their nuptial flight. The queens were marked individually (by "Edding 750 metallic" markers), and placed in boxes that were arranged for the different experiments. Each queen participated only in one experiment. The queens' behavior (e.g., walking, digging, social interactions) was recorded.

In 1991, the experiments were aimed at studying the effect of soil hardness and queen density on the queens' readiness to dig. Forty-three, 60 × 40 × 15 cm boxes, each filled with a 5 cm deep soil layer, were prepared. There were two types of boxes: 18 boxes with loose soil, and 25 boxes with hard soil, which contained the same type of soil, but pressed and hardened. The hardness of the soil was measured by the depth of penetration of a 4.5 mm thick nail, under the pressure of a 500 g weight: the nail penetrated to a depth of 2.0 cm in the loose soil, but only to 0.6 cm in the hard soil. A total of 125 queens were placed in these boxes, in different densities, either low (i.e., one or two queens in a box) or high (four or six queens in a box). Thus, each queen was subjected to one of four treatments, according to the type of soil (loose or hard) and to the density (low or high).

In 1992, the experiments were aimed at studying the effect of changes in soil hardness and in queen density on

the queens' readiness to dig. In the soil hardness experiments, two types of 60 × 40 × 15 cm boxes, each filled with a 5 cm deep soil layer, were prepared: boxes with loose soil, and boxes with hard soil. Each queen was subjected to one of four different treatments, as follows:

1. Eight queens were placed, one in a box, in hard soil boxes. After 15 min, each was transferred to her separate loose soil box (Hard to Loose).
2. Eight queens were placed, one in a box, in loose soil boxes. After 15 min, each was transferred to her separate loose soil box (Loose to Loose, control).
3. Eight queens were placed, one in a box, in loose soil boxes. After 15 min, each was transferred to her separate hard soil box (Loose to Hard).
4. Eight queens were placed, one in a box, in hard soil boxes. After 15 min, each was transferred to her separate hard soil box (Hard to Hard, control).

Four replicates of the first and the second treatments, and three replicates of the third and the fourth treatments were carried out (each time with different queens and fresh boxes).

In the density experiments, the boxes were 36 × 30 × 15 cm, filled with a 5 cm deep layer of loose soil, and the queens were unmarked. The experiment involved four different treatments, as follows:

1. Sixteen queens were placed, two in a box, in eight boxes. After 2 h, all 16 queens were transferred to a single box (Low to High).
2. Sixteen queens were placed in a single box. After 2 h, all 16 queens were transferred to another box (High to High, control).
3. Sixteen queens were placed together in a single box. After 2 h, these queens were transferred, and

randomly distributed to eight boxes, two in a box (High to Low).

4. Sixteen queens were placed, two in a box, in eight boxes. After 2 h, these queens were transferred and randomly distributed to other eight boxes, two in a box (Low to Low, control).

For each treatment, the number of queens that were digging was recorded in 5 min intervals during the 2 h before and the 2 h after transferring the ants.

It should be noted that the transfer itself has an enhancing effect on the digging. Queens that were transferred from box to box tend to start their digging earlier than queens that stayed in their original box (and this is the reason for conducting the control experiments in the way described above). As a possible explanation to this effect we speculate that maybe the ants perceive our handling as a predation trait, and react by accelerating their seeking for shelter by digging more readily.

## Results

### The soil hardness experiments

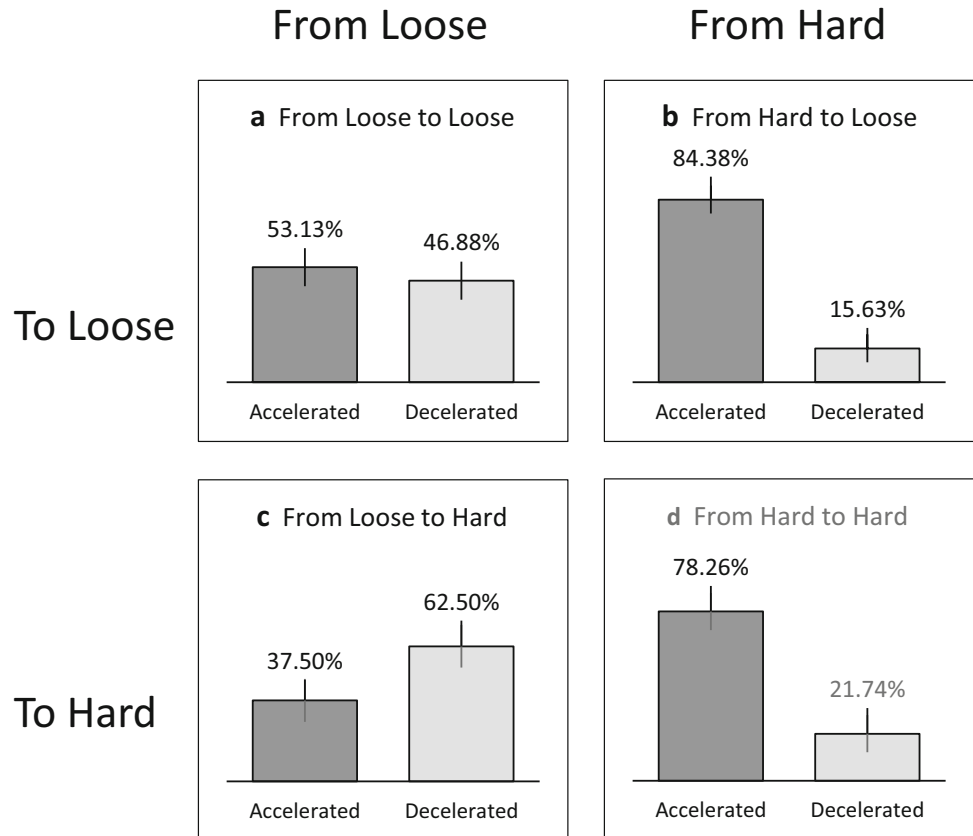
Digging started earlier in loose soil than in hard soil. [Wilcoxon's two-sample rank-sum test; the  $p$  value

calculated for data combined from several experiments (Lehmann 1975, pp 132–141) is smaller than 0.001.]

Queens that were transferred from hard to loose soil, started digging earlier (median time until start of digging: 5 min) than the control queens that were transferred from loose to loose soil (median: ~15 min): of the 32 queens that were transferred from hard to loose soil boxes, 27 (84.4 %) started digging earlier in the loose soil boxes to which they were transferred, than in the hard soil boxes in which they were placed first. On the other hand, of the 32 queens that were transferred from loose to loose soil boxes, only 17 (53.1 %) started digging earlier in the loose soil boxes to which they were transferred, than in the loose soil boxes in which they were placed first (Fig. 2a, b). Thus, the proportion of queens for which transferring shortened the time until digging, is larger in the first case (Hard to Loose), than in the control case (Loose to Loose). (Fisher's exact test,  $p = 0.007$ ).

Queens that were transferred from loose to hard soil, started digging later (median: 117.5 min) than the control queens that were transferred from hard to hard soil (median: ~77.5 min): of the 24 queens that were transferred from loose to hard soil boxes, 15 (62.5 %) started digging later in the hard soil boxes to which they were transferred, than in the loose soil boxes in which they were placed first. On the other hand, of the 23 queens that were transferred from hard to hard soil boxes (one managed to escape during the

**Fig. 2** The soil hardness experiments: percentage of queens ( $\pm$ SE) in each of the four treatments for which transfer accelerated/decelerated their digging



transfer), only 5 (21.7 %) started digging later in the hard soil boxes to which they were transferred, than in the hard soil boxes in which they were placed first (Fig. 2c, d). Thus, the proportion of queens for which transferring lengthened the time until digging is larger in the first case (Loose to Hard), than in the control case (Hard to Hard) (Fisher's exact test,  $p = 0.005$ ).

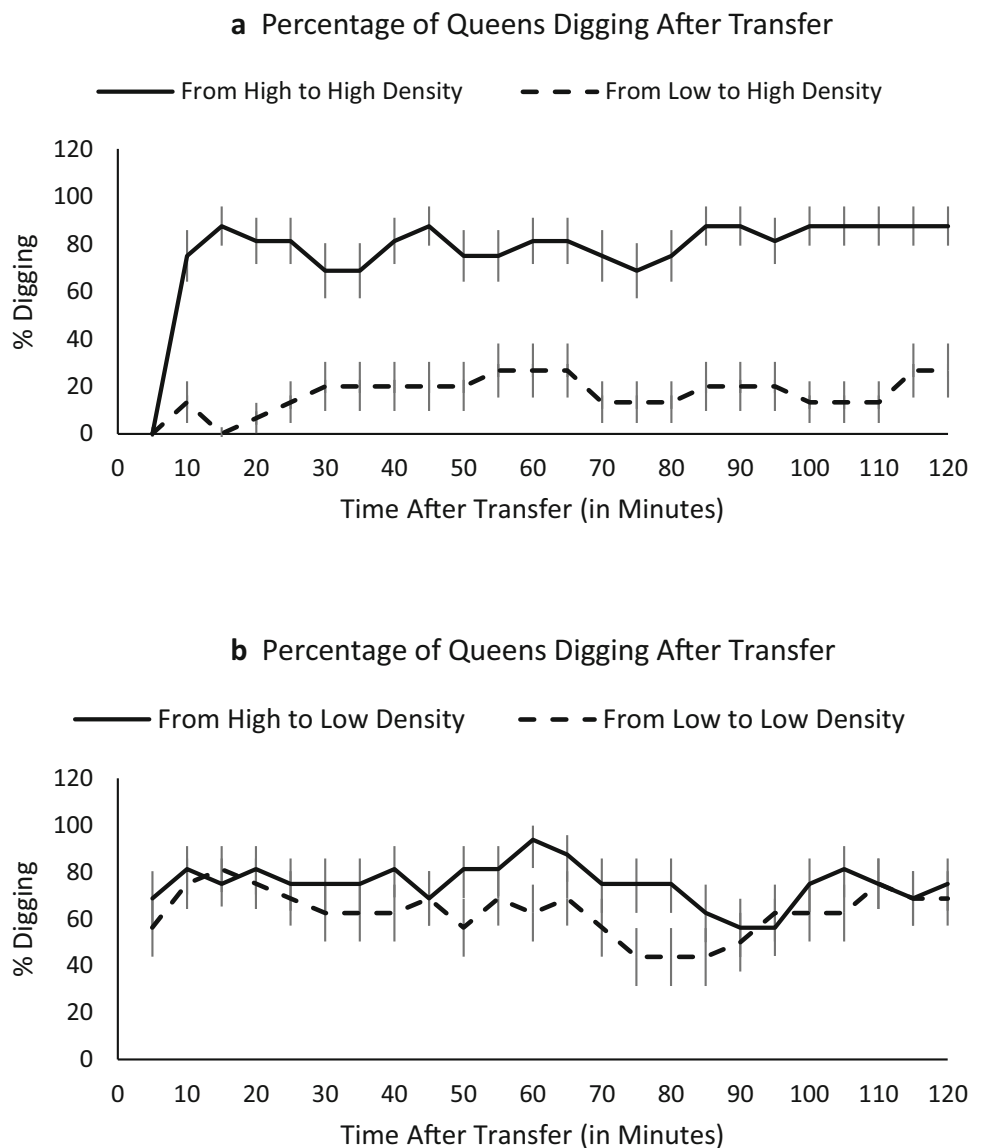
*The density experiments*

Digging started earlier in low densities (one or two queens in a box), than in high densities (four or six queens in a box). (Wilcoxon's two-sample rank-sum test; the  $p$  value calculated for data combined from several experiments is smaller than 0.05).

Queens that were transferred from low density (two in a box) to high density (16 in a box), were more reluctant to dig in their new location than the control queens that were transferred from high to high density ( $p = 0.005$ ). Since in this experiment the queens were unmarked, we could not use the same comparison method as in the soil hardness experiments. Instead, every 5 min (during the 2 h after transfer), the proportions of the queens that were digging in the two groups were compared (by Fisher's exact test), and a  $p$  value was obtained. The  $p$  value given above is the average of these 24 values. See Fig. 3a.

However, queens that were transferred from high density (16 in a box) to low density (two in a box), did not show a significantly greater inclination to dig in their new location than the control queens that were transferred from low to low density ( $p = 0.348$ , by the same method as described above), see Fig. 3b.

**Fig. 3** The density experiments: percentage of queens ( $\pm$ SE) that were digging as a function of time since transfer in each of the four treatments



## Discussion

After landing from their nuptial flight, the inseminated queens of *M. semirufus* have to search on the ground for a suitable nesting site, one that has the appropriate type of soil and is sufficiently far from other nests. In search of a suitable site, the young queen can spend a considerable time (sometimes even more than an hour and a half), exposed to predation and desiccation. Our observations showed that the searching period can vary considerably among different queens, indicating that the environment which they encounter upon landing is quite patchy, or that queens differ in their appreciation of habitat quality.

Kannowski (1959) and King and Tschinkel (2016) point out that sometimes a suitable environment can already be perceived from the air, directing the queens' landing accordingly (the macrohabitat selection phase). We have no information about selecting macrohabitat from the air in *M. semirufus*.

It should be pointed out that delayed digging by mated queens has also been observed in other species. As described by Hölldobler (1976), sympatric species of *Pogonomyrmex* in Arizona are separated by the timing, during the day, of their nuptial flight. Thus, the flight of one of the species, *P. maricopa*, is displaced to forenoon hours. Since the heat of midday prevents the queens of this species from beginning nest excavation, they delay their digging for 3 or 4 h, during which time they are subject to higher predation than the other species. However, this forced delay is a different phenomenon than the active, elective search exhibited by the queens of *M. semirufus*.

By recording the location of a searching queen at regular time intervals, our field observations revealed a positive correlation between the soil hardness at a location, and the linear distance to the next location on her search path. This phenomenon is similar to the "win stay, lose shift" strategy used by foraging bees and birds (see Motro and Shmida 1995 and references therein).

Moreover, we hypothesized that while walking, the young queens sample the environment, and react not only to the absolute digging conditions, but also compare the relative value of different sites. Our laboratory experiments indicate that soil properties (with respect to digging convenience), and queen density, are factors that affect the walking and searching time until digging. Furthermore, it turns out that young queens of *M. semirufus* are able to perceive changes, either an improvement or a deterioration, in soil hardness and in queen density: their digging decision is stimulated by an improvement, and impeded by a deterioration in these factors. Thus, queens that were transferred from hard to loose soil, started digging earlier than the control queens that were transferred from loose to loose soil. Likewise, queens that were transferred from loose to hard soil, started digging later

than the control queens that were transferred from hard to hard soil. Queens that were transferred from low to high density were more reluctant to dig in their new location than the control queens that were transferred from high to high density. However, queens that were transferred from high to low density did not show a significantly greater inclination to dig in their new location than the control queens that were transferred from low to low density. Unlike changes in soil hardness, which can immediately be perceived by the queens, a real decrease in density cannot be promptly detected. In reality, if a queen has realized that the density is high, temporarily not "seeing" other queens should not necessarily imply that they have disappeared right away, and are no longer there. Thus the decrease (but not the increase) of density in our experiment is expected to bring a somewhat indecisive queen reaction.

The sequential sampling strategy of the young queens can explain why we sometimes observe similar queens, occurring at the same type of soil, taking different digging actions, apparently due to their different past experience.

A similar result was obtained by Nonacs (1989), using a dynamic programming model to study decision making by Hymenoptera queens regarding the question of whether or not to join an already digging queen in a cooperative colony founding (pleometrosis). Assuming a fixed bound  $T$  to the possible searching time, Nonacs' model also demonstrates how similar queens, encountering similar conditions, can take different joining decisions, as a result of their different proximity to  $T$ .

These are examples of a more general phenomenon, in which different personal dispositions lead to different evaluations of the same objective situation.

**Acknowledgments** We thank two anonymous reviewers and the late Dr. Raja Szlez for important comments and helpful suggestions.

## References

- Baker MB, Rao S (2004) Incremental costs and benefits shape natal dispersal: theory and example with *Hemilepistus reaumuri*. *Ecology* 85:1039–1051
- Camargo RS, Forti LC, Fujihara RT, Roces F (2011) Digging effort in leaf-cutting ant queens (*Atta sexdens rubropilosa*) and its effects on survival and colony growth during the claustral phase. *Insectes Soc* 58:17–22
- Craig R, Crozier RH (1979) Relatedness in the polygynous ant *Myrmecia pilosula*. *Evolution* 33:335–341
- Donisthorpe HStJK (1915) British ants, their life-history and classification. William Brendon and Son, Plymouth
- Estes RD (1966) Behaviour and life-history of the wildebeest (*Connochaetes taurinus*). *Nature* 212:999–1000
- Franks NR, Dornhaus A, Hitchcock G, Guillem R, Hooper J, Webb C (2007) Avoidance of conspecific colonies during nest choice by ants. *Anim Behav* 73:525–534
- Freeman PR (1983) The secretary problem and its extensions: a review. *Int Stat Rev* 51:189–206

- Greaves T, Hughes RD (1974) The population biology of the meat ant. *J Aust Entomol Soc* 13:329–351
- Hölldobler B (1976) The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behav Ecol Sociobiol* 1:405–423
- Hölldobler B, Carlin NF (1985) Colony founding, queen dominance and oligogyny in the Australian meat ant *Iridomyrmex purpureus*. *Behav Ecol Sociobiol* 18:45–58
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard University Press, Cambridge
- Johnson RA (1992) Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. *Oecologia* 89:118–124
- Kannowski PB (1959) The flight activities and colony-founding behavior of bog ants in Southeastern Michigan. *Insectes Soc* 6:115–162
- Kawecki TJ (1992) Young queens of the harvesting ant *Messor semirufus* avoid founding in places visited by conspecific workers. *Insectes Soc* 39:113–115
- Keasar T, Motro U, Shmida A (2013) Temporal reward variability promotes sampling of a new flower type by bumblebees. *Anim Behav* 86:747–753
- King JR, Tschinkel WR (2016) Experimental evidence that dispersal drives ant community assembly in human-altered ecosystems. *Ecology* 97:236–249
- Lehmann EL (1975) *Nonparametrics: statistical methods based on ranks*. Holden-Day, San Francisco
- Luttbeg B (1996) A comparative Bayes tactic for mate assessment and choice. *Behav Ecol* 7:451–460
- Luttbeg B (2002) Assessing the robustness and optimality of alternative decision rules with varying assumptions. *Anim Behav* 63:805–814
- Motro U, Shmida A (1995) Near-far search: an evolutionarily stable foraging strategy. *J Theor Biol* 173:15–22
- Nonacs P (1989) Competition and kin discrimination in colony founding by social Hymenoptera. *Evol Ecol* 3:221–235
- Oaten A (1977) Optimal foraging in patches: a case for stochasticity. *Theor Popul Biol* 12:263–285
- Pamilo P, Varvio-Aho S-L (1979) Genetic structure of nests in the ant *Formica sanguinea*. *Behav Ecol Sociobiol* 6:91–98
- Pearson B (1983) Intra-colonial relatedness amongst workers in a population of nests of the polygynous ant, *Myrmica rubra* Latreille. *Behav Ecol Sociobiol* 12:1–4
- Pierre J-S, van Baaren J, Boivin G (2003) Patch leaving decision rules in parasitoids: do they use sequential decisional sampling? *Behav Ecol Sociobiol* 54:147–155
- Pyke GH (1978) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor Popul Biol* 13:72–98
- Real L (1990) Search theory and mate choice. I. Models of single-sex discrimination. *Am Nat* 138:901–917
- Silva EJ, Camargo RS, Forti LC, Travaglini RV (2014) Protein content of leaf-cutting ant queens before the nuptial flight and during the post-claustral phase. *Rev Bras Entomol* 58:333–336
- Silva EJ, Camargo RS, Forti LC (2015) Flight and digging effort in leaf-cutting ant males and gynes. *Sociobiology* 62:334–339
- Sommer K, Hölldobler B (1995) Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger*. *Anim Behav* 50:287–294
- Stamps JA, Davis JM (2006) Adaptive effects of natal experience on habitat selection by dispersers. *Anim Behav* 72:1279–1289
- Stamps JA, Krishnan VV, Reid ML (2005) Search costs and habitat selection by dispersers. *Ecology* 86:510–518
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- Talbot M (1972) Flights and swarms of the ant *Formica obscuripes* Forel. *J Kans Entomol Soc* 45:254–258
- Tenhumberg B, Keller MA, Possingham HP, Tyre AJ (2001) Optimal patch-leaving behaviour: a case study using the parasitoid *Cotesia rubecula*. *J Anim Ecol* 70:683–691
- Tschinkel WR (1993) Resource allocation, brood production and cannibalism during colony founding in the fire ant, *Solenopsis invicta*. *Behav Ecol Sociobiol* 33:209–223
- Tschinkel WR (1998) An experimental study of pleometrotic colony-founding in the fire ant *Solenopsis invicta*: what is the basis for association? *Behav Ecol Sociobiol* 33:209–223
- Waddington KD (1980) Flight patterns of foraging honeybees in relation to artificial flower density and distribution of nectar. *Oecologia* 44:199–204
- Ward PS (1983) Genetic relatedness and colony organization in a species complex of ponerine ants, I: phenotypic and genotypic composition of colonies. *Behav Ecol Sociobiol* 12:285–299
- Ward SA (1987) Optimal habitat selection in time-limited dispersers. *Am Nat* 139:883–891
- Wheeler WM (1916) The marriage-flight of a bull-dog ant (*Myrmecia sanguinea* F. Smith). *J Anim Behav* 6:70–73