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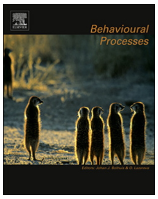

The effect of maze complexity on maze-solving time in a desert ant

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ABSTRACT

One neglected aspect of research on foraging behavior is that of the effect of obstacles that increase habitat complexity on foraging efficiency. Here, we explored how long it takes individually foraging desert ant workers (*Cataglyphis niger*) to reach a food reward in a maze, and examined whether maze complexity affects maze-solving time (the time elapsed till the first worker reached the food reward). The test mazes differed in their complexity level, or the relative number of correct paths leading to the food reward, vs. wrong paths leading to dead-ends. Maze-solving time steeply increased with maze complexity, but was unaffected by colony size, despite the positive correlation between colony size and the number of workers that searched for food. The number of workers observed feeding on the food reward 10 min after its discovery decreased with complexity level but not colony size. We compared our experimental results to three simulation models, applying different search methods, ranked them according to their fit to the data and found the self-avoiding random search to fit the best. We suggest possible reasons for the model deviations from the observational findings. Our data emphasize the necessity to refer to habitat complexity when studying foraging behavior.

1. Introduction

Foraging is one of the most important behaviors animals engage in with consequences for both reproduction and survival. Foraging should be selected for high efficiency for many reasons, such as competition with others over the food, predation risk while foraging and trade-offs over time with other important activities like mating (Kotler and Brown, 1988; Mitchell et al., 1990; Lemon, 1991; Abrahams, 1993; Gotthard, 2000). The optimal foraging mode or searching tactic depends on many factors, such as prey density, quality, or its spatial distribution pattern (Stephens and Krebs, 1986; de Knegt et al., 2007; Latty and Beekman, 2009; Scharf et al., 2009). Habitat complexity can be defined as the level of surface irregularities, from a completely homogenous surface to a heavily obstructed one (Taniguchi and Tokeshi, 2004). Habitat complexity affects many of such factors and is usually negatively correlated with foraging success (Gotceitas and Colgan, 1989; Warfe and Barmuta, 2004; Gibb and Parr, 2010).

Animals are influenced by the ground surface on which they move (e.g., vegetation cover affects beetle movement; Crist et al., 1992; Wiens et al., 1997). For example, animals must decide what to do when facing an obstacle that prevents them from exploring a desired direction: they can either turn back or follow its boundary, and then either choose a new direction or keep the current movement direction (Bengtsson et al., 2004; Casellas et al., 2008). Obstacles are important factors in foraging behavior, in increasing the actual distance between the forager and its food source, and the travel costs, while reducing foraging efficiency (Masden et al., 2010; Beyer et al., 2016). On the other hand, a complex habitat may offer a higher variety of shelters from predators (Thompson, 1982), indicating a trade-off between energy cost and predation risk. While it is clear that most habitats involve some degree of structure and obstacles, studies that consider the effect of obstacles, which limit accessibility to some parts of the habitat, are still relatively rare (but see, for example, Jeanson et al., 2003; Matthiopoulos, 2003). However, it is important to understand how animals cope with obstacles in order to understand their movement, dispersal, and conservation. Habitat complexity can be measured on various spatial scales and clearly depends on the studied animal. Mazes are typical tools used to study the effect of habitat complexity on navigation and route finding in small animals (e.g., Shumway, 2010; du Toit et al., 2012; Reid et al., 2012).

We focused here on the desert ant *Cataglyphis niger* and studied how habitat complexity affected its maze-solving time (defined as the time required for the first worker to discover the food reward). *Cataglyphis* ants are excellent navigators (Müller and Wehner, 1988; Wehner, 2003), and like all central-place foragers, they need not only to find food but also to return to their nest. *C. niger* workers forage

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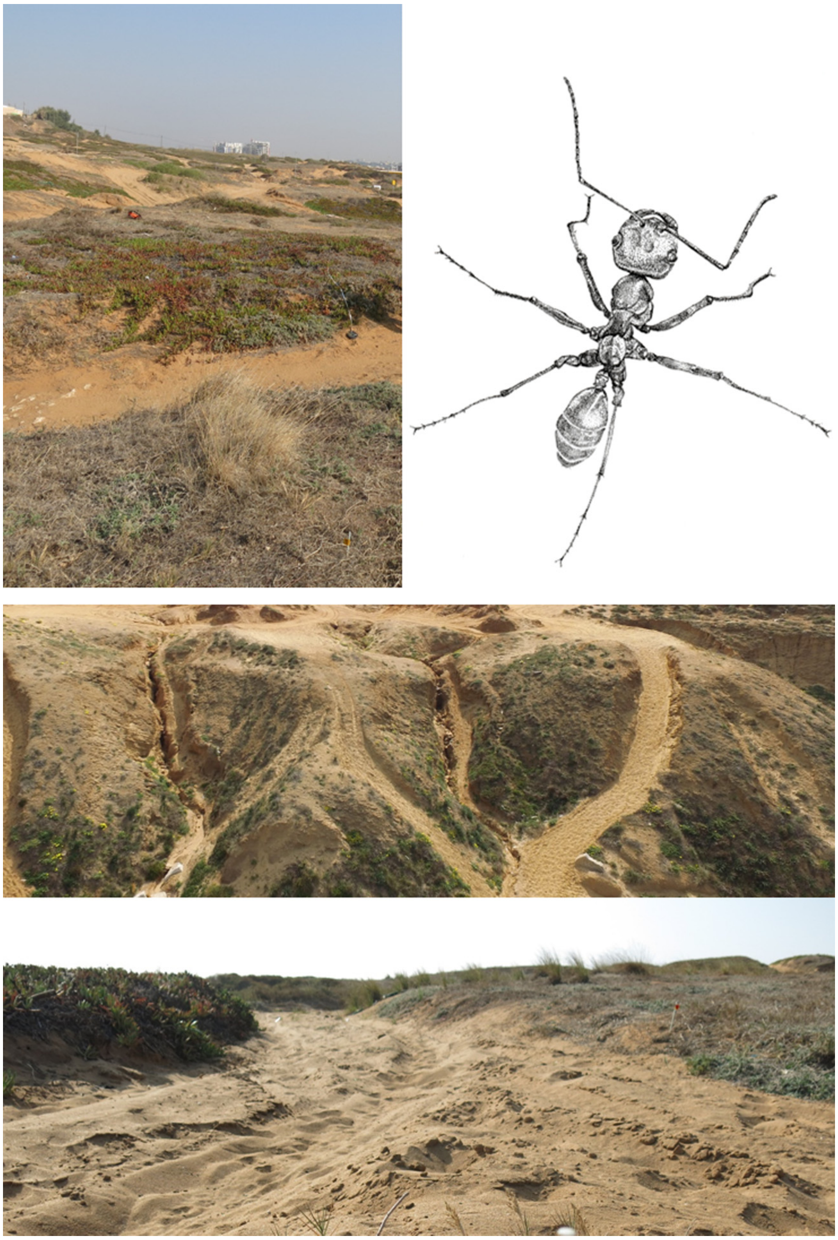

Fig. 1. Three photos of the habitat-of origin, comprised mostly of stabilized and semi-stabilized sand dunes, and a drawing of a *Cataglyphis niger* worker (by IS).

individually, do not mark trails with pheromone, and do not recruit other workers by using pheromones while foraging (Lenoir et al., 2009). Consequently, each worker must make individual decisions while foraging.

We expected increased maze complexity and increased number of workers searching to increase and decrease maze-solving time, respectively, and hence affect food discovery. This is because habitat complexity slows down movement, because animals reach dead-ends or face obstacles, which force them to use lengthier or more tortuous paths (Erlandsson et al., 1999; Cuddington and Yodzis, 2002). An extreme example is provided by predatory species that completely stop moving and switch to ambush predation when habitat complexity increases (Savino and Stein, 1989; James and Heck, 1994). A similar pattern probably holds true for foraging ants too, as studies on other ant species have demonstrated that increasing habitat complexity slows down foraging (Torres-Contreras and Vásquez, 2007; Radnan et al., 2018). That said, in a previous study on the same species studied here searching in similar but smaller mazes, maze complexity had little effect on maze-solving time and food discovery (Saar et al., 2017).

Here, we used a design of larger mazes and expected a stronger effect of maze complexity in the current design. If so, the apparent contradiction in the effect of complexity between large and small mazes could be a manifestation of the importance of scale in ecological studies (Levin, 1992). The motivation for the present study, therefore, was to examine whether high complexity levels introduced in large mazes would have an effect on maze-solving time in desert ants, in contrast to the only small effect detected when high complexity was examined in small mazes. Furthermore, in most of the studies demonstrating a link between habitat complexities and foraging behavior, habitat complexity was not precisely determined, and the experimental design merely comprised a “complex” vs. a “simple” habitat. An additional minor goal therefore was to test for the precise nature of the link between maze complexity and maze-solving time and to determine whether it is linear or not. A linear link would indicate that the increase in maze-solving time takes place at a similar rate to that of increasing complexity; while a non-linear link could indicate either an accelerating or a decelerating increase in maze-solving time with increasing complexity.

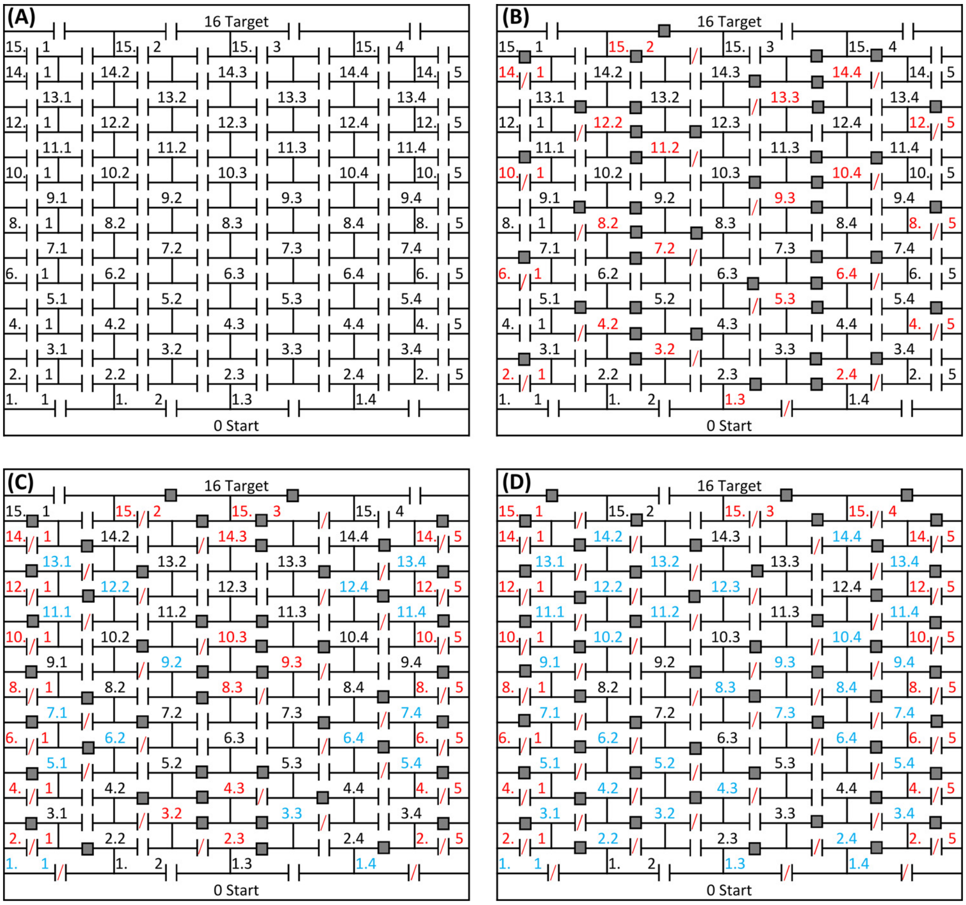

Fig. 2. The four mazes of increasing complexity levels used in the experiment. The maze is composed of cells (marked with numbers), the nest is located in the lower part of each maze (cell 0, start) and the food reward is in the upper part (cell 16, target). Cells are connected by paths. Two parallel lines connecting between cells indicate an open path through which the worker can move. The open paths leading to a dead-end are marked with a slant line, and we refer to them as wrong paths. A gray square indicates a closed path, through which movement is impossible. Dead-end cells are marked with a red number and are cells from which movement forward is impossible. A blue number indicates a cell that is not a dead-end but inevitably leads to a dead-end cell. (A) The least complex maze, with 120 correct paths. All paths in this case lead to the food reward. (B) The second least complex maze, with 55 correct paths leading to the food reward. (C) The third least complex maze, with 32 correct paths. (D) The most complex maze, with 16 correct paths.

We compared our findings to three simulations modelling the ant worker movement in the maze, calibrated to the data of maze-solving times in mazes of varying levels of complexity. The models assumed (a) depth-first search, (b) random search, or (c) a version of self-avoiding random search. Depth-first search is a common method for searching in mazes. It means searching longer and deeper into the maze, minimizing deviations to possible parallel routes, until reaching a dead-end, which when reached leads to turning back until reaching an unvisited cell (Korf, 1985; Schmajuk and Thieme, 1992; Reynolds, 2010). By random search, we mean that a searching worker has an equal probability to move in any possible, non-obstructed direction, irrespective of whether the worker has already visited this destination. Self-avoiding random search (Hayes, 1998; López Millán et al., 2012) starts as a random search, but the searching worker avoids re-entering destinations it has already visited that had led to dead-ends.

We also examined the contribution of colony size to maze-solving time, the number of workers searching in the maze, and the number of those feeding after initial discovery of the food reward. Previous studies on ants demonstrated that about 10% of the workers are involved in foraging (Porter and Jorgensen, 1981; Retana and Cerdá, 1990), and we therefore expected a positive correlation between colony size and the number of workers searching in the maze. A higher number of workers searching should also translate to faster maze-solving and more workers reaching the food, even due to chance alone.

2. Materials and methods

We collected 40 non-adjacent queenright colonies of *Cataglyphis niger* from Tel-Baruch sand dunes (32.132 N, 34.788 E) in October-December 2017 (Fig. 1). These semi-stabilized and stabilized sand dunes (~1.5 × 0.5 km) are an enclave of natural area, though disturbed by human activity, being surrounded by city neighborhoods in all directions, except for the Mediterranean coast to the west. See Saar et al. (2018a, b) for a description of the flora and other ant species in the habitat-of-origin. Colony size varied from 139 to 1575 workers (721 ± 393; mean ± 1 SD), covering the size of most colonies in the field, enabling us to test the effect of colony size on maze-solving time, and the number of workers searching and feeding, in addition to that of maze complexity. We kept the colonies in artificial Plexiglas nests (20 × 25 × 5 cm) in the laboratory (~28 °C; 12:12 L:D) and provided them constant access to water (water-filled tubes closed with cotton wool). We did not feed the colonies, to increase their motivation to forage. The experiment took place two days post collection after letting the colonies acclimate to laboratory conditions. The decision regarding acclimation duration of the colonies to laboratory conditions prior to the experiment considered two contrasting factors. On the one hand, colonies need to recover from collection stress; while on the other hand, too long a period in the laboratory has the potential to divert the colony from its natural behavior. We photographed each colony and counted the workers, referred to hereafter as colony size. Following the experiment, we fed the colonies and kept them in the laboratory for further experiments. No permits are required to collect this ant species and the experiment was non-lethal to the ants.

2.1. *Experiment: Searching in a maze of increasing complexity*

We tested each individual colony once in four mazes of equal size (1 × 0.6 m) but increasing complexity. Complexity was determined according to the number of correct paths leading to the food reward (see below): the higher the number of correct paths, the lower the complexity. The mazes were made of opaque Plexiglas, 5 cm height, and sealed from above with a transparent cover, preventing the workers from either escaping the maze or climbing the walls. The nests, in which the colonies were kept, were attached to the maze using a door, which was opened when the test began (Supplementary Material). The workers could therefore leave their nest and directly enter the maze. The mazes were placed in the laboratory below an artificial light source. We tested each colony only once, and did not expose it to the maze prior to the tests, as our aim was to study exploration behavior in a maze encountered for the first time and not to study spatial learning in a repeatedly encountered area. The mazes were composed of rectangular cells connected by paths (see Supplementary Material for a photo). In the simplest maze (Fig. 2a), for example, the cell 1.2 is connected to three cells (0, 2.2 and 2.3) through three paths. The mazes differed in the number of paths leading to a food reward (see below), hereafter referred to as “correct paths”, vs. paths leading to dead-ends, hereafter “wrong paths”. In the second simplest maze (Fig. 2b), for example, the cell 2.3 is connected only to cell 0 through one path leading to a dead-end, because its two other paths, leading forward in the maze, are blocked. The mazes were of four complexity levels and comprised of 120, 55, 32, or 16 correct paths (Fig. 2). We placed at the opposite end of the maze a food reward: 6-cm Petri dish with 0.5 g undiluted honey (similar to Saar et al., 2017). The workers might have smelled the honey, though we have no evidence for that; and we have no reason to believe that the smell would have disseminated differently in the mazes of different complexity levels. Workers, especially in the complex mazes, frequently reached dead-ends, at which there was no other choice but to turn back in the direction of the nest.

The maze was not intended to imitate the natural environment. The advantage of our maze is that its complexity level can be accurately defined and we can control for many confounding factors – a procedure impossible to implement in the field. The maze walls probably resemble dense vegetation through which ant workers cannot cross. The habitat-of-origin of the studied ants is composed not only of loose sand but also of stabilized dunes, forming obstacles that are difficult to cross. *Cataglyphis* can climb grass stalks or other small plants, to avoid heat stress (Boulay et al., 2017), but they are mainly ground foragers and do not forage on plants (Cerdá et al., 1992). Therefore, climbing bushes obstructing their way is less likely than turning back and seeking a different route, as simulated by the mazes we used. Workers may also encounter difficulty in climbing steep sand and may prefer to bypass it by finding a different route.

Cataglyphis offers a suitable model by which to study the effect of habitat complexity on foraging for several reasons: (1) this genus occurs in diverse habitats, from dunes of shifting sand completely free of plants to habitats covered with vegetation (Vonshak and Ionescu-Hirsch, 2009); (2) the long travel distance of the foragers while searching for food, because their food sources are usually scattered (Lenoir et al., 2009); and (3) their reliance on various navigation tools (Wehner, 2003). We documented the maze-solving time (the time till the first worker found the food reward). Following maze solving, we waited for 10 more minutes to allow more workers to reach the food reward in addition to the first one discovering it, and we then documented by visual counting: (a) the number of workers searching in the maze; (b) the number of workers feeding on the food reward; and (c) the mass of the food collected by the ant workers 10 min after maze solving (by weighing). Each colony was observed for up to 3 h. If the colony did not solve the maze within this time, the experiment was stopped and the colony was removed from all further analyses because it provided no values for either (a), (b), or (c) above. This held true for a total of five colonies (out of the 40 tested colonies, 10 per treatment): two and three in the most and second-most complex mazes, respectively. Setting the maze-solving time of the colonies not solving the maze to the maximal observation time (3 h) and including them in the analysis led to qualitatively identical results (see Supplementary Material). We therefore preferred to use a conservative approach and removed them. We used whole colonies and did not limit our test to solely foraging individuals, because we were interested in the effect of colony size on the number of workers searching and in the number of workers searching on maze-solving time. The mazes were cleaned with ethanol between tests to remove possible odors left by foraging ant workers.

2.1.1. Statistical analysis

We used two multiple linear regressions to test for the effect of the number of correct paths and colony size on maze-solving time and on the number of workers that searched for food. We then used a multiple linear regression to test for the effect of the number of correct paths and number of workers searching on the number of workers feeding on the food reward provided. Colony size and the number of workers searching demonstrated a tight positive correlation ($r = 0.755$) and could therefore not be simultaneously used as explanatory variables (violating the no multicollinearity assumption of linear regression). Maze-solving time did not differ from normal distribution, but the number of workers searching and feeding did, and they were both square-root transformed prior to the analysis. The mass of the food collected and the number of workers feeding were tightly correlated ($r = 0.862$). We therefore analyzed only the number of workers feeding, but the results were similar when replacing it with the mass of food collected as a response variable. We used a model selection procedure, the Akaike information criterion corrected for a small sample (AICc; Johnson and Omland, 2004), to examine whether the link between maze complexity and maze-solving time is better described by (a) a linear model ($y = ax + b$); or (b) a polynomial model ($y = ax^2 + bx + c$). All statistics were performed using SYSTAT v. 12 (Systat Software Inc., Chicago, IL, USA).

2.2. Modeling ant searching

We designed three individual-based simulation models in order to examine possible search methods for the workers in the maze, suggest mechanistic explanations for the results, and evaluate how well each of the models fit the observed results, expressed in maze-solving time. An individual-based model fits best here, because *Cataglyphis* spp. are solitary foragers, so foragers search independently of each other. The model was written in MATLAB 2017 (MathWorks, Natick, MA, USA). The search methods we applied were: (a) depth-first search algorithm, chosen because it is simple to compute and requires little memory by the ants; (b) random search, meaning that a worker has an identical probability of moving in any possible direction (excluding blocked paths), even if it revisits the same maze cell several times; and (c) self-avoiding random search, which is similar to random search, with the important exception of avoiding previously encountered dead-ends.

The depth-first search model adopts the simplifying assumption that workers know where their nest is and move away from the nest direction. *Cataglyphis* ants may do so using landmarks and smell (Mayade et al., 1993; Ziegler and Wehner, 1997; Steck et al., 2010). Specifically, workers might have used some slight differences in the maze walls, corners, or the reflection of the artificial light in the maze, as landmarks. Both the depth-first search model and the self-avoiding random search model assume that workers remember recently visited dead-ends, in order to avoid entering the same ones again. The assumption that workers possess short-term memory longer than our experiment duration is supported in the literature (Ziegler and Wehner, 1997; Beugnon et al., 2005). All three models are not meant to predict precisely the worker’s behavior, but should be simply referred to as “null models” tailored to the specific mazes used here, and assuming basic, unsophisticated movement patterns.

2.2.1. The algorithm of the depth-first search model

(1) The simulation starts when the worker leaves the nest. The worker moves for each time step one cell from a lower to an upper level in the maze, against the nest direction. (2) The worker first needs to choose one of four possible cells (Fig. 1a, cells 1.1–1.4). (3) For each further step, the worker can choose between two cells at the most (e.g., Fig. 2a, cell 1.2 leads to 2.2 and 2.3). The small corner cells in our maze lead only to a single cell in the higher level (e.g., Fig. 2a, cell 2.1 leads

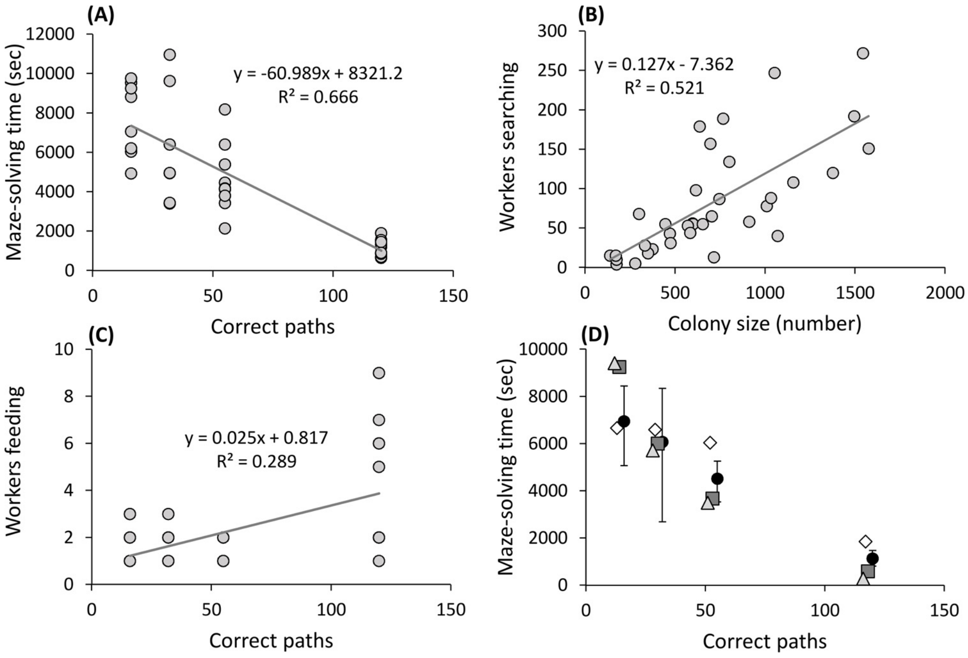

Fig. 3. (A) Maze-solving time (the time required to reach the food reward) as a function of the number of correct paths leading to the food reward (all data points are presented). (B) The effect of colony size on the number of workers searching in the maze, measured 10 min after reaching the food reward. (C) The effect of the number of correct paths on the number of workers feeding on the food reward, 10 min after reaching it. (D) A comparison between the expected maze-solving time according to the three simulation models, calibrated with half of the data (dark gray squares = depth-first search, grey triangles = random search, and white diamonds = self-avoiding random search), vs. the second half of the observed data [black circles; means ± 95% confidence intervals. Please see (A) for all data points].

only to 3.1). Cells leading to a dead-end also lead only to a single cell (e.g., Fig. 2c, cell 1.1, leading only to to 2.1) and a dead-end cell leads nowhere (e.g., Fig. 2c, cell 2.1). (4) If a worker encounters a dead-end it will go back, one cell each time step, until it reaches a cell that enables it to move in a different direction. Assuming short-term spatial memory, the worker will re-enter neither already visited dead-ends nor cells leading to these dead-end cells. (5) The simulation ends when the worker reaches the target cell containing the food reward. (6) The simulation's output is the number of time steps required to reach the target cell (maze-solving time) and the number of dead-ends that the worker encounters while searching (see the Supplementary Material for examples of simulated movements through the different mazes).

2.2.2. *The algorithm for the random search model*

(1) The simulation starts when the worker leaves the nest. The worker moves for each time step one cell in the maze. (2) The worker first needs to choose one of four possible cells (Fig. 1a, cells 1.1–1.4). (3) For each further step, the worker chooses randomly with equal probability among four cells at the most, either against the nest direction or back to the nest (e.g., Fig. 2a, cell 2.3 leads to 3.2, 3.3, 1.2 and 1.3). (4) If there is only a single path, as in dead-ends, the worker will use it. (5) The simulation's ending and output are the same as in the previous algorithm.

2.2.3. *The algorithm for the self-avoiding random search model*

(1) The simulation starts when the worker leaves the nest. The worker moves for each time step one cell in the maze. (2) The worker first needs to choose one of four possible cells (Fig. 1a, cells 1.1–1.4). (3) For each further step, the worker chooses randomly with equal probability among four cells at the most, either against the nest direction or back to the nest. (4) If a worker encounters a dead-end it will go back, one cell each time step, until it reaches a cell that enables it to move in a different direction. Assuming short-term spatial memory, the worker will re-enter neither already visited dead-ends nor cells leading to these dead-end cells. (5) The simulation's ending and output are the same as in the previous algorithm.

2.3. *Calibrating the model*

We randomly chose half of the data derived from each of the four treatments (17 of the 35 colonies we have data for). We used the maze-solving times of these selected colonies to calibrate the model. We used a linear regression to estimate the amount of real time (seconds) that equals: (1) a single time step in the model, which is the time required to move between two adjacent cells; and (2) how long a worker requires to find out that the current cell is a dead-end before turning back. We achieved this by running each of the three simulations for 10,000 times, and calculating the average maze-solving time and the number of dead-ends encountered for each maze type, which were maze-specific (see Results). We then fitted an equation linking between the observed maze-solving time, the average simulation duration (number of time steps) in each of the four mazes, and the average number of dead-ends encountered in each of the four mazes. The equation was: Maze-solving time = average simulation time steps × a + average number of dead-ends encountered × b. The regression estimated both a and b, while a and b were estimators of the time it took to move from one cell to the next, and of the time it took to turn back at a dead-end, respectively. We calculated the expected maze-solving time according to each simulation for each maze type. We next compared the expected maze-solving time for each maze type according to the simulation using the other half of the data that had not been used to calibrate the model. This provided an estimation of the predictive power of each of the three models and also their points of weakness.

3. Results

3.1. *Experiment: Searching in a maze of increasing complexity*

Maze-solving time and hence food discovery decreased with the increasing number of correct paths ($t = -7.707$, $P < 0.001$, $n = 35$; model $R^2 = 0.668$; Fig. 3a). Colony size had no effect on maze-solving time ($t = 0.460$, $P = 0.649$). In contrast, colony size positively affected the number of workers searching ($t = 6.225$, $P < 0.001$, model $R^2 = 0.580$; Fig. 3b), while the number of correct paths had no effect on the same response variable ($t = -0.880$, $P = 0.386$). The number of workers feeding on the food reward was positively affected only by the number of correct paths ($t = 3.974$, $P < 0.001$; model $R^2 = 0.333$; Fig. 3c), with no effect of the number of workers searching ($t = 1.723$, $P = 0.095$).

The linear model better described the link between maze complexity

Table 1
Mean maze-solving time (MST) or the number of cells visited during the simulation, and number of dead-ends (DE) encountered for each of the maze types for each of the three simulations computed (depth-first search, random search, and self-avoiding random search). Each mean is based on 10,000 simulation runs. In the simplest maze (first row of the Table; Fig. 2a) there are no dead-ends, and therefore the average time a worker spends in dead-ends is zero. "*a*" refers to the calibrated time it takes for a worker to cross a single cell in the maze according to each model, and "*b*" refers to the time spent in each dead-end visited, both "*a*" and "*b*" after calibration to the data.

	Depth-search first		Random search		Self-avoiding random search	
Maze type / correct paths	MST	DE	MST	DE	MST	DE
120 (Fig. 2a)	16	0	243.48	0	242.32	0
55 (Fig. 2b)	23.13	3.57	397.67	61.48	301.38	12.74
32 (Fig. 2c)	36.17	5.9	591.02	101.88	311.31	14.38
16 (Fig. 2d)	67.95	8.5	1270.25	160.29	404.66	12.18
a (sec)	37.5		1.2		7.6	
b (sec)	789.2		49.3		293.3	

and maze-solving time than the polynomial model (AICc of the linear model = 627.90; AICc of the polynomial model = 629.10; ΔAICc = 1.20), although this difference is too small to completely rule out the possibility that a polynomial model also fits the data.

3.2. *Modeling ant searching in a maze design*

The average maze-solving time and the number of dead-ends encountered per maze type for the three models are given in Table 1. The models and their fit to half of the data provided different estimations (Table 1), regarding *a* (the time a worker requires to move between adjacent cells in the maze) and *b* (the delay induced by a dead-end). Specifically, *a* was 1.2, 7.6, and 37.5 s, and *b* was 49.3, 293.3, and 789.2 s in the random search, self-avoiding random search, and depth-search first models, respectively. The maze-solving times predicted by each of the three models and calibrated using half of the data were compared to the observed maze-solving time according to the other half of the data (Fig. 3d). All models deviated to some extent from the observed results. However, the model deviating the least was the self-avoiding random search model (a total deviation between the four pairs of the observed and expected points of 3,052 s) followed by the depth-first search model (3,727 s) and the random search model (4,662 s). We also used a bootstrap procedure to calculate the 95% confidence intervals for the observed results. Regarding the overlap with the confidence intervals of the observed results, neither the self-avoiding random search nor the depth-first search models overlapped with two of the four complexity levels, while the random search model did not overlap with three of the four complexity levels (Fig. 3d). Finally, the self-avoiding random search provided, in our opinion, the most logical values of *a* and *b*, because 1.2 s for the time a worker requires to move between adjacent cells as calibrated for the random search seems too short to be realistic, while 789.2 s spent in a dead-end, as predicted by the depth-first search seems too long.

4. Discussion

Habitat complexity, or specifically here the number of correct paths leading to the food reward, had a strong effect on maze-solving time and consequently on food discovery. Complexity explained ~66% of the variance in maze-solving time – a high value for a single variable. Maze-solving time increased linearly with maze complexity. While colony size had a strong positive effect on the number of workers searching, it was translated neither to a positive effect on maze-solving time, nor to the number of workers feeding 10 min after the first worker had discovered the food reward. The latter was negatively affected by complexity. We consider the self-avoiding random search model to be the best one describing the movement of the workers in the maze, while the depth-search model was the second-best model. The latter model overestimated the time required to solve the maze in complex mazes and underestimated it in simple mazes, while the self-avoiding random search model overestimated the time required to solve the maze in simple mazes. We discuss possible reasons for these deviations.

The strong link between habitat complexity, maze-solving time, and the number of workers feeding emphasizes the importance of referring to habitat complexity when predicting movement patterns and time. The findings from our study also imply that two habitats, similar in food abundance, spatial distribution pattern, and substrate type may still greatly differ in the foraging efficiency of animals searching for food, if the habitats differ in complexity. This is supported by other studies demonstrating the negative effect of habitat complexity or heterogeneity on foraging success, such as of parasitoid encounter rates with their hosts (Romeis et al., 2005; Bezemer et al., 2010), or other ant species searching for food (Torres-Contreras and Vásquez, 2007; Radnan et al., 2018). The effect of habitat complexity is not limited to movement patterns and foraging, but can also lead to slower growth and impaired survival and reproduction. Habitat complexity may more strongly affect dominant species than subordinate ones, making it harder for the former to monopolize resources (Höjesjö et al., 2004; Sarty et al., 2006). In this sense, complexity has a positive contribution to species coexistence. In a previous study with the same study species searching in smaller mazes of lower complexity levels, the latter had only little effect on maze-solving time (Saar et al., 2017). We demonstrate here the strong effect of complexity when searching in larger, more complex mazes. This contradiction in the findings of different studies emphasizes the importance of testing phenomena on the right scale, and suggests that larger mazes, as used here, are required in order to demonstrate the negative effect of complexity on navigation in desert ants. The link between maze complexity and maze-solving time was linear. This suggests that the effect of complexity or added obstacles is additive, at least for the range tested. It also suggests that the search behavior of the studied ant remains constant across complexity levels, though this remains to be validated in future studies.

Because some ant species repeatedly choose either right or left turns, the time taken to solve the maze also depends on the number of inconsistent turns (i.e., change in movement direction) that workers need to take while moving along the correct path, leading to the food reward (Jander, 1990; Macquart et al., 2008; Grüter et al., 2015). The number of required turns in our mazes increased from the most complex maze till the second simplest one. Therefore, if the latter finding is valid for the studied species here, this could have moderated the effect of complexity in the current design but could not have increased it. The studied species occurs in sand dunes, which is not as open and obstacle-free a habitat as one might imagine, due to an ongoing process of dune stabilization and the growth of dense vegetation. Furthermore, *C. niger* workers sometimes encounter difficulty in climbing steep sand (D Bega, personal observation), which presents another possible obstacle, forcing the foraging workers to use a lengthier or a more tortuous route, probably making it harder to detect food sources. Our findings support this suggestion.

The number of workers searching was about 10% of the colony size. This observation fits studies in other ant species reporting a similar proportion of foragers (e.g., Porter and Jorgensen, 1981; Retana and Cerdá, 1990; but see Torres-Contreras and Vásquez, 2007 for a decrease in the ratio of foragers to colony size with increasing colony size). A valid assumption is that the number of workers searching should affect maze-solving time and food retrieval (Cole et al., 2014). This, however, did not hold true in the present study. There are several examples demonstrating a similar pattern – larger colonies are not more efficient in collecting resources than smaller ones (Thomas and Framenau, 2005; Flanagan et al., 2012). There is probably a difference concerning this aspect between individually foraging ant species, similar to our focal species, and group-foraging species that recruit nestmates while foraging. Being able to recruit many workers is certainly beneficial in depleting large food sources. We have no single good explanation as to why a higher number of workers searching in the maze did not translate to faster solving times. It could be that the presence of many workers in the maze slows them down as they frequently encounter and interact with each other. It could also be that the advantage that large colonies have regarding the number of foragers is not immediately evident, because not all foragers leave the nest at the same time. In this case, discovery time depends mostly on the number and timing of the first few workers leaving the nest, which might not greatly differ according to colony size.

The random search model was the least suited to the observed data, probably either because the workers' movement was not random, but more directional against the nest's direction, or due to the short-term memory ability of workers preventing them from reentering already visited dead-ends. Self-avoiding random search fitted somewhat better than depth-first search. The depth-first search model underestimated the time needed to reach the food in a simple, open maze, while self-avoiding random search overestimated it. Workers probably do not simply go directly through the maze, as the depth-first search model assumes, but occasionally spend time thoroughly searching a single cell or even turn back and return to the nest. Both behaviors, of turning back in the nest direction and of spending some time in dead-ends, were observed when conducting the experiment. Food retrieval therefore may not be the sole goal of these ants, with acquiring general knowledge on the immediate surroundings of the colony also being important. Acquiring such knowledge might assist the workers under more complex situations in the future, unrelated to foraging (e.g., nest relocation: Franks et al., 2007; Healey and Pratt, 2008). Such knowledge of their new surroundings will surely also aid in foraging-related situations. However, removing any movement directionality might lead to too many steps within a narrow range of cells, as expressed in the overestimation of maze-solving time in the two least complex mazes by the self-avoiding random search model. We therefore believe that the assumption that workers remember the nest's direction and move against it when searching for food is not exaggerated. The depth-search first model overestimated the time required to solve the most complex maze. This suggests that workers either stopped less frequently than expected by the model or moved faster. In short, enabling the simulated workers at least some degree of moving back in the direction of the nest seems to improve the model's fit to the data.

All models assumed similar movement speed and delay times when facing a dead-end irrespective of the number of correct paths. Two other simplifying assumptions of the model are those of no change in behavior throughout the test and no effect of possible interactions between workers. Every model has simplifying assumptions, and some of them can be relaxed, but at the cost of increasing model complexity and decreasing its generality. Plotting the maze-solving time of different ant species against the complexity level might result in different slopes, depending on each species' ability to cope with high complexity. Ant species demonstrating a moderate slope might populate more complex habitats while those characterized by a steep slope might do better in open areas. In conclusion, we demonstrate here the negative effect of maze complexity on maze-solving time and on the number of workers feeding after initial discovery of the food reward. In addition, while the number of workers searching was positively correlated with colony size, colony size had no effect on feeding intensity.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.beproc.2019.103893.

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