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Random choice of the tropical fire ant in the enclosed space

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ABSTRACT: The tropical fire ant *Solenopsis geminata* is an invasive ant species in Taiwan. In the present study, we investigated the turning behaviour of the tropical fire ant in the T-maze when external cues were shielded. In total, 1800 observations (600 workers × 3 choices) were conducted in the study. Workers presented eight types of left–right choice after three choices in the T-maze experiment. We demonstrated that the turning behaviour of *S. geminata* workers was not significantly affected by the four cardinal directions. Moreover, eight types of left–right choice of workers were divided into four groups. The result shows that the ratio of the four groups is 1.33:3.27:3.25:1 (≈1:3:3:1). Notably, based on the binomial expansion, the left–right choice of workers is random. The workers' choices did not exhibit a leftward or rightward turning bias after three choices in the experiment. Thus, we speculate that in the absence visual cues, *S. geminata* workers might navigate using random choice strategies when exploring the enclosed space.

KEY WORDS: Left–right choice, Random choice, *Solenopsis geminate*, T-maze, Turning behaviour.

INTRODUCTION

Ants have various signals and cues available for orientation, including pheromone trails, visual cues, tactile information, idiothetic cues, and geomagnetic information (Jaffé *et al.*, 1990; Wittlinger *et al.*, 2006; Freas and Schultheiss, 2018). A study on giant tropical ants *Paraponera clavata* revealed that workers use pheromonal trails and visual cues during orientation and that foragers change cue hierarchies with experience: naive *P. clavata* foragers use pheromone trails to find food sources, whereas experienced foragers use local landmark cues for orientation (Harrison *et al.*, 1989). For example, desert ants *Cataglyphis fortis* use path integration (an innate strategy) to return home and revisit locations (Müller and Wehner, 1988). They have the ability to learn food odours and use olfactory cues to return to nest (Huber and Knaden, 2018). Buehlmann *et al.* (2018) observed *C. fortis* foragers' walking speed and found that *C. fortis* foragers slow down when approaching the nest. Ant foragers, primarily use a visual system as their navigational sensor. Australian Jack Jumper ants *Myrmecia croslandi* navigate using landmarks to find their way home (Narendra *et al.*, 2013; Zeil *et al.*, 2014).

Different ant species exhibit different navigational strategies (Knaden and Graham, 2016). Many ant species use idiothetic memory, a form of spatial memory, for orientation in the absence of pheromonal, visual, and other external cues (Jaffé *et al.*, 1990; Gerbier *et al.*, 2008). Cosens and Toussaint (1985) reported that wood ants *Formica aquilonia* can use idiothetic information to locate a feeding site in the laboratory. *Formica pratensis* foragers use some idiothetic left–right turning memory in T-maze laboratory experiments (Aksoy and Camlitepe, 2005). Desert ants *C. fortis* memorise their stride length and azimuth and use these values to guide foraging and homing (Wittlinger *et al.*, 2006). Corpse-carrying workers of *Myrmica rubra* depend on their own spatial memory when they remove dead nestmates far from the nest (Diez *et al.*, 2011). However, some ant species do not depend on idiothetic cues (Goss *et al.*, 1989; Shen *et al.*, 1998; Salo and Rosengren, 2001).

Many ants use a combination of cues for navigation. In addition to using innate guidance (pheromone or visual cues) and idiothetic information, foraging ants can navigate home using panorama-based guidance and learned information (Steck *et al.*, 2009; Knaden and Graham, 2016; Freas and Schultheiss, 2018). *Cataglyphis* ants use terrestrial cues for landmark guidance by performing well-structured learning walks back to the nest. These ants use panorama-based navigation through multiple preforaging learning walks (Fleischmann *et al.*, 2017; Fleischmann *et al.*, 2018). Moreover, the behaviour of ants is represented by deterministic walks in a random environment for orientation (Li *et al.*, 2014). Basari *et al.* (2014) suggested that former follower ants of *Temnothorax albipennis* learn landmarks during tandem running and use this information to make strategic decisions.

Recent research has found that ants show turning biases in branching mazes. (Hunt *et al.*, 2014) indicated that rock ants *T. albipennis* exhibit a leftward turning bias when exploring unknown nest sites. (Basari *et al.*, 2014) observed that *T. albipennis* worker ants use their right eye more than their left eye to recognise landmarks for navigation. Hunt *et al.* (2018) also provided evidence that turning bias may be associated with significant differences in ommatidia number between the left and right eyes.

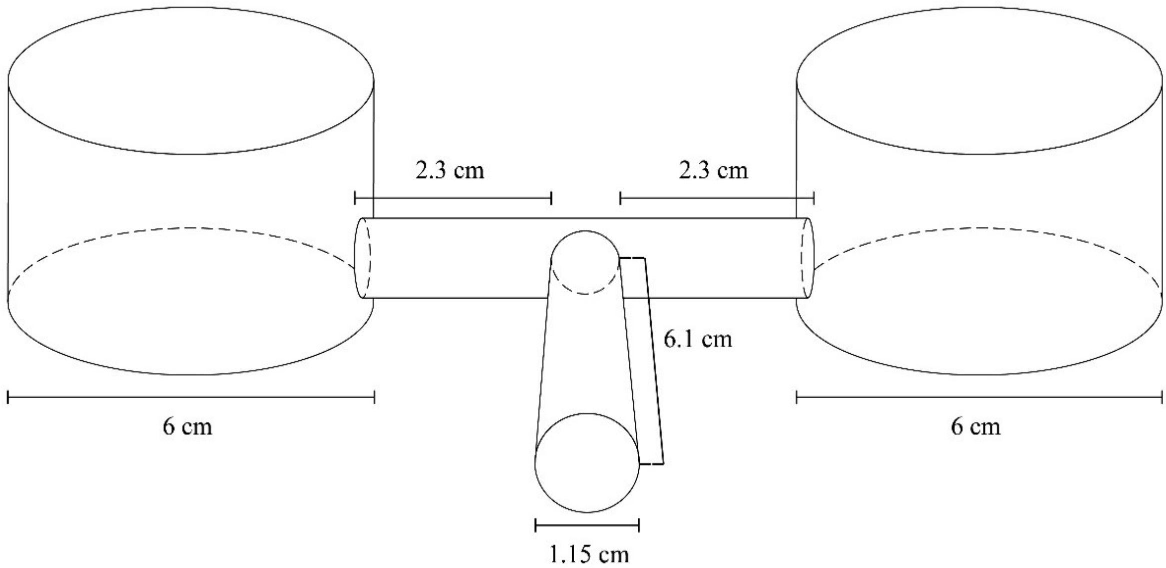

Fig. 1. The T-maze was connected to two plastic containers covered by the red cellophane-paper. We oriented the T-maze entrance along four paths corresponding to the cardinal directions (south, north, east, and west).

In this study, we focus on the tropical fire ant *Solenopsis geminata*, an invasive ant species widely distributed in agricultural fields and weedy areas in Central, Southern, and Eastern Taiwan (Lai *et al.*, 2009; Lai *et al.*, 2018). In general, invasive ant species expand their range through exploring novel environments and establishing new nest sites. Based on behaviour studies of *S. geminata*, we may gain more understanding of their exploration behaviour in the ecosystem in Taiwan. In our experiment, a simple T-maze is used to investigate the turning bias of tropical fire ants when shielded from external cues. We also investigate whether workers' choices (making left or right turns) are affected by the four cardinal directions.

MATERIALS AND METHODS

The ants

Three *S. geminata* colonies were excavated from Taichung (24°15′N, 120°31′E), Taiwan between October 2018 and May 2019. Each colony was transported in a plastic container coated with Fluon (NP115; Northern Products Inc., Woonsocket, RI, USA) to prevent the ants from escaping. All *S. geminata* colonies were moistened regularly and maintained at room temperature (26°C–27°C). The workers were provided with water, frozen crickets (*Gryllus bimaculatus*), and commercial insect jellies (Beetle Jelly, Han Shuo Food Co., Chang-Hua, Taiwan) ad libitum. After acclimatisation for 1 week in the laboratory, the colonies were used in behavioural experiments.

Experimental design

To understand whether *S. geminata* workers have a turning bias while shielded from external cues, we used a red cellophane-coated T-maze (entrance arm: 1.15 cm in diameter, 6.1 cm long; left-right arms: 1.15 cm in diameter, 2.3 cm long) connected to two plastic containers (6 cm in diameter) which were also covered with red cellophane (Fig. 1). The plastic container's interior walls were coated with Fluon to prevent ants from climbing the walls and escaping. The T-maze entrance along four paths corresponding to the cardinal directions (south, north, east, and west). Workers walked into the T-maze from south to north (S–N), north to south (N–S), east to west (E–W), and west to east (W–E). To take a S–N direction, for example, a worker walked into the T-maze from south to north when the T-maze is positioned in a S–N direction. By contrast, when the T-maze is rotated, a worker will walk into the T-maze from the north to south (N–S) directions. We also observed whether the four cardinal directions affect workers' choices to turn left or right.

In each trial (S–N, N–S, E–W, and W–E), 50 workers on the nest surface were randomly collected from each colony. Each worker had three choices in each direction tested (i.e., three replications for each worker). Thus, 200 workers were used from each of the three colonies in the four cardinal directions tested. Workers used in each test were isolated in separate containers away from the nest. In total, 1800 observations (50 workers × 3 choices × 4 cardinal directions × 3 colonies) were conducted in this study. In the first trial, an individual worker was placed at the entrance of the T-maze using a paintbrush. After the first left-right choice, the worker was removed from the plastic container and placed in a separate Fluon-coated plastic container - labelled with L_1/R_1 - until the other workers completed the experiment. Each worker in

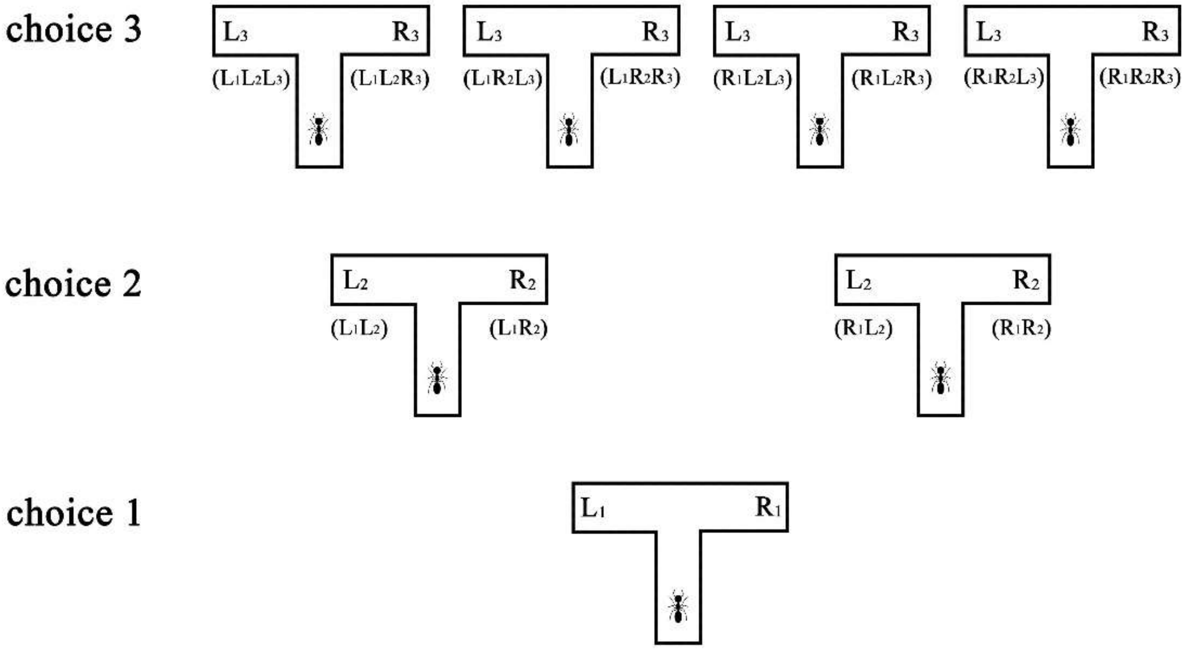

Fig. 2. Three choices for workers in the T-maze experiment. In the first choice (choice 1), each individual worker was introduced into the entrance of the T-maze using a paintbrush. After the first left–right choice, the worker was placed in a plastic container which labelled L_1 or R_1. Each worker in the L_1 plastic container was then reintroduced into the entrance of the T-maze to make the second choice (choice 2). After the third choice (choice 3), eight left–right choice combinations were possible ($L_1L_2L_3$, $L_1L_2R_3$, $L_1R_2L_3$, $L_1R_2R_3$, $R_1L_2L_3$, $R_1L_2R_3$, $R_1R_2L_3$, and $R_1R_2R_3$).

the L_1 plastic container was introduced into the entrance of the T-maze to make the second choice. For instance, if a worker turned left as both its first and second choice, the worker would be placed in the plastic container labelled L_1L_2. By the second left–right choice, a worker's choice combinations might be L_1L_2, L_1R_2, R_1R_2, or R_1L_2. After the third left–right choice, a worker could have made any of the eight possible combinations of left–right choices: $L_1L_2L_3$, $L_1L_2R_3$, $L_1R_2L_3$, $L_1R_2R_3$, $R_1L_2L_3$, $R_1L_2R_3$, $R_1R_2L_3$, and $R_1R_2R_3$ (Fig. 2). The T-maze and plastic containers were cleaned with 75% ethanol to remove any pheromone residue left by the workers after each worker walked through the maze. Between each choice, the workers were placed in the plastic container for at least 10 minutes to acclimatise. If a worker made a U-turn and exited through the entrance of the maze, it was moved and placed in a plastic container to acclimatise for 10 min before retesting.

To determine the number of left–right turning biases in workers' choices, we generated predictions of turning frequency by using the binomial expansion listed subsequently. After the experiment, the eight combinations of left–right choice (CLRC) of all workers are expected, given by

$$\mathbf{CLRC = (L_1+R_1) \times (L_2+R_2) \times (L_3+R_3),} \quad \mathbf{(1)}$$

where CLRC denotes the types of left–right choice, L represents turning left, R represents turning right, and the subscripts 1, 2, and 3 represent the first, second, and third choices. Assuming that the workers' first, second, and third choices are independent, we set

$$\mathbf{L_1 = L_2 = L_3 = L} \quad \mathbf{(2)}$$

and

$$\mathbf{R_1 = R_2 = R_3 = R.} \quad \mathbf{(3)}$$

By substituting Eqns 2 and 3 in Eqn 1, we obtain

$$\mathbf{CLRC = (L+R)^3 = L^3 + 3L^2R^1 + 3L^1R^2 + R^3.} \quad \mathbf{(4)}$$

Statistical analysis

We used SPSS (version 25) for statistical analysis. The left–right choice data were analysed with binomial tests. The chi-square test was performed to test whether the four cardinal directions affected the workers' left–right choices.

RESULTS

Our results indicated that the workers' choices to turn left or right were not significantly associated with the four cardinal directions ($\chi^2 = 2.323$, $df = 3$, $P = 0.508$). In total, 1800 observations on 600 workers were conducted in a T-maze experiment (Table 1). Workers were more likely to make three left turns ($L_1L_2L_3$: 90 workers × 3 choices = 270 left–right choices) than to make three right ($R_1R_2R_3$: 68 workers × 3 choices = 204 left–right choices). However, this does not show a significant turning bias for workers, even though the total number of left–right choices was 934 (51.89%) for left choices and 866 (48.11%) for right choices (P = 0.114; Table 1).

Table 1. Left–right choices of workers after three choices in the T-maze experiment.

Type of workers' choices	Worker number (left–right choices) Cardinal Directions				The total number of workers
	S–N	N–S	E–W	W–E	
$L_1L_2L_3$	20 (60L)	25 (75L)	23 (69L)	22 (66L)	90 (270L)
$L_1L_2R_3$	20 (40L, 20R)	12 (24L, 12R)	17 (34L, 17R)	19 (38L, 19R)	
$L_1R_2L_3$	24 (48L, 24R)	24 (48L, 24R)	17 (34L, 17R)	24 (48L, 24R)	222 (444L, 222R)
$R_1L_2L_3$	18 (36L, 18R)	19 (38L, 19R)	17 (34L, 17R)	19 (38L, 19R)	
$L_1R_2R_3$	15 (15L, 30R)	18 (18L, 36R)	24 (24L, 48R)	16 (16L, 32R)	
$R_1L_2R_3$	25 (25L, 50R)	23 (23L, 46R)	16 (16L, 32R)	11 (11L, 22R)	220 (220L, 440R)
$R_1R_2L_3$	18 (18L, 36R)	15 (15L, 30R)	16 (16L, 32R)	23 (23L, 46R)	
$R_1R_2R_3$	10 (30R)	14 (42R)	20 (60R)	24 (72R)	68 (204R)
Total	**(242L, 208R)**	**(241L, 209R)**	**(227L, 223R)**	**(224L, 226R)**	**600 (934L, 866R)**

S–N: south–north (a worker entered the T-maze from the south and walked north when the T-maze was positioned in a south–north direction); N–S: north–south; E–W: east–west; W–E: west–east; L: left choice; R: right choice; 1: first choice; 2: second choice; 3: third choice.

Table 2. Four left–right choice groups after three choices in the T-maze experiment.

Group of workers' choices	Cardinal Directions				The total number of workers	Percentage of choices (%)	Ratio
	S–N	N–S	E–W	W–E			
Group Ⅰ (L^3)	20	25	23	22	90	15	1.33
Group Ⅱ (L^2R^1)	62	55	51	54	222	37	3.27
Group Ⅲ (L^1R^2)	58	56	56	50	220	36.7	3.25
Group Ⅳ (R^3)	10	14	20	24	68	11.3	1

S–N: south–north (a worker entered the T-maze from the south and walked north when the T-maze was positioned in a south–north direction); N–S: north–south; E–W: east–west; W–E: west–east; L: left choice; R: right choice; L^3 ($L_1L_2L_3$); L^2R^1 ($L_1L_2R_3$, $L_1R_2L_3$, and $R_1L_2L_3$); L^1R^2 ($L_1R_2R_3$, $R_1L_2R_3$, and $R_1R_2L_3$); R^3 ($R_1R_2R_3$).

The number of worker ants for each of the eight types of left–right choices in the T-maze experiment is presented in Table 1. The eight combinations could be divided into four groups according to Eqn 4: I (for L^3), II (for L^2R^1), III (for L^1R^2) and IV (for R^3; Table 2). Moreover, based on Eqn 4, when L = R, the L^3:L^2R^1:L^1R^2:R^3 ratio is 1:3:3:1. Of all 600 workers, 90 (15%), 222 (37%), 220 (36.7%), and 68 (11.3%) appeared in group I, II, III, and IV, respectively—thus presenting a L^3:L^2R^1:L^1R^2:R^3 ratio of 1.33:3.27:3.25:1, which is nearly equal to 1:3:3:1 (Table 2). Approximately half of all included workers chose the right or left direction randomly.

DISCUSSION

Animals can use innate guidance, idiothetic, or learned information for navigation (Knaden and Graham, 2016). Ants have different search strategies to find targets when they are in uncertain environments (Schultheiss *et al.*, 2015; Wehner *et al.*, 2016). Workers explore new nests in closed/underground environments that are typically dark, narrow, and maze-like networks. Thus, T-mazes are tools for studying the exploration behaviour of *S. geminata* workers in this study. We noted workers exhibited a random choice even when the orientation of the entrance to the T-maze was changed. Therefore, our workers' choices appear to have not been significantly affected by any of the four cardinal directions.

Worker ants have no previous knowledge of the environment outside of their nests before they leave the nests. Thus, an inexperienced worker would be guided by internal inherited strategies (Schultheiss *et al.*, 2015). Our present experiments showed that *S. geminata* workers did not exhibit a significant turning bias while in the T-maze, even though the total number of left choices was more than that of right choices. When no external cues are available, ant workers might use different types of search strategies for the location of their nest. For example, the wall-following (i.e., thigmotactic) behaviour has been observed in other ants as well (Dussutour *et al.*, 2005; Hunt *et al.*, 2014; Endlein and Sitti, 2018). Thigmotactic behaviour is possibly a search strategy for ants to explore unknown areas with boundaries (Endlein and Sitti, 2018) or a simply connected maze (Walker, 1986). However, it is difficult to determine whether workers' incidental contact with either the left or right side of the wall of a maze leads to their wall-following behaviour in this study. The turning bias of individual ants without possible interference of a wall contact will be the focus for the future investigation.

In our results, workers presented a nearly equal ratio of eight types of left–right choice in this study. Therefore, we suggest that *S. geminata* workers exhibit random search behaviours in the enclosed spaces. The random walk is a search strategy used by some animals to explore unknown areas (Bartumeus *et al.*, 2005; Schultheiss *et al.*, 2015). Deneubourg *et al.* (1986) showed that foragers exit their nest for the first time in random directions around the nest. The Argentine ants

(*Linepithema humile*) have been observed to choose directions randomly when encountering novel areas (Mahavni *et al.*, 2019). Naive foragers tend to explore different compass directions around the nest during their learning walks (Zeil and Fleischmann, 2019).

According to Eqns 2–4, if L^3:$3L^2R^1$:$3L^1R^2$:R^3 = 1:3:3:1, then $L_1 = L_2 = L_3 = R_1 = R_2 = R_3$. We speculate that these workers' choices to turn left or right are not affected by their previous choices, although we do not know yet whether workers remember the direction they have chosen after testing. However, Goss *et al.* (1989) trained foragers of the Argentine ants to visit the feeding site and found that workers were unable to memorize directional information. Even though ant workers of *Formica uralensis* could memorize the location of a food resource and make repeated trips to it, they still forage randomly in the absence of visual and olfactory cues (Salo and Rosengren, 2001). It will be important in the future to investigate whether repeated testing of the same individual leads to worker's memory formation.

In conclusion, we investigated the turning behaviour of *S. geminata* workers in the absence of external orientation cues through a T-maze experiment and noted that after three left–right choices, the workers did not exhibit left–right turning bias in the T-maze. Moreover, the workers' left–right choices are random. Thus, we speculate that *S. geminata* workers might navigate using a random choice strategy to explore an enclosed space when no visual cues are provided. In other words, the random exploration might be an effective strategy for *S. geminata* workers to explore unknown areas.

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