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Searching Behavior in the Tropical Fire ant *Solenopsis geminata* (Hymenoptera: Formicidae)

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Social insects have evolved different search strategies to find target objects in unknown environments. In the present study, the searching behavior of the tropical fire ant *Solenopsis geminata* was investigated in a circular arena. The average time, search path, speed, and search patterns of worker ants in a circular arena were determined. The results showed that fire ant workers followed six major search patterns. The variation in the searching patterns of workers may explain the different levels of exploration. Most workers (56.8%) tended to search in small loops and progressively increase the search area size. These workers mostly turned in one direction, either clockwise or counterclockwise. The number of workers whose turning directions were consistent was significantly higher than that of workers which changed the turning directions. Moving speed was also higher in workers who maintained their turning directions than in those that changed directions. We thus propose that following search patterns consisting of loops of increasing size may be an effective strategy. The tropical fire ant *S. geminata* is a globally invasive species that was introduced to Taiwan 40 years ago and has continued to threaten residents. Based on behavioral studies of *S. geminata*, we may gain a better understanding of their exploratory behavior in the ecosystem in Taiwan.

Key words: *Solenopsis geminata*, Searching behavior, Searching patterns, Loops, Invasive species.

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BACKGROUND

Ants use a variety of cues and navigational strategies for orientation (Jaffé et al. 1990; Wehner et al. 2016; Freas and Schultheiss 2018). In most ant species, the predominant cues are trail pheromones used for orientation on paths between the nest and resources (Vilela et al. 1987). However, most trail pheromones evaporate and degrade rapidly, especially at high surface temperatures (van Oudenhove et al. 2011). Certain ant species use visual signals for navigation; for example, giant tropical ants (*Paraponera clavata*) initially use olfactory cues, and experienced foragers may then switch from olfactory to visual cues for orientation (Harrison et al. 1989). Ants of the genus *Cataglyphis* have high visual ability and use sun-compass navigation (Wehner et al. 1996). Desert ants (*Cataglyphis fortis*) navigate using path integration to return to the nest and revisit locations (Müller and Wehner 1988). However, path integration can be error-prone (Merkle et al. 2006; Huber and Knaden 2015). To overcome potentially accumulating errors of the path integrator, foragers use visual and olfactory cues to pinpoint their nests. In addition, some ant species rely on idiothetic cues, the self-motion cues, for orientation. For instance, wood ants (*Formica aquilonia*) can use idiothetic information for their foraging activity, as shown under laboratory conditions (Cosens and Toussaint 1985). Foragers of *F. pratensis* can navigate using idiothetic left/right turning memory in T-maze experiments (Aksoy and Camlitepe 2005).

Forager ants may encounter unpredictable and diverse navigational challenges in dynamically changing environments. Thus, foragers use multiple information sources to navigate between the nest and forage sources. There is evidence that pheromone trails improve route learning when black garden ants (*Lasius niger*) forage in a maze (Czaczkes et al. 2013). Buehlmann et al. (2012) found that *C. noda* foragers can use magnetic and vibrational landmarks to locate their nest position. They use terrestrial cues for landmark guidance on multiple pre-foraging learning walks back to the nest (Fleischmann et al. 2018). Moreover, desert ants can memorize food odors (Huber and Knaden 2018) and use visual information for foraging and homing (Buehlmann et al. 2018). Interestingly, Buehlmann et al. (2018) found that *C. fortis* foragers were more alert to visual changes closer to the nest. Thus, foraging ants also use panorama-based guidance and learned information for navigation (Knaden and Graham 2016; Freas and Schultheiss 2018).

In addition to innate guidance, some ant species show a turning bias for orientation. Black garden ants (*L. niger*) exhibit a right-turning bias on their foraging trails (Heuts and Brunt 2005). Leaf-cutting ants (*Acromyrmex lundii*) show an innate preference for turning counterclockwise (CCW) in the absence of external cues. They have a similar leftward turning bias in the Y-mazes (Endlein and Sitti 2018). Rock ants (*Temnothorax albipennis*) exhibit leftward turning bias in mazes (Hunt et al. 2014), and this bias may be associated with a left-right asymmetry in ommatidia numbers of the workers' eyes (Hunt et al. 2018). Nevertheless, many ant species apply random search strategies to explore unknown areas or to locate resources (Bartumeus et al. 2005; Pearce-Duvet et al. 2011; Schultheiss et al. 2015; Lai and Chao 2021). Schultheiss et al. (2015) suggested that desert ants exhibit a composite Brownian search distribution in their search patterns. Argentine ants (*Linepithema humile*) explore in random directions when encountering novel areas (Mahavni et al. 2019). Learning-naive ants have been observed to explore different directions in proximity to their nest during learning walks (Zeil and Fleischmann 2019).

In this study, we investigated whether tropical fire ants (*Solenopsis geminata*) would exhibit different searching behaviors to explore unknown areas. In previous studies, these fire ants exhibited a random choice strategy in a T-maze when external cues were excluded (Lai and Chao 2021). However, worker ants may exhibit wall-following (*i.e.*, thigmotactic) behavior to explore a maze when no external cues are available (Walker 1986; Dussutour et al. 2005; Hunt et al. 2014;

Endlein and Sitti 2018). To exclude potential biases due to wall-following behavior, we used an open area in which worker ants were allowed to move freely without any wall contact. Furthermore, we observed whether these fire ants would exert a particular search strategy when exposed to an unknown environment.

MATERIALS AND METHODS

Ants

Three colonies of *S. geminata* were examined in the present study. Colonies of *S. geminata* were collected from Taichung City, Central Taiwan. Each colony (a whole nest) was excavated and maintained with soil in a plastic container (37.5 × 23.5 × 15 cm) coated with Fluon (NP115; Northern Products Inc., Woonsocket, RI, USA) to prevent the ants from escaping. All colonies were moistened regularly and maintained in the laboratory at room temperature (26–27°C). There is a place to put food on the nest surface. Ants were provided *ad libitum* with water, commercial insect jelly (Beetle jelly; Han Shuo Food Co., Ltd, Taiwan), and frozen crickets (*Gryllus bimaculatus*). Workers were used for behavioral experiments after acclimatization to the laboratory conditions for one week. Some workers may stay in the lab for more than one week due to the time-consuming behavioral experiments. However, the colonies were maintained in the laboratory before using in behavioral experiments for a maximum of 30 days.

Experimental design

The orientation of fire ants was observed in an open circular arena (a 9-cm diameter circle drawn on an A5 paper sheet). The A5 paper sheet was placed in a plastic container (37.5 × 23.5 × 15 cm). Workers were randomly collected from the nest surface and placed in the center of the arena to observe their exploratory behavior until workers left the arena. To this end, a chopstick with a toothpick that bore a nylon bristle (taken from test tube brushes) was used to collect an individual worker ant ascending the bristle. Then, we placed the chopstick in the center of the arena and let the ant descend onto the paper sheet. Each worker was used in only one test and was not transferred back to the nest afterwards, but was placed in a separate container. After each test, the plastic container was cleaned using 75% ethanol, and the A5 paper was replaced to exclude potential pheromone residues left by the workers.

Each worker ant's trajectories in the circular arena were video-recorded using a digital camera (Stylus TG-4 Tough, Olympus, Japan) for further analysis. We investigated whether ants would exhibit a particular search strategy or turning preference when placed in an unknown circular arena. The search paths of individual ants were reproduced using the video analysis tool Tracker (Tracker 5.0.6). The image of the searching paths was a combination of different positions of ants at intervals of 0.5 s, and each position was connected with a line. The mean velocity (in mm/s) was determined (hereafter referred to as mean speed).

Statistical analyses

The searching patterns of most workers showed a clockwise (CW) or counterclockwise (CCW) direction, thus the searching behavior of each worker was characterized by 1) the direction of the first turn and 2) change of direction during the test (until the ant left the arena).

The direction of the first turn was defined as the direction (CW or CCW) of the searching track which was consistent within the first 3 s. Data of workers that changed their turning directions within the first 3 s were removed from the data set. The proportion of individual ants showing CW and CCW search paths was tested for equality using Pearson's chi-squared test. The significance indicates workers preferred a direction rather than randomly chose a way to turn. The speed (mm/s) of workers showing each of the directions at the first turn was compared using a Mann-Whitney *U* test.

The change of direction during the examination was defined by whether the ant changed its searching track direction during the examination. The speed of ants changing direction was compared with that of ants following the same direction using a Mann-Whitney *U* test. The statistical analyses were performed using R software (R Core Team 2009) with the function “prop.test” and “wilcox.test”.

RESULTS

Searching patterns

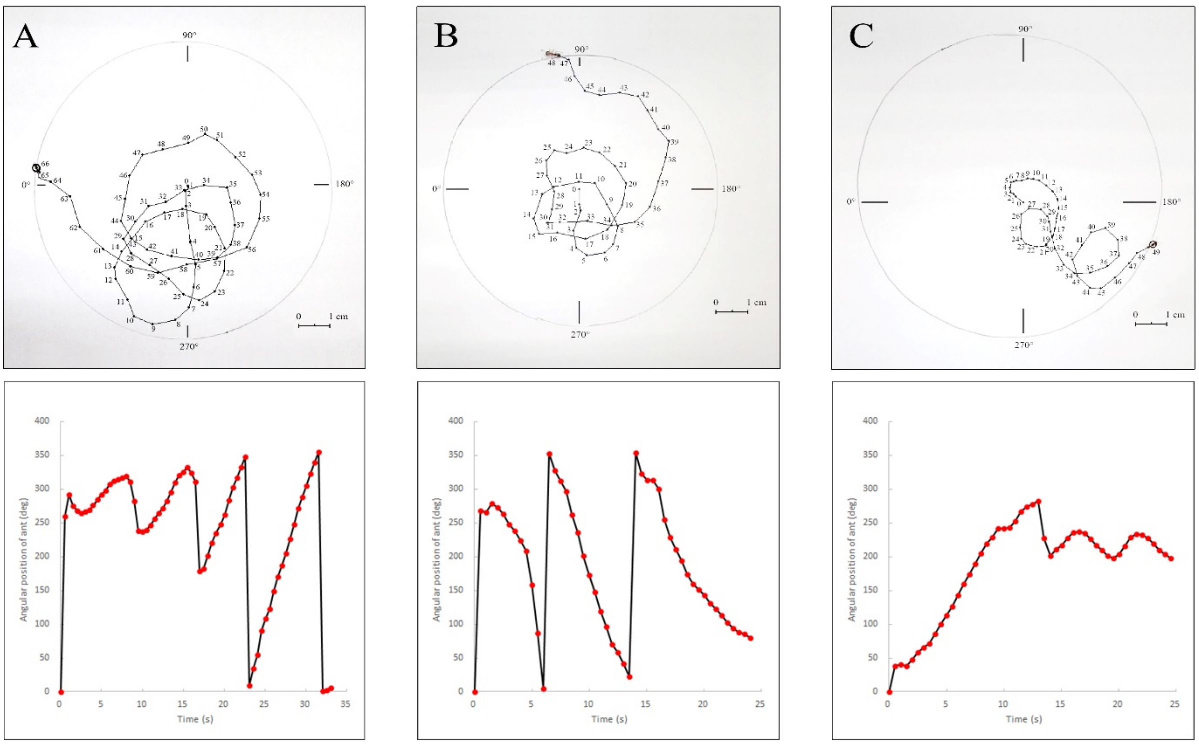
Search patterns of 176 ants were analyzed, and the average time (mean ± standard deviation) an ant spent moving in the circular arena was 17.41 ± 16.90 s (2–120 s). The average searching path length was 218.70 ± 162.47 mm (39.29–888.20 mm). During searching, the ants were continuously moving at a mean speed of 14.76 ± 4.93 mm/s (4.35–27.20 mm/s). In many cases, the ants initially moved forward over a short distance and then turned right or left. They kept turning in one direction, frequently moving by more than 360°, and the searching patterns became wider so that the whole area expanded. Thus, the search pattern consisted of loops of increasing size. Occasionally, the ants reversed their turning directions i.e., switching between CW and CCW turns.

Six major turn patterns were observed (Table 1; Fig. 1A–F): CW (29.5%), CCW (27.3%), initially CW then CCW (CW-CCW; 11.4%), initially CCW then CW (CCW-CW; 4%), straight-line paths to immediately exit the arena (SL; 5.1%), and some ants moved in tortuous searching patterns (T; 17%). In addition, the following patterns were exhibited only by a few ants: CW-CCW-CW (2.8%), CCW-CW-CCW (0.6%), CW-CCW-CW-CCW (0.6%), CCW-CW-CCW-CW (1.1%), and CW-CCW-CW-CCW-CW-CCW (0.6%; Table 1).

Table 1. Searching patterns of *Solenopsis geminata* workers moving in the circular arena

Search path	Total number of workers (%)	Average searching time (sec)	Average searching path (mm)	Speed (mm/sec)
CW	52 (29.5%)	18.5 ± 15.2	258.9 ± 169.7	15.7 ± 4.8
CCW	48 (27.3%)	17.2 ± 13.7	235.9 ± 151.3	15.1 ± 4.3
CW-CCW	20 (11.4%)	25.4 ± 12.9	299.4 ± 128.6	12.7 ± 3.8
CCW-CW	7 (4%)	23.2 ± 9.3	274.5 ± 113.8	12.2 ± 3.8
CW-CCW-CW	5 (2.8%)	38.4 ± 30.7	298.3 ± 127.7	10.2 ± 5.5
CCW-CW-CCW	1 (0.6%)	31	310	10
CW-CCW-CW-CCW	1 (0.6%)	120	750	6
CCW-CW-CCW-CW	2 (1.1%)	25.5 ± 4.9	304 ± 70.2	11.9 ± 0.5
CW-CCW-CW- CCW-CW-CCW	1 (0.6%)	37.5	339	9
SL	9 (5.1%)	2.8 ± 0.6	47.5 ± 6.6	17.7 ± 4.1
T	30 (17%)	5.1 ± 3.6	62.1 ± 19.9	15.2 ± 6.1

CW: clockwise; CCW: counterclockwise; SL: straight-line path; T: tortuous path.



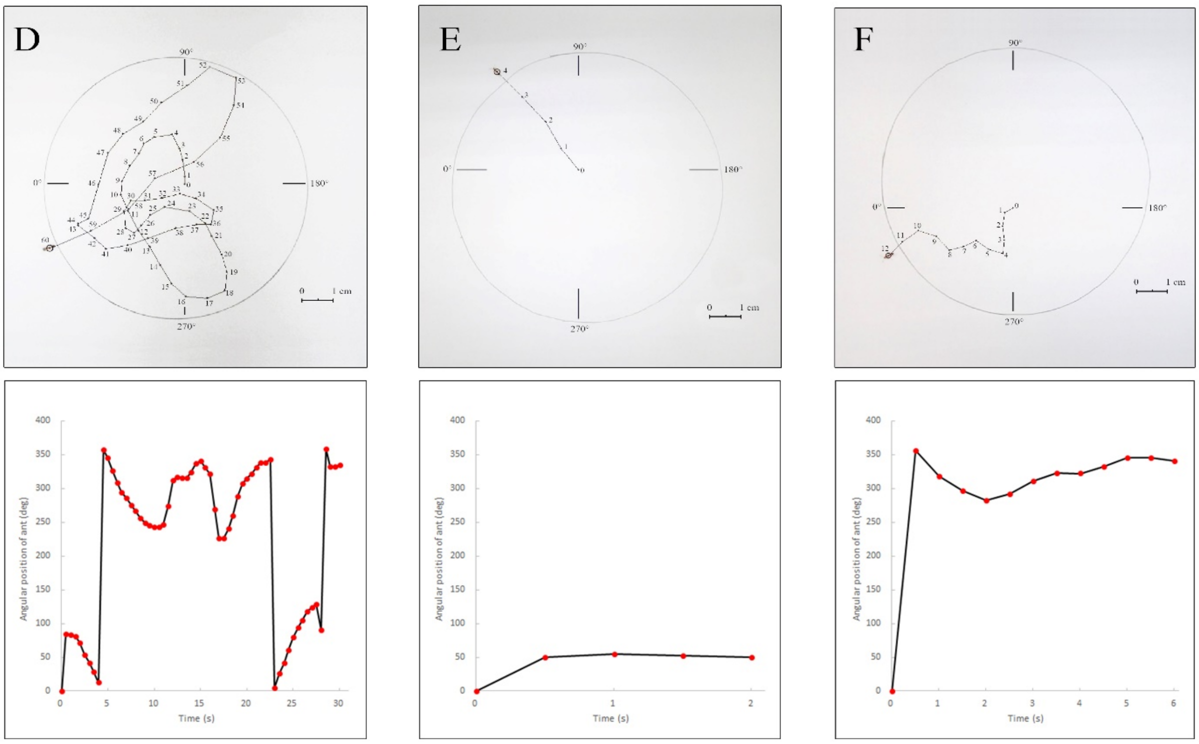


Fig. 1. Examples of six predominant search patterns (top figures) and angular position (bottom figures) of *S. geminata* workers in a circular arena. (A) clockwise (CW) turning; (B) counterclockwise (CCW) turning; (C) CW-CCW turning; (D) CCW-CW turning; (E) straight-line path; (F) tortuous path. Circled data points refer to the positions of the worker at 0.5 s intervals.

Direction of the first turn

Forty-six workers were removed from the data set which includes 30 workers who were in tortuous searching patterns, 9 workers that moved in straight-line paths, and 7 workers that changed their turning directions within the first 3 s. In total, 130 (176-46 = 130) workers were analyzed regarding the direction of the first turn, and 74 (56.92%) turned CW within the first 3 s, whereas 56 (43.08%) turned CCW. This difference in proportions was not significantly different ($X^2 = 2.22$; *d.f.* = 1; $P = 0.136$). The mean speed did also not differ significantly between ants first turning CW (14.45 ± 5.00 mm/s) and CCW (14.66 ± 4.29 mm/s; $U = 2177$; $P = 0.623$; Fig. 2).

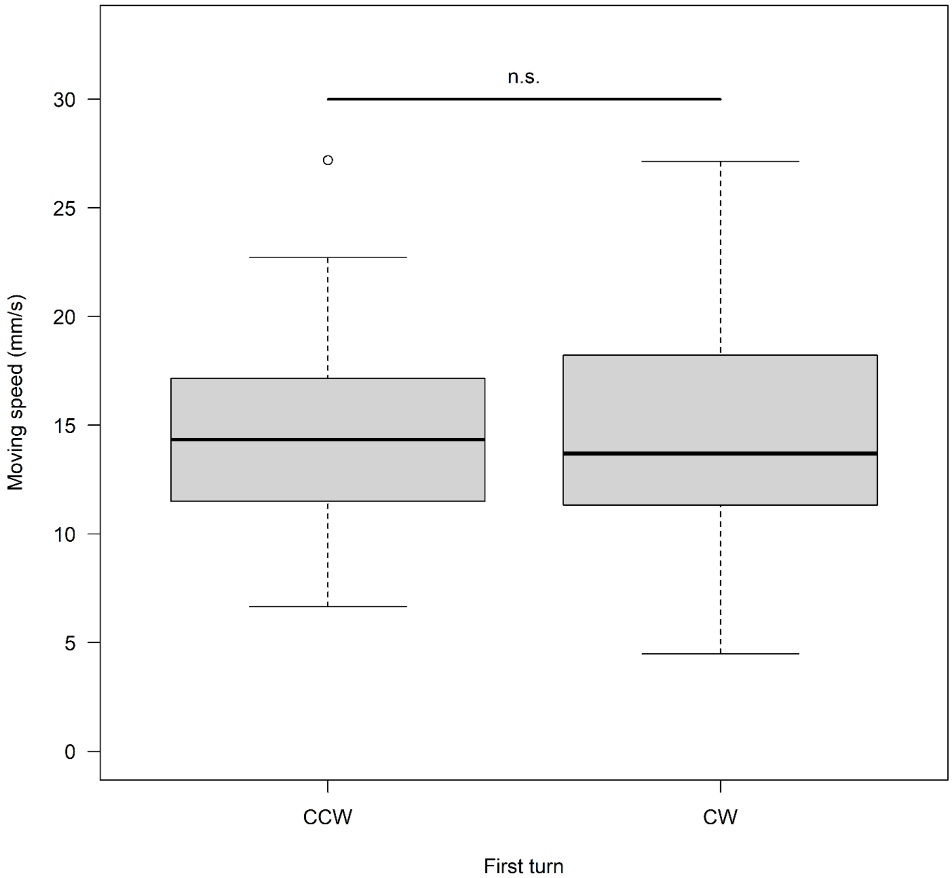


Fig. 2. Moving speed of workers showing counterclockwise (CCW) and clockwise (CW) direction on their first turn, respectively; n.s. – not statistically significant.

Change of direction

Among the 130 workers examined, 100 individuals (76.92%) consistent turning direction. Moving speed was significantly higher in ants maintaining consistent direction (15.43 ± 4.54 mm/s) than in those changing direction (11.57 ± 3.95 mm/s; $U = 2231$; $P < 0.001$; Fig. 3).

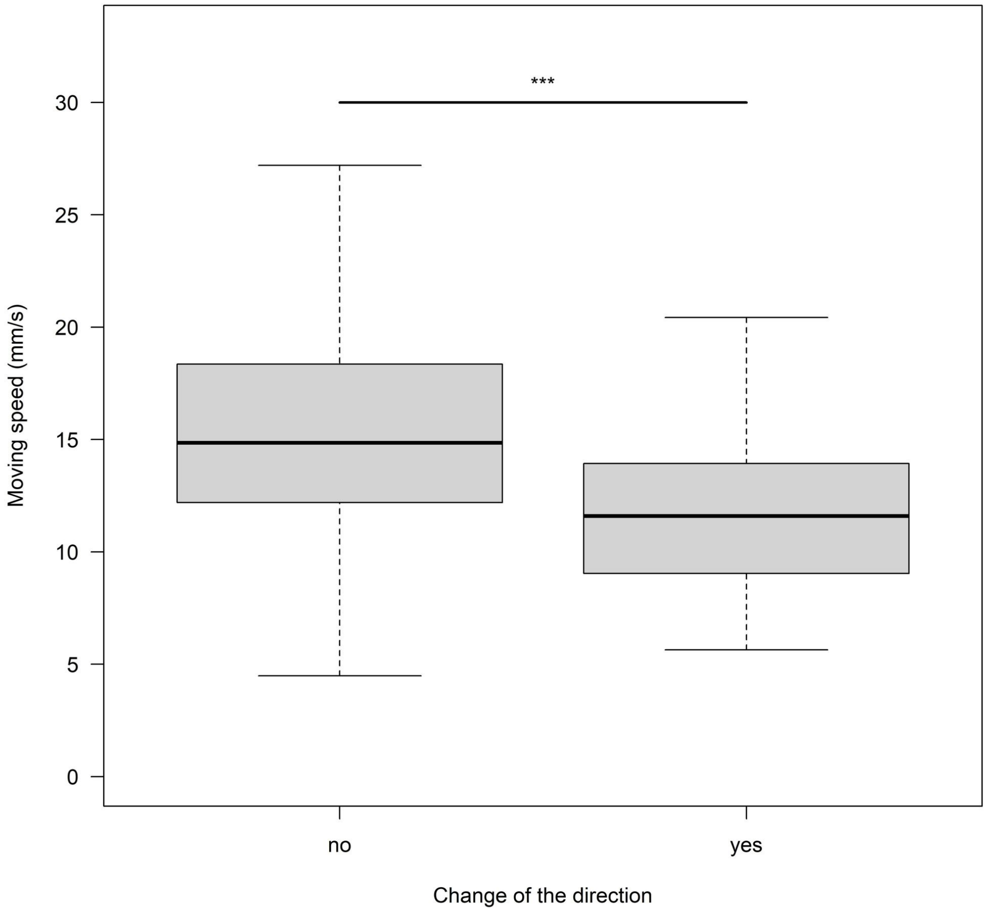


Fig. 3. Moving speed of workers changing or not changing direction; asterisks indicate a significant difference (*P* < 0.001).

DISCUSSION

We investigated the searching behavior of a tropical fire ant in a circular arena without any bias due to wall contact. Turning occurred spontaneously when workers explored the unknown circular arena, and most worker ants consistently turned in one direction (CW or CCW). Individual workers may rely on information from their nestmates or personal experience for their foraging trips (Kolay et al. 2020). Therefore, variation in orientation direction indicates that ants may exert different searching strategies according to their foraging roles (Imirzian et al. 2019). We cannot confirm that all workers that were randomly collected from the nest surface in this study were foragers, however, the innate turning preferences of individual workers and their foraging roles require further research.

Our results showed that fire ant workers tended to turn in a looping pattern during searching. Besides turning in one direction, workers kept moving outwards along an expanding trajectory to increase their search areas. Significantly more ants turned consistently in the same direction than changed the search directions. Therefore, moving speed was higher in workers that maintained their search directions than in those that changed direction. Such a searching pattern that kept turning in one direction minimizes the average time required to find the target. Also, workers initially searched in small loops and progressively increased the search area size to maximize the probability of finding their target (*e.g.*, the nest). Similar search patterns were also found in *Cataglyphis* ants which exhibit search patterns of loops increasing in size while they get lost (Wehner and Srinivasan 1981). It is assumed that workers moving in the system of origin-centered loops is an effective strategy to search for the location of the nest (Müller and Wehner 1994). In addition, search patterns of worker ants consist of loops that are optimal for searching for the target when the surrounding environment is unknown (Schultheiss et al. 2015).

In the current study, some fire ant workers were observed to change their turning direction while searching. That is, they switched from CW to CCW direction, or vice versa. A few workers even changed their turning direction repeatedly. We found that fire ant workers tended to expand their search areas to enhance their discovery success. Imirzian et al. (2019) analyzed foraging trajectories of carpenter ants (*Camponotus rufipes*) and found that most foragers walk in straight lines overlapping the same areas (low exploration). However, there are a group of foragers who showed high exploration. This high exploration may increase the probability of finding food resources but simultaneously increase the ant's exposure to potential risks; the researchers thus suggested that foragers show low levels of exploration, especially moving in straight lines, which may reduce such risks (Imirzian et al. 2019). We also observed that 5.1% of fire ant workers progressed in straight lines and directly exited the arena. Pearce-Duvet et al. (2011) investigated 10 ant species and found that searching speed and turning are species-specific; moreover, they found that workers enhance discovery success through their foraging behavior by reducing the frequency of turning. They also suggested that workers moving in straighter lines increase their chances of discovering forage sources. However, the resource conditions, search area, the worker's experience, and other environmental factors may also determine the search behavior (Schultheiss et al. 2015). More detailed investigation of search patterns and strategies of individual workers is thus required.

Ants can use innate, idiothetic, or learned information for navigation (Knaden and Graham 2016). Li et al. (2014) proposed that ants are controlled by hunting, homing, and path building objectives during foraging. In general, a naïve worker typically uses an internal strategy to engage in a freely ranging search. In contrast, experienced workers can move into unexplored areas to avoid searching the same area repeatedly (Schultheiss et al. 2015). However, some ant species prefer one direction over the other. A similar turning bias has also been found in rock ants (Hunt et al. 2014) and leaf-cutting ants (Endlein and Sitti 2018). Our previous study showed that *S. geminata* workers exhibited a random choice strategy in a T-maze when external cues were shielded (Lai and Chao 2021). In the current study, *S. geminata* workers presented different searching behaviors when placed in an unknown environment and the absence of a specific target. The variation in searching patterns of workers may explain different levels of exploration. It is also interesting to note that 56.8% of fire ant workers turned consistently in one direction (CW or CCW). We thus assume that searching in small loops and progressively increasing the search area size is an effective strategy.

CONCLUSIONS

In this study, we observed six predominant search patterns of *S. geminata* workers. The variation in searching patterns may explain the different levels of exploration. Most workers (56.8%) tended to search in small loops and progressively extended the search area. Thus, the ants mostly turned in one direction, either CW or CCW, and some ants switched between directions. This result shows that moving speed was higher in workers that maintained their search directions than in those that changed direction. We suggest that workers showing a looping pattern of increasing size and searching in one direction might be an effective strategy. Our results improve the understanding of the exploratory behavior of the invasive ant species, *S. geminata*, in their introduced range in Taiwan.

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Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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