Journal of Entomology and Zoology Studies

Available online at www.entomoljournal.com

JEZS

Journal of Entomology and Zoology Studies

E-ISSN: 2320-7078
P-ISSN: 2349-6800
JEZS 2015; 3 (1): 27-32

Received: 06-12-2014
Accepted: 06-01-2015

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Antagonistic interactions among common tropical household ant species (Hymenoptera: Formicidae)

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Abstract
Antagonistic interactions are a common phenomenon among different ant species. Laboratory bioassays were conducted on five species of co-occurring household ant pests i.e. *Solenopsis geminata*, *Monomorium latinode*, *Paratrechina longicornis*, *Tapinoma melanocephalum* and *Camponotus variegatus* to examine interspecific antagonistic behavior. Although all the chosen ant species were found within a household environment, the study was conducted to observe aggressive behavior and interference competition if any, existing between the five ant species. Aggression was more pronounced in *S. geminata* than in *M. latinode*, *P. longicornis*, *T. melanocephalum* and *C. variegatus. P. longicornis* took less time to locate a food source than *M. latinode*, *S. geminata*, *T. melanocephalum* and *C. variegatus*, but could not continue to defend the food source against the aggressive *S. geminata*. Although the arrival of *S. geminata* was delayed at the food source, it dominated and defended the food from other ant species. The results of this study indicated that *S. geminata* is more aggressive and displayed dominance over other co-occurring household ant species.

Keywords: Aggression, behavior, interference competition, Formicidae, household ants

1. Introduction

Interspecific competition is a common behavior in ant communities [1]. Ant species aggressively fight for food and space; competition among ant species brings about aggressive or antagonistic behaviors which include intense fights, escape and/or submissive behaviour [2, 3]. The degree of aggressiveness varies in a fight between different ant species, and as a result, a dominance hierarchy exists among sympatric ant species [4, 5, 6]. Dominant ant species within a community control the occurrence of other ant species with regard to the protection of its nest, food sources and territories [7, 8]. Evidence regarding competition suggests that not only individual behaviors, but the influence that one population has on another also contributes to dominance [9]. Ant species compete with each other either directly through aggressive fight, which may result in the death of opponents or indirectly through exploitation of common space or food resources [1, 10]. A dominant territorial ant species outcompetes other ants in a community [1]. Ants are known to fight by using various means i.e. bites, stings, toxic smears and repellents [1, 11]. Invasive ant species in particular have several characteristics that enable them to dominate other ant species, including elevated levels of aggression, better efficiency in locating as well as defending food resources and often occur at high densities in invaded areas [12, 13, 14, 15, 16].

Co-existing ant species alter their foraging strategy by either foraging on different food resources or have different foraging timings [17]. Urbanization destroys the habitat of many specialist species and often creates an attractive habitat for generalist species which have a wide adaptability to urban conditions [18]. Invasive ant species are found to adapt to a wider range of climatic conditions [19] and thereby occur as common household pests. A number of studies on interspecific aggression among invasive ant species have been carried out both in the field and laboratory [20, 21, 22, 23]. Information on the competitive ability and dominance on food resources of tropical household ant species is lacking. Hence, a study was conducted in the Insect Science Laboratory at Bangalore University, Bengaluru, India. In this study, we investigated interspecific antagonistic behavior of five commonly occurring household ant species *viz*., *Solenopsis geminata* (Fabricius), *Monomorium latinode* (Mayr), *Tapinoma melanocephalum* (Fabricius), *Paratrechina longicornis* (Latreille) and *Camponotus variegatus* (Fr. Smith). The tropical fire ant, *S. geminata* native to tropical and temperate regions of the New World has spread worldwide through human means. It invaded parts of Africa and Asia (including India and Japan), some Indian Ocean islands (including Madagascar) and various

Pacific Ocean islands (including New Caledonia and the Hawaiian and Galapagos archipelagos) [13, 24]. *C. variegatus* is native to south-east Asia [25]. *M. latinode* is spread across the Indo-Australian region [26]. *P. longicornis*, a common 'tramp species' native of West Africa has spread pan-tropically [27]. The origin of *T. melanocephalum* is ambiguous and is assumed to be either from Africa or the Oriental region [28]. Knowledge obtained from the study on the interactions between common household ant species could be useful to understand their dominance hierarchy and the effects it could have on co-existing ant species.

2. Materials and methods

Interspecific aggression between workers of five ant species *viz*., *S. geminata*, *M. latinode*, *T. melanocephalum*, *P. Longicornis* and *C. variegatus* was examined in the laboratory over a period of six weeks during March-April 2011 to observe the highest level of aggression in different sympatric ant species, range of aggressive behaviors between ant species, time taken by different ant species to locate a food source and ability to dominate a food source.

2.1 Collection and maintenance of ant species in the laboratory

Worker ants of monomorphic species *T. melanocephalum* and *P. longicornis* and minor workers of polymorphic species *S. geminata*, *M. latinode* and *C. variegatus* were collected for the study. The worker ants that were moving away from the nest in search of food were collected a day prior to the experiment with the help of an aspirator. The ants that were collected neither had their gasters full nor were they carrying any food back to the nest. The collected ants were kept in a temporary plastic box (22 x15 x10 cm) containing a thin layer of damp sand at the bottom to maintain moisture for the better survival of ants. In the laboratory, the ants were fed on water supplied with a cotton bung.

2.2 Aggression bioassay

Aggression assays were carried out in Petri dishes (20 cm in diameter). The inner wall of the Petri dish was coated with Fluon™ to prevent the ants from escaping. A food source was kept in the centre of the Petri dish. Bait is commonly used in antagonistic behavioral studies as it reduces escape and brings about aggressive behaviors [12, 29]. Based on our earlier studies, food sources were chosen in the experiment based on their greater attraction to a particular food [30] (Table 1). The procedure for aggression bioassay was based on the method of Chong and Lee [20] with modifications. Ten worker ants of two different species were aspirated separately into glass tubes (15 cm height and 4 cm diameter). The tubes were then inverted at opposite ends in the Petri dish and the tubes were gently removed once the ants had settled down on the Petri dish. Observations were made for 90 min to record the aggressive behavior of ant species. Duration of observation time was standardized based on the preliminary studies. The rationale behind these trials was to observe interactions between different ant species. Owing to the small arena, accidental collisions were bound to occur. But the main component of this study was to observe and record aggressive behavior following initial collision.

Aggression was scored following the method of Suarez *et al*. [31] using four behavioral indices: 1= touch including prolonged antennation, 2= avoid and retreat in opposite directions immediately upon contact, 3= aggression which includes lunging, biting, pulling legs/antenna or stinging and 4= prolonged fight including death. Only behaviours with scores of 2 and above were considered aggressive. Pairing of five ant species formed ten combinations. The total aggressive index indicating the aggression of each ant species was calculated by totalling the behavioral index scores of 2 and above. The method of Grover *et al*. [32] was used to calculate aggressive index. For each 90 min trial, the number of ants which were involved in each behavioral category every 15 min were recorded. The average for that category was calculated. The average obtained was multiplied by the aggression scale for that behavior. The result was then summed along with the averages obtained for the other behavioral scales to get the final aggressive index.

Table 1: Combination of different household ant species and food presented in aggression bioassays

Sl. No.	Ant combination	Food
1	*Tapinoma melanocephalum vs Solenopsis geminata*	Boiled egg yolk
2	*Tapinoma melanocephalum vs Monomorium latinode*	Boiled egg yolk
3	*Tapinoma melanocephalum vs Paratrechina longicornis*	Honey
4	*Tapinoma melanocephalum vs Camponotus variegatus*	Honey
5	*Solenopsis geminata vs Monomorium latinode*	Boiled egg yolk
6	*Solenopsis geminata vs Paratrechina longicornis*	Honey
7	*Solenopsis geminata vs Camponotus variegatus*	Cockroach
8	*Monomorium latinode vs Paratrechina longicornis*	Mixed fruit Jam
9	*Monomorium latinode vs Camponotus variegatus*	Boiled egg yolk
10	*Paratrechina longicornis vs Camponotus variegatus*	Honey

The time taken by the first individual of an ant species to locate the food source was recorded (in minutes) as the food discovery time. The species with the most individuals found on the food at the end of the experimental period was recorded as the dominant species. Ant species were ranked based on the method of Cerdá *et al*. [33] where interspecific interactions at the food source was categorized as expulsion (in which one ant species chases away another), co-existence (where workers of both ant species occur on a food source without any aggression) and escape (when an ant species which had occupied a food source was forced to abandon the bait following attack from another ant species). The dominance index was taken as the percentage of time that an ant species was dominant in expulsion and escape behaviors in 10 trials. Each experiment (involving a set of 10 ants belonging to different species) was repeated 10 times with a fresh set of ants and food source.

2.3 Statistical analysis

To test the overall aggression among different ant species, a one-way Analysis of Variance (ANOVA) was conducted separately for individual scales of aggressive behavior and time taken to locate a food and dominance on a food, and significant difference between species were determined by Tukey HSD test at $P< 0.05$ [34].

3. Results

3.1 Aggressiveness and dominance of different ant species:

The aggressive index of *S. geminata* was significantly higher than that of *P. longicornis*, *M. latinode*, *C. variegatus* and *T. melanocephalum* (Fig. 1; $F_{4, 195}$= 24.58; P = 0.01). Aggression among *P. longicornis*, *M. latinode*, *C. variegatus* and *T. melanocephalum* was not significantly different. In interspecific interactions (expulsion, co-existence and escape) a clear transitive dominance hierarchy existed among the five ant species in which the dominance index of *S. geminata* was the highest (Table 2).

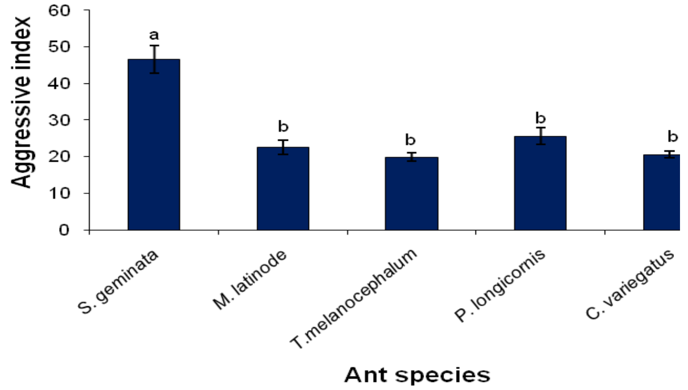

Fig 1: Aggressive index of different household ant species. Bars with different small letters indicate significant differences in total aggressive index among different ant species at *P*<0.05 (One way ANOVA-Tukey HSD test). (Vertical lines indicate ± SE of the mean of the total aggression displayed by an ant species towards its opponent).

Table 2: Dominance hierarchy of household ant species at a food source based on their interspecific interactions

Ant species	Expulsion (%)	Co-existence (%)	Escape (%)	Dominance index (%)
Solenopsis geminata	80.7	0.0	2.5	83.2
Paratrechina longicornis	65.1	15.1	12.5	77.6
Monomorium latinode	60.8	12.5	10.2	71.0
Camponotus variegatus	40.5	10.2	5.7	46.2
Tapinoma melanocephalum	6.1	18.5	11.5	17.6

P. longicornis found food faster than *S. geminata, M. latinode, T. melanocephalum* and *C. Variegatus* (Fig. 2; $F_{4, 195}$= 12.16; *P*=0.01), though these species also differed significantly among themselves (*P*= 0.01).

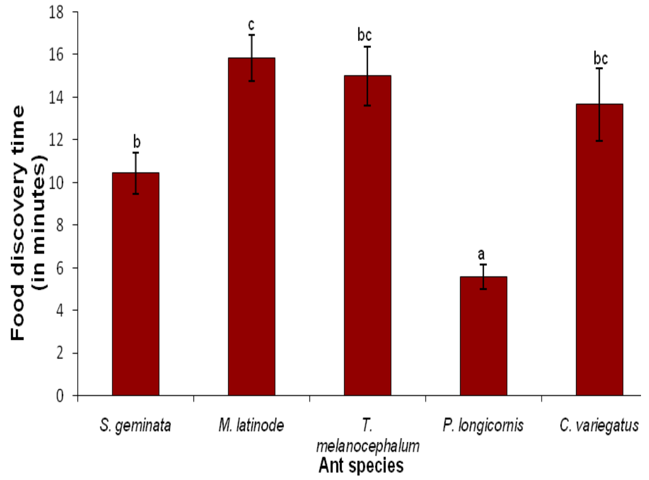

Fig 2: Time taken by different household ant species to discover a food source. Bars with different small letters indicate significant differences in food discovery time among different ant species at *P*<0.05 (One way ANOVA-Tukey HSD test). (Vertical lines indicate ±SE of the mean time taken by ant species to discover a food source).

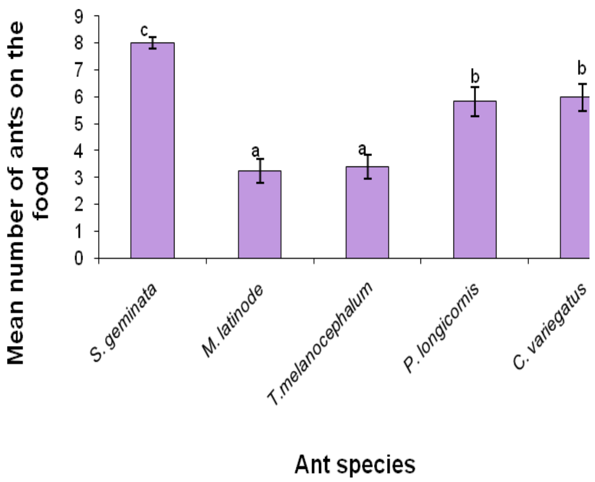

Fig 3: Dominance of different household ant species over a food source. Bars with different small letters indicate significant differences in dominance among different ant species at *P*<0.05 (One way ANOVA-Tukey HSD test). (Vertical lines indicate ±SE of the mean number of ant species present on a food source).

Dominance of the food source by *S. geminata* was significantly greater than the other four species (Fig. 3; $F_{4, 195}$= 19.01; *P*= 0.01). Similarly, dominance by *P. longicornis* and *C. variegatus* exceeded that of *T. melanocephalum* and *M. latinode* (*P*= 0.01).

3.2 Behavioral repertoire of different ant species upon confrontation:

a) *T. melanocephalum*

T. melanocephalum displayed greater avoidance behavior towards *S. geminata, M. latinode* and *C. variegatus* than to *P. longicornis* (Table 3; $F_{3, 36}$=6.74; P= 0.01). Indeed, whenever

T. melanocephalum came across any other ant species, it ran around the Petri dish rapidly with its gaster raised. Avoidance behavior among *S. geminata*, *M. latinode* and *C. variegatus* was not significantly different.

b) *M. latinode*

M. latinode displayed both avoidance and aggression behaviors. It exhibited greater avoidance to *P. longicornis* and *S. geminata* than to *T. melanocephalum* and *C. variegatus* (Table 3; $F_{3, 36}$= 5.525; *P*= 0.01). *M. latinode* displayed greater aggressive behavior towards *S. geminata* than towards *T. melanocephalum* and *C. variegatus* (Table 3; $F_{3, 36}$= 44.37; *P*= 0.01). Whenever *M. latinode* encountered *S. geminata*, *T. melanocephalum* or *C. variegatus*, it displayed lunging and upward bending of gaster. *M. latinode* avoided *S. geminata* in the first encounter, but displayed aggression towards *S. geminata* in subsequent meetings. Normally, *M. latinode* avoided its opponents and clustered at the edge of the Petri dish. Rarely *M. latinode* attacked whenever a competitor came within a range of 2-4 mm. The movement of *M. latinode* was slow.

Table 3: Behavioral index of household ant species interacting with an opponent species.

Ant species combination	Behavioral index (Mean ± SEM)*			
	1	2	3	4
Tapinoma melanocephalum *vs* *Solenopsis geminata*	10.20 ± 2.23a	23.80 ± 1.24b	0.00 ± 0.00a	0.00 ± 0.00a
Monomorium latinode	6.50 ± 1.34a	23.30 ± 2.03b	0.20 ± 0.01a	0.00 ± 0.00a
Paratrechina longicornis	4.60 ± 1.61a	14.00 ± 2.09a	0.00 ± 0.00a	0.00 ± 0.00a
Camponotus variegatus	7.50 ± 1.56a	17.00 ± 1.92ab	1.10 ± 0.00b	0.00 ± 0.00a
Monomorium latinode *vs* *Solenopsis geminata*	0.00 ± 0.00a	15.70 ± 2.39ab	22.20 ± 2.44c	1.20 ± 0.51b
Tapinoma melanocephalum	3.50 ± 0.70b	10.00 ± 0.84a	7.60 ± 1.60b	0.00 ± 0.00a
Paratrechina longicornis	3.40 ± 0.89b	19.30 ± 1.70b	0.00 ± 0.00a	0.00 ± 0.00a
Camponotus variegatus	1.10 ± 0.28a	11.30 ± 1.93a	2.29 ± 0.48ab	0.00 ± 0.00a
Paratrechina longicornis *vs* *Monomorium latinode*	4.50 ± 0.98ab	4.70 ± 1.15a	1.70 ± 0.53a	0.00 ± 0.00a
Tapinoma melanocephalum	4.60 ± 1.60ab	18.80 ± 1.53b	12.90 ± 1.44c	6.40 ± 0.95b
Solenopsis geminata	0.40 ± 0.40a	25.60 ± 1.21c	7.10 ± 1.45b	0.60 ± 0.26a
Camponotus variegatus	7.20 ± 1.17b	16.50 ± 1.99b	6.20 ± 1.80ab	2.10 ± 0.99a
Camponotus variegatus *vs* *Tapinoma melanocephalum*	7.50 ± 1.56b	21.60 ± 1.18ab	0.00 ± 0.00a	0.00 ± 0.00a
Monomorium latinode	2.70 ± 0.73a	23.50 ± 2.40b	0.00 ± 0.00a	0.00 ± 0.00a
Paratrechina longicornis	9.30 ± 1.56b	19.40 ± 1.53ab	1.00 ± 0.70b	0.00 ± 0.00a
Solenopsis geminata	1.60 ± 0.40a	16.30 ± 1.23a	0.00 ± 0.00a	0.00 ± 0.00a
Solenopsis geminata *vs* *Paratrechina longicornis*	1.20 ± 0.44a	21.00 ± 2.04a	33.60 ± 3.93b	10.90 ± 1.99b
Camponotus variegatus	3.00 ± 0.58a	16.30 ± 1.23a	5.30 ± 1.30a	0.80 ± 0.44a
Tapinoma melanocephalum	10.20 ± 2.23b	21.70 ± 1.68a	8.70 ± 2.54a	0.90 ± 0.48a
Monomorium latinode	0.00 ± 0.00a	17.10 ± 1.78a	37.30 ± 2.94b	12.80 ± 1.14b

*Means followed by different letters within a column are significantly different. Behavioral index: 1= touch, 2 = touch and immediate avoidance, 3= aggression (lunging, biting/pulling), 4 = Fighting (continuous aggression including abdomen curling) [31]

c) *P. longicornis*

The avoidance behavior of *P. longicornis* was greater towards *S. geminata* than to *T. melanocephalum*, *C. variegatus* and *M. latinode* (Table 3; $F_{3, 36}$= 33.24; P= 0.01). Similarly, its avoidance towards *T. melanocephalum* and *C. variegatus* was greater than that towards *M. latinode* (Table 3; $F_{3, 36}$= 16.90; P= 0.01). *P. longicornis* escaped from its opponents by swift movement. *P. longicornis* avoided any opponent initially, later on it displayed more aggression towards *T. melanocephalum* than to *S. geminata*, *C. variegatus* and *M. latinode* (Table 3; $F_{3, 36}$= 10.93; *P*= 0.01). *P. longicornis* always moved away from the food source whenever the more aggressive *S. geminata* invaded the food.

d) *C. variegatus*

C. variegatus displayed greater avoidance behavior towards *M. latinode* than to *T. melanocephalum*, *P. longicornis* and *S. geminata* (Table 3; $F_{3, 36}$= 3.49; *P*= 0.01). *C. variegatus* moved rapidly around the Petri dish and avoided confrontation with competitors.

e) *S. geminata*

S. geminata suddenly retreated in its first encounter with *M. latinode*, *P. longicornis*, *T. melanocephalum* or *C. variegatus* (Table 3; $F_{3, 36}$= 2.54; *P*=0.07). In the subsequent encounters, it fought more aggressively with *M. latinode* and *P. longicornis* than with *T. melanocephalum* and *C. Variegatus* by biting, pulling and injuring the opponents, and this often lead to fatalities (Table 3; $F_{3, 36}$= 33.98; *P*= 0.01; $F_{3, 36}$= 28.73; *P*= 0.01).

4. Discussion

S. geminata was found to be a very antagonistic species. Although *S. geminata* recruits came later during the course of the experiment and thereby taking more time to find a food source, it was able to aggressively defend and monopolize the food resource by not allowing *M. latinode*, *T. melanocephalum*, *P. longicornis* or *C. variegatus* near the food. Similar behavior has been reported in *S. geminata* [35], *S. invicta* Buren [36], *Anoplolepis gracilipes* (Fr. Smith) [37, 38] and *Linepithema humile* [14, 39].

P. longicornis located the food faster than the other household ant species. However, soon after the arrival of dominant *S. geminata*, it readily gave up the food source without a fight as observed for interactions with this species and *Pheidole radoszkowskii* Mayr [35] and *Tapinoma sessile* Say [14]. The rapid discovery of food by *P. longicornis* could be due to their fast movements compared to *S. geminata*, which moves slowly. However, after the discovery of food, workers of *S. geminata* that were present on the food defended it from *P. longicornis.* Similar behavior has been observed in *P. longicornis* and *S. geminata* in the field [40]. The efficient foraging of *P. longicornis* would help to exploit the environment on a larger scale and provide an advantage over aggressive ant species. Similar behavior has been reported in *A. gracilipes* [6, 12, 38, 41]. The opportunistic behavior of *P. longicornis,* whereby it is able to exploit a food source before the arrival of an aggressive *S. geminata* appears to be an optimal successful foraging strategy for interactions with dominant species with which it coexists [42], such as *Pheidole megacephala* Fabricius, *Camponotus* species or *Solenopsis* species.

Several ant species are able to co-exist with other ant species by employing different foraging strategies [35, 43]. In our study, all the five ant species exhibited different strategies in order to deal with the opponent ant species. *T. melanocephalum,* the smallest of the ant species studied was always found to escape from its opponents and avoid any confrontation with its competitors. *T. melanocephalum* became excited when it faced another ant species and began to run erratically as observed in *T. sessile* [39]. Small sized ants defend themselves by being very quick in their movements, producing chemical repellents, becoming immobile or displaying submissive behavior when attacked [11]. Similar behavior has been reported in species of *Monomorium* and *Tapinoma* [20]. In our study, *T. melanocephalum* was extremely submissive and gave up baits without any fight, similar to interactions observed between *T. sessile* and *L. humile* [14].

M. latinode avoided other ant species by becoming immobile and sometimes clustered at a point. Similar observations were made in other *Monomorium* spp. [20]. Slow moving *Monomorium* spp. and *S. geminata* become motionless when they are confronted, but *T. melanocephalum, P. longicornis* and *Camponotus* spp. escape from confrontation due to their fast and erratic movements [44]. *T. melanocephalum*, *C. variegatus* and *P. longicornis* were found to explore the food area quickly and were able to avoid direct collision with *S. geminata* and *M. latinode*. Similar behavior has been reported in *A. gracilipes* in interactions with several ant species [20].

Formicines usually bite or use chemical repellents against competitors [11]. However, *P. longicornis* and *C. variegatus* made use of their speed and they rarely attacked their opponents. *S. geminata* and *M. latinode* (Myrmicinae) attacked their opponents while *T. melanocephalum* (Dolichoderinae) was extremely evasive and surrendered baits without a fight.

Study of aggressive behavior between ant species confined to small arenas may not reflect true behavior that would occur in the field. However, studies conducted in the laboratory do give insights into the aggressive nature of the ant species involved whose behavior might be masked in the field due to the presence of other ant species [44]. The present study focused on the interspecific interactions between ant species commonly found within a household environment.

Our study indicates that *S. geminata* is a very hostile and dominant species, which displaces other household ant species from food resources. The presence in large numbers and possession of dominant traits of *S. geminata* in the environment could bring about displacement of other ant species within a habitat and make this species a more formidable and persistent pest within a household environment. Based on these observations, additional studies at a colony level in the field can elucidate the natural interactions among these household ants.

5. Acknowledgements

The authors thank Dr. T. Musthak Ali, Department of Entomology, University of Agricultural Sciences, Bengaluru, India for identifying the ant species. The first author acknowledges the University Grants Commission (UGC), New Delhi, India for the sanction of Faculty Development Programme (FDP) to pursue doctoral degree.

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