

Workers' Extra-Nest Behavioral Changes During Colony Fission in *Dinoponera quadriceps* (Santschi)

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Abstract

Ant colonies can reproduce by two strategies: independent foundation, wherein the queen starts a new colony alone, and dependent foundation, in which workers assist the queen. In the queenless species *Dinoponera quadriceps* (Santschi), the colony reproduces obligatorily by fission, a type of dependent foundation, but this process is not well understood. This study describes a colony fission event of *D. quadriceps* in the field and analyzes the influence of the fission process on workers' extra-nest behavior. Based on observations of workers outside the nest, five distinct stages were identified: monodomic stage, polydomic stage, split stage, conflict stage, and post-conflict stage. The colony was initially monodomic and then occupied a second nest before it split into two independent colonies, indicating a gradual and opportunistic dependent foundation. After the fission event, the daughter colony had aggressive conflicts with the parental colony, resulting in the latter's disappearance. Colony fission affected workers' extra-nest behavior by increasing the frequency of rubbing the gaster against the substrate (which probably has a chemical marking function) and by decreasing the frequency of foraging during the split stage. After the fission event, the number of foragers was halved and foragers remained nearer to the nest during extra-nest activity. The spatial closeness of the parental and daughter colonies led to competition that caused the extinction or migration of the parental colony. Intraspecific competition was indicated by foraging directionality at the colony level, whereby areas of neighbor colonies were avoided; this directionality was stronger while both colonies coexisted.

Introduction

Ant colonies can behave as superorganisms due to their high level of organization, division of labor among individuals, and their ability to reproduce, regenerate, feed, and protect themselves (Bourke & Franks 1995). They can reproduce by independent foundation, with the queens rearing the first offspring generation alone without assistance from their parental colony workers, or by dependent foundation, in which the colony splits into two autonomous groups (fission) and the queens are assisted by workers (Peeters & Ito 2001). During colony fission, all the benefits of group living are maintained, including greater defense capability, higher success in finding food and rearing offspring, and

lower mortality of the sexuals (Peeters & Ito 2001, Macedo 2006, Cronin *et al* 2013). In contrast, during independent foundation, there is an obligate solitary phase during which the queens are at greater risk (Peeters & Ito 2001).

In *Dinoponera*, a ponerine genus comprising only queenless ant species such as *Dinoponera quadriceps* (Santschi), independent foundation is not known, and colonies reproduce by fission (Monnin & Peeters 1997, Hart & Ratnieks 2005, Lenhart *et al* 2013). A *D. quadriceps* colony consists of morphologically similar workers (Monnin *et al* 1998), and all of them are able to sexually reproduce (Monnin & Peeters 1998). However, only one aggressively dominant worker (alpha) mates and becomes the reproductive female of the colony, called thereafter the gamergate

(Monnin & Peeters 1998, Lenhart *et al* 2013). In *Dinoponera* colonies, monogyny and monandry increase kinship among the offspring and decrease the conflict between gamergates and other workers (Hart & Ratnieks 2005). Most of the eggs in a *D. quadriciceps* colony are laid by the gamergate, but a small fraction of the unfertilized eggs can be laid by subordinate workers. Subordinate workers' eggs are usually eaten by the gamergate. Nevertheless, the ovarian development and egg-laying of subordinate workers enable fast replacement of the gamergate in case of its decline or colony fission (Monnin & Peeters 1997).

Dinoponera quadriciceps inhabits the Caatinga and Atlantic Forest areas of northeastern Brazil, where it nests in the soil (Kempf 1971, Paiva & Brandão 1995). In its natural environment, nests are overdispersed. This pattern is shown by most ant species studied. An overdispersion of nests indicates that intraspecific competition is an important factor determining nest distribution (Levings & Traniello 1981, Vasconcellos *et al* 2004). Colonies have only one gamergate and have an average population of 80 workers (range, 26–238) (Monnin & Peeters 2008, Lenhart *et al* 2013). Without a winged queen, *D. quadriciceps* gene flow, dispersion and colonization are restricted, and thus escaping from deteriorating habitats is difficult. These features of its biology likely make it more vulnerable to extinction than other ant species (Peeters & Ito 2001). Thus, it is important to expand knowledge about the colony fission process, as it is still poorly understood in this species. Because colony fission is usually an unpredictable event, observations of spontaneous fission events in a natural setting are valuable. This study describes a *D. quadriciceps* colony fission event in the wild and analyzes how the colony fission process affects workers' extra-nest behavior.

Material and Methods

Data collection

The study was carried out in a secondary Atlantic forest area in the Floresta Nacional de Nísia Floresta (06°05'S, 35°12'W), Instituto Chico Mendes de Conservação da Biodiversidade, Nísia Floresta, Brazil. We observed a *D. quadriciceps* colony from August 2007 to June 2009. The collection effort was approximately 12 h (from 5:30AM to 5:30PM) once per week, totaling 962 h of collection effort and 210 h of direct observation.

The workers were marked individually before and during the study using a colored plastic tag with a unique alphanumeric combination for each individual. It was affixed to the thorax with adhesive based on cyanoacrylate ester, following the technique of Corbara *et al* (1986). A total of 220 workers were marked; however, only 97 were observed throughout the study.

Marked workers were followed during their extra-nest activity. The observation began when a worker left the nest and finished when it returned to the nest. Each worker was followed in at least two consecutive trips. Instantaneous focal-animal sampling was used as the observation method (Altmann 1974). Worker behavior was recorded every minute within 15-min blocks, with 5-min intervals between observation blocks (Martin & Bateson 1994). During the observations, we did not make any intervention affecting the colony, and handling of workers was restricted to marking. The following behavior categories were recorded: foraging, food capture and transport, antennal contact between nestmates, agonistic interaction, rubbing the gaster against the substrate, inactivity, locomotion, and auto-grooming (Azevedo 2009). Regardless of whether they were followed, all marked workers observed outside the nest were recorded to estimate the number of workers engaged in extra-nest activity.

The routes traveled by workers were also recorded. Every 5 min of observation, a numbered flag was placed at the worker's location. Later, angles and distances between flags were measured (modified from Turchin 1991). These data were used to draw the routes of each worker. The angles between the nest entrance and each flag spot were measured to obtain data on foraging route direction. The maximum distance from the nest reached by the worker on each trip was also recorded.

During the study, the colony that was being monitored spontaneously underwent a fission process. Based on observation of worker behavior outside the nest, five distinct stages were identified. Data were collected on the parental colony until its disappearance, at which point data collection began on the new colony.

Data analysis

Frequency data for each behavioral category, the number of workers engaged in extra-nest activity in each observation day, and the maximum distance reached in each trip were analyzed by one-way analysis of variance (ANOVA) and Fisher's least significant difference post hoc test or by the Kruskal-Wallis test (H) and Games-Howell post hoc test, depending on the results of a Kolmogorov–Smirnov test for normality, with stage of fission process as the independent variable. Because season may influence the ants' extra-nest activity, variables that differed significantly among the stages of fission were analyzed by generalized linear models with stage of fission (five-level factor) and season (two-level factor) as independent variables to confirm the influence of fission when taking into account the effect of seasonality. Based on rainfall data from Empresa de Pesquisa Agropecuária do Rio Grande do Norte, we considered March to August as the rainy season and September to February as the dry season. The models were performed with a normal

distribution (Gaussian family) and identity as link function in R 2.15.3 (The R Foundation for Statistical Computing 2013). The full models were simplified by applying an analysis of deviance to remove non-significant effects. Response variables that deviated from a normal distribution were analyzed with a Kruskal-Wallis test (H) and Games-Howell *post hoc* test, with the combination of fission stage and season as the independent variable. Foraging direction data were analyzed by a Rayleigh test (Z) using the Oriana 2.0 software (Kovach Computing Services 2004). All tests were performed with a two-tailed level of significance of 5%.

Results

The first stage observed in this study was called the monodomic stage (MS) and lasted for four and a half months (from August 2007 to 15 December 2007), when the colony had not yet started the fission process and had only one nest. Following that, a new nest 3.34 m away from the monitored nest was also occupied by the colony, marking the beginning of the polydomic stage (PS), which lasted 4 months (from 19 December 2007 to 19 April 2008). The new nest was found when workers from the monitored nest that were being followed entered another nest that was covered by leaves and lacked any sand mound outside. We did not observe the construction of the new nest, which was probably derived from the preexisting hole of an abandoned nest or of rotten roots. During the polydomic stage, the colony occupied both nests, but the old one remained the main nest, with much more intense traffic of workers than the new one. The nests did not seem to have any underground connection, as workers moved between them on the surface.

When the colony split into two independent colonies at the beginning of the split stage (SS), some of the workers remained in the old nest and others became a new colony in the new nest. Once the colony was divided, worker traffic increased around the new nest. Near the entrance of the old nest, many workers, probably from the newly founded colony, chemically marked the substrate by rubbing their gasters against it. The frequency of rubbing the gaster against the substrate by workers from the old nest also increased. During the split stage, which lasted for five and a half months (from 26 April 2008 to 11 October 2008), ants from both nests exhibited the expected behavior for workers from different colonies, producing agonistic interactions when they occasionally came into contact. In this stage, the nests were no longer shared and workers from one nest did not enter the other.

Then, there was a conflict stage (CS) that lasted for 2 months (from 25 October 2008 to December 2008), when workers from the new colony began to get closer to the old nest, often reaching the nest entrance and sometimes

entering the old nest to start agonistic interactions with workers from the old colony. Agonistic interactions also occurred during occasional encounters during foraging. The conflict stage resulted in the disappearance of the old colony, probably due to extinction of the colony from death of the workers, or due to colony migration to another location. In the post-conflict stage (PCS), from February 2009 to June 2009, there was only the new colony, which began to be monitored in this stage.

The frequency of foraging ($F=4.5$, $N=76$, $df=4$, $p=0.003$) (Fig 1a), rubbing the gaster against the substrate ($F=4.4$, $N=76$, $df=4$, $p=0.003$) (Fig 1b), and auto-grooming ($F=2.9$, $N=76$, $df=4$, $p=0.029$) during workers' extra-nest activity differed significantly among the stages. However, when taking into account the effect of season, the effect of the fission process on auto-grooming was not significant. For the frequencies of foraging and rubbing the gaster against the substrate, the effect of season was not significant. Thus, after the removal of the non-significant effect of season from the full models, the final model for foraging and rubbing the gaster against the substrate included only the effect of fission (Table 1). The number of workers engaged in extra-nest activity ($F=9.8$, $N=87$, $df=4$, $p<0.001$) (Fig 1c), and the maximum distance reached by workers during extra-nest activity ($H=117.8$, $N=337$, $df=4$, $p<0.001$) (Fig 1d) also differed significantly among the stages of the fission process. Despite a significant effect that season had on the number of workers engaged in extra-nest activity, the effect of fission stage was significant when both season and fission were taken into account (Table 1). The maximum distance varied significantly when the combination of fission stage and season was tested as the independent variable ($H=121.4$, $N=337$, $df=8$, $p<0.001$), but it did not differ between seasons within the same stage, whereas differences between stages within the same season were significant (Table 2). The frequency of food capture and transport ($p=0.504$), antennal contact between nestmates ($p=0.114$), agonistic interaction ($p=0.532$), inactivity ($p=0.093$), and locomotion ($p=0.070$) did not differ significantly among the five stages.

Regarding the direction taken by workers during extra-nest activity, both old and new colonies had directionality regardless of the stage analyzed (MS, $Z=44.8$, $N=737$, $p<0.001$; PS, $Z=100.5$, $N=535$, $p<0.001$; SS, $Z=55.8$, $N=539$, $p<0.001$; CS, $Z=25.4$, $N=347$, $p<0.001$; PCS, $Z=19.7$, $N=332$, $p<0.001$) (Fig 2). From the beginning of observations, the old nest showed a directional tendency, avoiding the area of a neighbor colony located at 110° and a distance of 13.6 m. Workers foraged preferentially in the opposite direction, as indicated by their mean vectors (MS, $\mu=253.6^\circ$; PS, $\mu=284.1^\circ$; SS, $\mu=267.8^\circ$; CS, $\mu=273.1^\circ$).

The stage with highest directionality was the polydomic stage, which had the longest mean vector length (MS, $r=0.25$; PS, $r=0.43$; SS, $r=0.32$; CS, $r=0.27$). In the polydomic

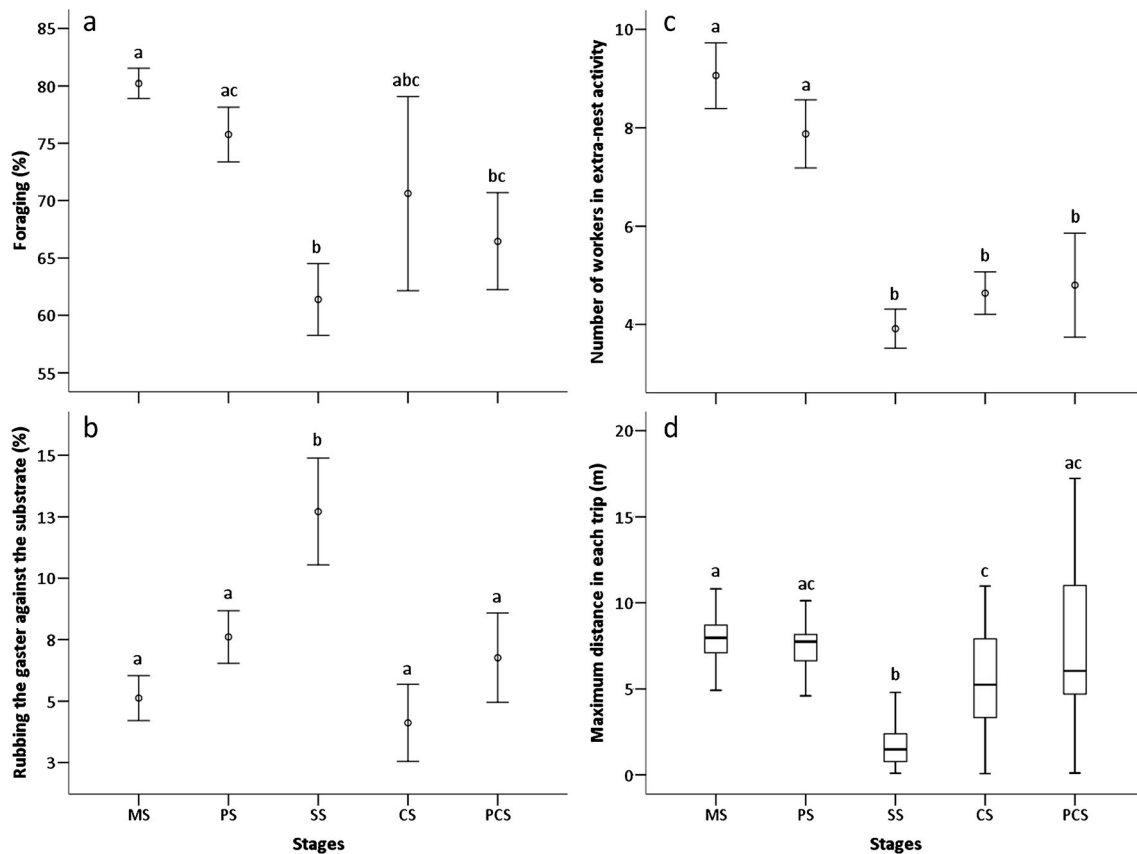


Fig 1 Changes in **a** foraging frequency (mean \pm SE), **b** rubbing the gaster against the substrate frequency (mean \pm SE), **c** number of workers engaged in extra-nest activity (mean \pm SE), and **d** maximum distance reached during extra-nest activity (median, first and third quartiles, and non-outlier range) throughout a *Dinoponera quadriceps* colony fission process. MS: monodomic stage; PS: polydomic stage; SS: split stage; CS: conflict stage; PCS: post-conflict stage. Different letters indicate significant differences among the stages.

stage, the area of the new nest, at 176° from the old nest, also seemed to be avoided (Fig 2). This phenomenon also occurred, although less intensely, during the split and conflict stages, which had longer mean vector lengths than the monodomic stage but shorter lengths than the polydomic stage. The new colony, in the post-conflict stage, had a mean vector length ($r=0.24$) similar to that of the old colony during its monodomic stage. Workers from the new colony avoided the area of two neighbor colonies at 14.6 m and 290° and 17.4 m and 185° from the new nest. The preferred direction was opposed to these neighbor colonies, as indicated by the mean vector ($\mu=50.6^\circ$).

Discussion

Although dependent colony foundation occurs as a regular stage of the colony cycle in many species, in species with opportunistic dependent colony foundation, the separation of the daughter colony from the parental colony is unpredictable and field documentation is rare, as it requires long-term observations of neighboring nests with marked individuals (Peeters & Ito 2001, Cronin *et al* 2013). Opportunistic

dependent foundation can occur in polydomic species in which nests of the same colony may become isolated from one each other due to a gradual decrease in the traffic among them (Cronin *et al* 2013). According to our results, this seems to be the case in *D. quadriceps*.

In the monodomic stage, the frequency of extra-nest behaviors were similar to those previously recorded for *D. quadriceps* (Araújo & Rodrigues 2006, Azevedo 2009), with a high percentage of time spent outside the nest to forage. In this stage, workers reached a mean distance of 8.2 m during foraging, which is also similar to the foraging distance recorded for *Dinoponera gigantea* (Perty) (Fourcassié & Oliveira 2002). Thus, the workers showed features of an unaltered colony, and in the polydomic stage, none of the analyzed variables differed from those in the monodomic stage.

The existence of a polydomic stage before the colony split indicates that colony fission in *D. quadriceps* occurs gradually. In bees, the split between parental and daughter colonies can occur either abruptly or gradually. In honeybees, there is no contact between colonies after a swarm moves to the new nest site, but in stingless bees, the construction of the new nest is initiated prior to fission and construction material

Table 1 Final generalized linear models investigating the effects of fission process stage and season on the variation of workers' extra-nest behavior in *Dinoponera quadriceps*.

Response variable		Estimates (SE)	t-value	pvalue
Foraging	(Intercept)	80.21 (3.53)	22.74	<0.001
	Polidomic stage	-4.45 (5.07)	-0.88	0.382
	Split stage	-18.83 (4.92)	-3.83	<0.001
	Conflict stage	-9.6 (5.8)	-1.66	0.102
	Post-conflict stage	-13.76 (5.15)	-2.67	0.009
Rubbing the gaster against the substrate	(Intercept)	5.12 (1.54)	3.33	0.001
	Polidomic stage	2.48 (2.21)	1.12	0.265
	Split stage	7.59 (2.15)	3.54	<0.001
	Conflict stage	-1.01 (2.53)	-0.4	0.691
Number of workers engaged in extra-nest activity	(Intercept)	9.48 (0.74)	12.76	<0.001
	Rainy season	-1.78 (0.77)	-2.32	0.023
	Polidomic stage	-0.82 (1.05)	-0.79	0.433
	Split stage	-4.33 (1.01)	-4.27	<0.001
	Conflict stage	-4.84 (1.16)	-4.16	<0.001
	Post-conflict stage	-3.26 (1.07)	-3.04	0.003

is transferred from the old nest to the new nest for up to 6 months after the swarm occupies the new nest (Peeters & Ito 2001, Cronin *et al* 2013).

The split stage differed significantly from the monodomic and polydomic stages in terms of the frequency of foraging and rubbing the gaster against the substrate, the number of workers engaged in extra-nest activity, and the maximum distance in each trip, indicating that workers' extra-nest behavior is influenced by the colony fission process. In this

Table 2 Significance results of multiple comparisons between seasons and between stages of colony fission in relation to the maximum distance reached by *Dinoponera quadriceps* workers during extra-nest activity.

	p-value
Monodomic stage: rainy season × dry season	0.460
Polidomic stage: rainy season × dry season	1.000
Split stage: rainy season × dry season	0.693
Post-conflict stage: rainy season × dry season	1.000
Rainy season: monodomic stage × polidomic stage	1.000
Rainy season: monodomic stage × split stage	0.022
Rainy season: monodomic stage × post-conflict stage	0.996
Dry season: monodomic stage × polidomic stage	0.467
Dry season: monodomic stage × split stage	< 0.001
Dry season: monodomic stage × conflict stage	0.026
Dry season: monodomic stage × post-conflict stage	1.000

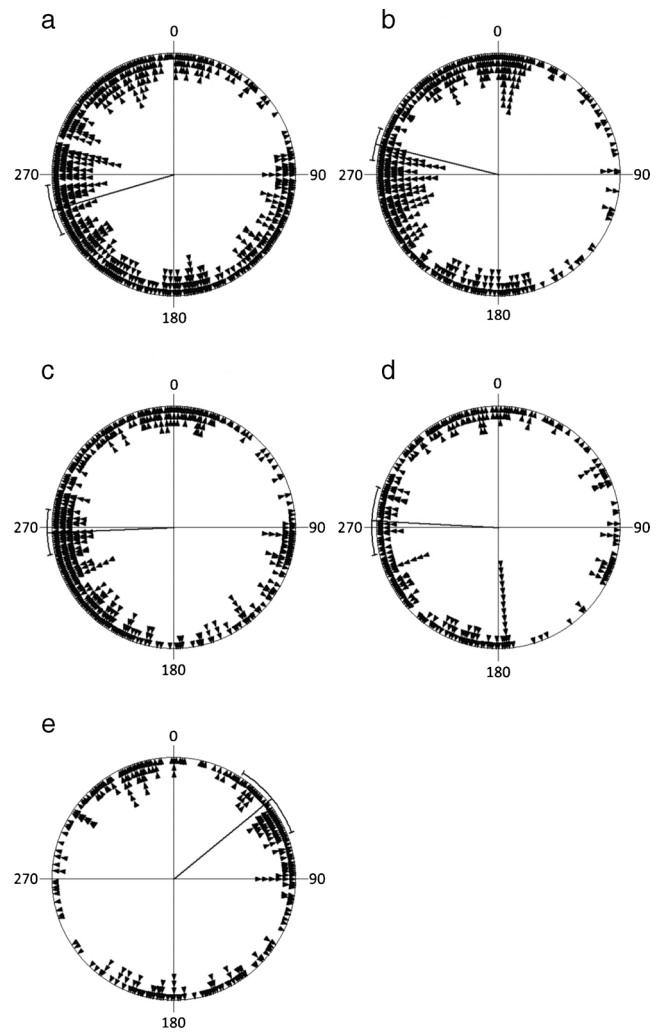


Fig 2 Distribution of workers around the colony during extra-nest activity in the a monodomic stage, b polidomic stage, c split stage, d conflict stage, and e post-conflict stage of the colony fission process in *Dinoponera quadriceps*. The arrows indicate the positions of workers recorded every 5 min of observation. The vector indicates mean and confidence interval.

stage, probably due to the presence of a new colony so close, there was an increase in the frequency of rubbing the gaster against the substrate. With this increase, there was a decrease in the percentage of time spent by workers foraging during extra-nest activity, reaching a mean of 61.4%. Rubbing the gaster against the substrate probably has a chemical marking function and was previously observed by Araújo & Rodrigues (2006), who suggested that this behavior could be related to the establishment of individual trails. Based on our results, we suggest that it can also be related to the establishment of colony territory. A uniform colony odor can be achieved by the transference of hydrocarbons among ants from the same nest, as occurs in *Pachycondyla apicalis* (Latreille), *Aphaenogaster senilis* (Mayr), and *Camponotus fellah* (Dalla Torre) (Soroker *et al* 2003). Territory signaling can play an important role in determining the results of

agonistic encounters if the bourgeois strategy is adopted, as in *Cataglyphis niger* (André), in which the owner of the territory is usually the winner (Wenseleers *et al* 2002).

The number of workers engaged in extra-nest activity was influenced by season, with a significant decrease during the rainy season. The influence of season on foraging activity has previously been observed in *D. quadriceps* and in other ant species. Seasonal changes in environmental conditions that affect foraging activity are mainly related to food availability, temperature, and humidity (Levings 1983, Cogni & Oliveira 2004, Medeiros *et al* 2012). Nevertheless, independent of the influence of season, colony fission had a significant effect on the number of workers engaged in extra-nest activity. In the split stage, the number of workers engaged in extra-nest activity was halved in comparison to the monodomic and polydomic stages. Thus, the number of workers engaged in extra-nest activity seemed to reflect colony population. Species with small colonies, such as *D. quadriceps*, may be able to split only if they increase the production of workers enough to make colonies viable after fission. However, the priority is to replace dead workers (Peeters & Ito 2001), which explains why the number of workers that were engaged in extra-nest activity did not increase again in any stage after fission until the end of the study.

The split stage also showed a decrease in the maximum distance reached in each trip. Workers remained closer to the nest during extra-nest activity relative to other stages. Azevedo (2009) suggested that food is first depleted near the nest, an area visited by all foragers, and then foragers are pushed to forage at increasing distances to obtain food. This might be the cause of workers reaching farther distances in the stages leading up to fission, when the colony had a high number of foragers, compared with the stages following fission, when there were few workers engaged in extra-nest activity to deplete food items in the nearby area.

In the conflict stage, which occurred more than 5 months after the fission event, the frequencies of foraging and rubbing the gaster against the substrate returned to levels similar to those in the monodomic stage. The two colonies formed by fission were too close, causing the conflict between them. Whereas the distances from the parental colony to other neighbor colonies were 13.60, 18.85, 13.22, and 20.30 m, the distance to the daughter colony was only 3.34 m. The restriction in dispersion distance is a feature of queenless ant species that have dependent colony foundation, as gamergates are wingless. This represents a severe restriction that limits the distance that can separate parental and daughter colonies (Peeters & Ito 2001). While ant species with independent colony foundation can disperse up to 1.6 km, dependent colony foundation has a maximum range of 32 m (Cronin *et al* 2013).

The extinction or migration of the parental colony as a result of the conflict probably helped to maintain the overdispersion in nest distribution, lending support to the

hypothesis that intraspecific competition has an important role in determining the spatial arrangement of nests (Vasconcellos *et al* 2004). The maintenance of this type of distribution in ants can require territorial behavior that excludes workers, colonies, or founding queens that are in the foraging area of an established colony (Hölldobler & Wilson 1990). Foraging distance varied from 0.07 to 32.07 m in the parental colony and from 0.10 to 38.62 m in the daughter colony; thus, each colony was within the foraging area of the other. However, other neighbor colonies that were also within this area did not produce conflicts, except in the form of agonistic interactions in occasional encounters during extra-nest activity. This is likely because distant areas are rarely reached during foraging. The median foraging distance in the parental colony was 6.25 m and 6.05 m in the daughter colony. Therefore, only the two monitored colonies were within the frequently visited area of one another. Furthermore, due to the short distance between the nests, the agonistic encounters always occurred near them, which may have elevated the level of aggression between colonies as a behavior of nest defense. In *Cataglyphis fortis* (Forel), the level of aggression is higher when workers are near their nests than when they are distant (Knaden & Wehner 2003). Indeed, agonistic interactions that occurred at the nest entrance of the parental colony or very close to it, typical of the conflict stage, lasted longer and were more intense than those that occurred during foraging and far from the nest entrance.

As demonstrated by the extinction or migration of the parental colony, colonies founded by dependent colony foundation are good competitors from the moment of foundation because they have enough adult workers to build safe nests, care for the brood, and forage efficiently, unlike colonies founded independently that are initially quite vulnerable (Peeters & Ito 2001). Nevertheless, the new colony did not start the conflict with its parental colony immediately after its foundation. The conflict stage started five and a half months after colony fission, which is probably the time needed for the new colony to reach a more mature stage. Furthermore, the parental colony underwent an army ant attack during the split stage, which may have contributed to its posterior decline.

In the post-conflict stage, the new colony had a lower frequency of foraging and a lower number of workers engaged in extra-nest activity than the parental colony had during the monodomic and polydomic stages. These differences probably reflect inter-colony differences and the stage of each colony: one colony was more than 5 years old (it had been observed since 2003) and was about to undergo fission, and the other was a newly founded colony that was about 1 year old. Furthermore, during the post-conflict stage, some workers from a neighboring colony aggressively approached the entrance of the new nest, just as workers

from the new colony had done during the conflict stage, but in this case, the new colony was able to repel the attackers, and the conflict did not persist.

The results hitherto discussed indicate the occurrence of intraspecific competition in *D. quadriceps* colonies that are too close to each other as a result of colony fission, but the colonies' directionality during foraging indicates that competition between farther neighbor colonies also occurs in this species. There was a directional preference at the colony level in all stages, with areas near neighbor colonies avoided. The colonies foraged preferentially in the opposite direction to these neighbor colonies. The same occurs in colonies of *Veromessor pergandi* (Mayr). Their colonies tend to forage away from conspecific neighbors when there is resource shortage, whereas colonies that had their neighbors experimentally removed forage randomly (Ryti & Case 1988). In *D. quadriceps*, although there was colony directionality in all stages, it was higher while the parental and daughter colonies coexisted.

Based on this observation of a spontaneous *D. quadriceps* colony fission event in its natural environment, we conclude that colony fission affected workers' extra-nest behavior by increasing the frequency of rubbing the gaster against the substrate and by decreasing the frequency of foraging. After the fission event, the number of foragers was halved, and foragers remained nearer the nest during extra-nest activity. The closeness of the parental and daughter colonies led to competition that caused the extinction or migration of the parental colony.

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