

Nest distribution varies with dispersal method and familiarity-mediated aggression for two sympatric ants

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Dispersal mechanisms and competition together play a key role in the spatial distribution of a population. Species that disperse via fission are likely to experience high levels of localized competitive pressure from conspecifics relative to species that disperse in other ways. Although fission dispersal occurs in many species, its ecological and behavioural effects remain unclear. We compared foraging effort, nest spatial distribution and aggression of two sympatric ant species that differ in reproductive dispersal: *Streblognathus peetersi*, which disperse by group fission, and *Plectroctena mandibularis*, which disperse by solitary wingless queens. We found that although both species share space and have similar foraging strategies, they differ in nest distribution and aggressive behaviour. The spatial distribution of *S. peetersi* nests was extremely aggregated, and workers were less aggressive towards conspecifics from nearby nests than towards distant conspecifics and all heterospecific workers. By contrast, the spatial distribution of *P. mandibularis* nests was overdispersed, and workers were equally aggressive towards conspecific and heterospecific competitors regardless of nest distance. Finally, laboratory experiments showed that familiarity led to the positive relationship between aggression and nest distance in *S. peetersi*. While unfamiliar individuals were initially aggressive, the level of aggression decreased within 1 h of contact, and continued to decrease over 24 h. Furthermore, individuals from near nests that were not aggressive could be induced to aggression after prolonged isolation. Overall, these results suggest that low aggression mediated by familiarity could provide benefits for a species with fission reproduction and an aggregated spatial distribution.

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At a large scale, species' spatial distributions are often set by habitat conditions such as resource availability (Doncaster 1981; Boyce & McDonald 1999; Kaspari et al. 2000). At a more local scale, a population's spatial distribution becomes increasingly influenced by other factors such as dispersal methods and competitive strategies (Ricklefs & Schluter 1994; Fangliang et al. 1997; Nathan & Muller-Landau 2000). For populations of sessile organisms, there is often a trade-off between dispersal and competitive traits (Smith & Fretwell 1974; Yu & Wilson 2001; Cadotte et al. 2006), so that spatial distribution reflects a combination of ability to colonize a site and ability to persist at that site following colonization (e.g. Levins & Culver 1971; Hubbell 1979; Sousa 1984; Schupp 1990).

Ant colonies with discrete nest sites are sessile organisms that have evolved a range of dispersal strategies (reviewed in Hölldobler & Wilson 1990). In many species, young queens establish new colonies after a mating flight, which allows them to disperse far from their home nest (Zera & Denno 1997) and colonize new, empty

habitats (Hölldobler 1981). In some species, however, queens do not depart on mating flights, and new colonies are produced either by a single wingless queen departing from her home nest to establish a new one, or by group fission, in which a group of individuals leaves the home nest to establish a new one (Vargo & Porter 1989; Peeters & Ito 2001). Colonies originating without a mating flight often disperse shorter distances than colonies from winged queens, and colonies originating from group fission are often initially more competitively capable than colonies originating from single queens (Peeters & Ito 2001). Therefore, fission dispersal is expected to lead to high levels of competitive pressure among nearby conspecific colonies (Chéron et al. 2011), which can have far-reaching effects on the relationship between spatial distribution and behaviour among conspecific competitors (Gaudreault & Fitzgerald 1985; Dyson & Passmore 1992).

Although fission is a common means of reproductive dispersal in social insects (Peeters & Ito 2001), spiders (Avilés 2000), marine invertebrates (McFadden 1991) and social mammals (Cant et al. 2001; Waterman 2002), relatively little is known about the behavioural and ecological factors associated with this process for many species (Chéron et al. 2011), although fission dispersal has received much attention in honeybees (Seeley & Buhman 1999,

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2001; Seeley 2003, 2010; Rangel & Seeley 2008). We investigated the relationship among nest distribution, competitive overlap and aggressive behaviour (intraspecific and interspecific) in two sympatric ant species that differ in their methods of reproductive dispersal. The first is *Streblognathus peetersi*, a species in which the queen caste has been secondarily lost, and all individuals maintain reproductive potential (Peeters 1991). This species reproduces by group fission, with new colonies being created when a group of unmated workers leaves the parental nest (Monnin & Peeters 2008). After becoming locally established, a single reproductive individual mates with a winged male near her nest entrance (Peeters 1991; Cuvillier-Hot et al. 2004). In the second species, *Plectroctena mandibularis*, unmated and wingless queens disperse individually on foot from the parental nest, mate with winged males, and then establish new nests as singletons (Villet 1999).

Because competitive overlap can affect spatial distribution as well as competitive strategies, we first compared foraging behaviour between species by investigating when and where workers forage, and what items they collect. Second, we determined the nest spatial distributions for each species. Nest distribution could differ according to dispersal mechanism. Alternatively, competitive interactions among non-nestmates could lead to overdispersion for each species, regardless of differences in reproductive dispersal (Levings & Traniello 1981; Wiernasz & Cole 1995; Soares & Schoereder 2001). Third, to see whether aggressive behaviour is correlated with nest spatial distribution, we determined the relationship between nest distance and aggression among workers for each species, including aggression towards nestmates as well as non-nestmate conspecifics and heterospecifics. Finally, using laboratory experiments, we tested whether the relationship between nest distance and aggression in *S. peetersi* is sensitive to familiarity through repeated contact among workers.

METHODS

The field site was a large (ca. 20 ha) montane grassland meadow surrounded by mixed deciduous–coniferous forest, located near Magoebaskloof, Limpopo province, South Africa (23°53.3'S, 29°59.7'E, 1395 m elevation). To avoid edge effects and other difficulties associated with changing habitat type, we limited the study site to a ca. 12 ha rectangle (300 × 400 m) within the meadow. During an initial survey, we marked with acrylic paint 60 *S. peetersi* (five each from 12 colonies) and 40 *P. mandibularis* (five each from eight colonies) foragers to track individuals while they were foraging, and to determine whether they entered or left multiple nests.

Temporal Analysis

To establish each species' daily foraging routines, we recorded the time that the first forager left its nest and the time that the last forager returned to its nest for 15 nests of each species. During preliminary observations, we found that both species forage in two discrete efforts each day, one in the early morning and a second in the late afternoon. To compare foraging times between *S. peetersi* and *P. mandibularis*, we compared the foraging time midpoints of both morning and afternoon efforts (i.e. time between first forager leaving and last forager returning to the nest within a foraging effort) for all species–effort combinations with an ANOVA followed by Tukey's multiple comparisons test. We also recorded with what items (arthropod, annelid or plant material) foragers returned to their nests during this survey, and compared the similarity of diets between species using Fisher's exact contingency table test.

Spatial Analysis

We searched the study site and used GPS to record nest locations of each species. Preliminary visual inspection of the overall nest distribution (Fig. 1) suggested that nest spatial intensity could be inhomogeneous, a violation to most stationary null model spatial statistics (Baddeley & Silverman 1984; Ripley 1988; Baddeley et al. 2000). To determine the appropriate null model for our analysis, we tested for stationary structure using a likelihood ratio test comparing the null homogeneous Poisson model to an inhomogeneous Poisson model (Baddeley 2008). Because the inhomogeneous model better explained the underlying nest spatial structure ($AIC_{\text{homogeneous}} = -1386$, $AIC_{\text{inhomogeneous}} = -1389$, $P = 0.030$), we used nonstationary spatial point patterns (i.e. a null model assumption of an inhomogeneous Poisson process) for all spatial analyses.

To determine whether conspecific nest distribution was overdispersed, random or aggregated for each species, we used separate Ripley's *K* functions (Ripley 1977; Baddeley 2008) for conspecific between-nest intensities with isotropic corrections for rectangular sampling sites (Ripley 1988), and 95% confidence intervals using Monte Carlo simulations (Ripley 1981; Diggle 2003; Baddeley & Turner 2005). To determine whether nests within the site were spatially segregated by species, we tested for nest segregation using Dixon's (1994) nearest-neighbour contingency table test (Rajala 2011).

To find each species' use of foraging space, we divided the study site into a series of 10 × 10 m quadrats. We randomly chose 100 of these 100 m² quadrats to census forager presence/absence for each

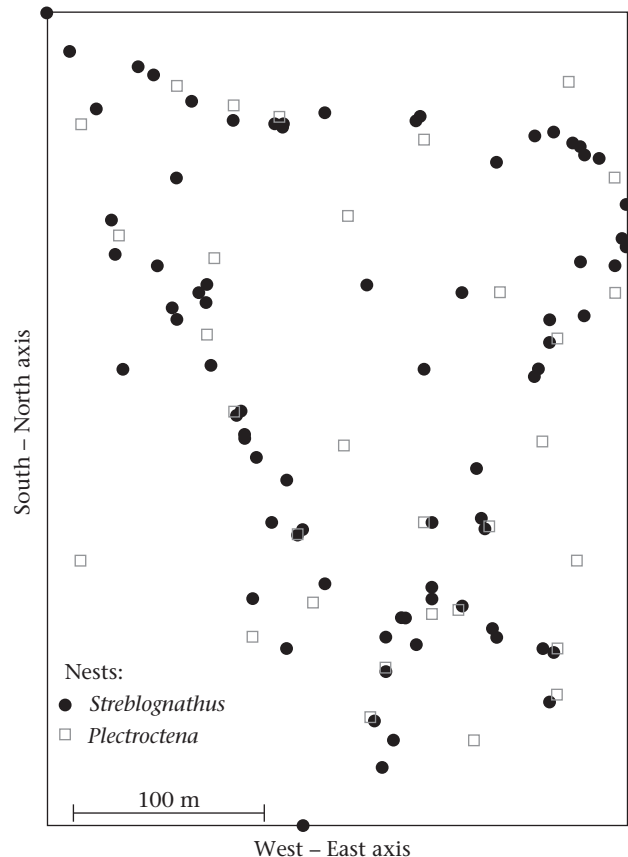


Figure 1. Ant nest spatial arrangement within the study site (ca. 12 ha rectangular plot within a ca. 20 ha grass meadow; see Methods for full description).

species during each of the two foraging time intervals (0630–0930 and 1600–1900 hours).

Behaviour Assays

We conducted behaviour assays in the field to investigate how foragers behave towards conspecific and heterospecific competitors from nests at various distances. These assays measured aggression of a focal individual towards a conspecific or heterospecific individual either near or far from the focal ant's nest ($N = 30$ replicates per species–distance–competitor combination). Control assays were with a focal individual and a nestmate ($N = 30$ per species). Near-nest assays included a focal individual and a forager from its nearest-neighbour nest (conspecific and heterospecific). For *S. peetersi*, the average nearest-neighbour nest distances were 12.5 m and 15.7 m for conspecific and *P. mandibularis*, nests, respectively. For *P. mandibularis*, the average nearest-neighbour nest distances were 34.5 m and 14.2 m for conspecific and *S. peetersi* nests, respectively. Far-nest assays included a focal individual and a conspecific or heterospecific forager from a nest ≥ 100 m away. For each assay, the focal ant and its competitor were placed in isolated containers (15 cm diameter) for 5 min. After this acclimation stage, both ants were simultaneously placed into an assay arena (15 cm diameter) for 3 min, while we recorded the number of times the focal ant was aggressive (biting, lunging, gaster flexing and fighting) as well as the number of nonaggressive interactions (antennation or contact without the above aggressive behaviours). We compared the number of aggressive interactions among nestmates, near and far conspecifics and heterospecifics for each species using an ANOVA (square-root transformed to meet parametric assumptions) followed by Tukey's multiple comparisons test to determine whether aggression differed according to competitor identity.

To determine how behaviour between *S. peetersi* foragers is affected by competitor familiarity, we set up a series of laboratory nest pairs (dark 24 h, 26 °C, 60–70% relative humidity) in which each pair was connected to a single foraging area (light:dark 12:12 h, 20:28 °C night:day, 40–50% relative humidity). Each experimental nest contained 20–30 individuals, and each nest pair included two nests that were collected from far apart (≥ 100 m) in the field. For 7 days, the foraging area was divided in half with a solid wall to preclude contact between ants from different nests. Because diet can influence nestmate recognition in some ant species (Liang & Silverman 2000; Ichinose et al. 2009), foragers from one colony received one mealworm every 3 days and sugar–water ad libitum, while foragers from the other colony received one cockroach every 3 days and honey–water ad libitum (this amount of food per individual is similar to what we found foragers returning to the nest with, and on many days the previous food item was not finished before a new one was added). On the 8th day, we removed the solid divider so that foragers from both nests shared a common foraging area. Using digital video cameras, we recorded in 10 min intervals the number of aggressive and nonaggressive interactions (as defined in the field assays) among *S. peetersi* foragers in the common area 10 min, 1 h and 24 h after removing the divider. We compared the number of aggressive interactions between consecutive observation time points for each nest pair separately using chi-square tests. We then pooled these results among replicate nest pairs for each comparison of time points using Fisher's omnibus test (Sokal & Rohlf 1995). Finally, we observed all colonies 7 days after removing the divider to examine the effects of competition on each colony.

Using four additional colonies, we followed the above nest-pairing protocol for a second *S. peetersi* laboratory experiment to compare the effects of isolation on individuals from colonies that

differed in nest distance when in the field. In the first nest pair, individuals came from nests that were nearby (10 m) in the field and did not exhibit aggression in the field assay. In the second nest pair, individuals came from nests that were distant (105 m) in the field and did exhibit aggression in the field assay. For 8 weeks before the experiment, all four colonies were isolated, and all received a similar diet of mealworms, water and sugar–water ad libitum. In the experimental nests, we removed the solid dividers in the common foraging areas of each nest pair 7 days after starting the experiment and recorded the numbers of aggressive and nonaggressive interactions for two 10 min intervals (10 min and 1 h after barrier removal).

RESULTS

Temporal Analysis

We found a significant difference (ANOVA: $F_{3,56} = 38.327$, $P < 0.001$) among temporal foraging midpoints for all species–foraging effort combinations. This difference was a result of each species having two discrete foraging efforts per day, one in the morning and another in the late afternoon (Fig. 2). Neither the morning nor the afternoon foraging period, however, differed between species (Tukey's multiple comparison: morning: $P_{\text{adjusted}} = 0.160$; afternoon: $P_{\text{adjusted}} = 0.913$).

In addition to foraging at similar times of the day, *S. peetersi* and *P. mandibularis* foraged for similar prey items (Fisher's exact test: $P = 0.832$). Of the 300 *S. peetersi* foragers observed returning to their nests, 17 returned with arthropods, five with annelids and two with plant/seed material. Of the 220 *P. mandibularis* foragers observed returning to their nests, nine returned with arthropods, one with an annelid and one with plant/seed material.

Spatial Analysis

Nests of *S. peetersi* were spatially aggregated (Fig. 3a), with observed Ripley's K values above critical ($\alpha = 0.05$) at all radius distances. By contrast, the spatial distribution of *P. mandibularis*

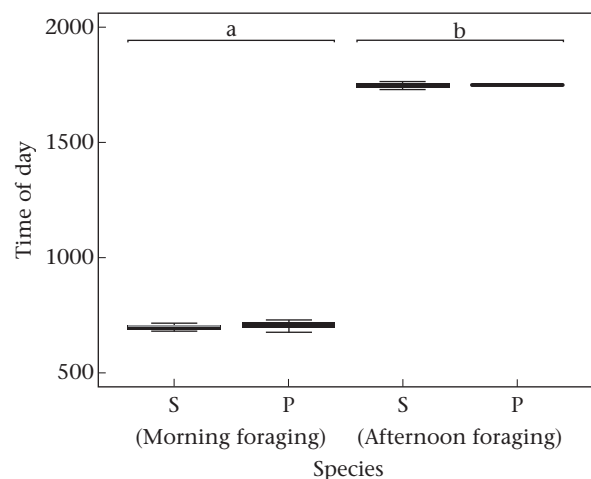


Figure 2. Distributions (median, quantiles, minimum and maximum values) for time of day when each species foraged (midpoint between when the first forager left a nest and when the last forager returned) for 15 nests of each species. Foragers from each species make two foraging trips per day, and remain in the nest during the afternoon. S: *Streblognathus peetersi*; P: *Plectroctena mandibularis*. Letter groupings (a and b) reflect significant differences between groups (Tukey's multiple comparisons; $P < 0.001$).

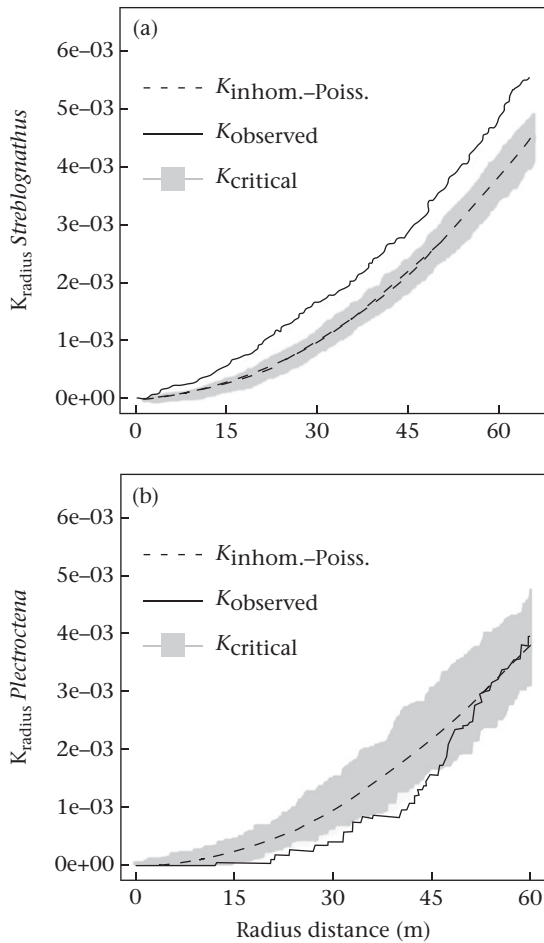


Figure 3. Ripley's K values, measure of spatial intensity, as a function of increasing radius distance for nest distribution of (a) *Streblognathus peetersi* and (b) *Plectroctena mandibularis*. K_{observed} are actual values, $K_{\text{inhom.-Pois.}}$ are predicted values assuming an inhomogeneous Poisson distribution, and K_{critical} are Monte Carlo simulations testing upper and lower bounds ($\alpha = 0.05$) of K values at each radius distance. K_{observed} values $\geq K_{\text{critical}}$ are evidence of conspecific nest aggregation beyond the underlying spatial structure, while K_{observed} values $\leq K_{\text{critical}}$ are evidence of conspecific nest overdispersion.

nests was overdispersed at radius distances ≤ 45 m, and randomly dispersed at larger radius distances (Fig. 3b). Finally, nests within the site were not spatially segregated between species ($C = 0.310$, $P = 0.143$).

Besides sharing space for nests, *S. peetersi* and *P. mandibularis* also foraged at similar locations. During the morning quadrat survey, we found *S. peetersi* in 46 and *P. mandibularis* in 18 of the 100 sample quadrats. Sixteen of the 100 quadrats contained both species, which provided a significant positive correlation for forager presence/absence between these two species (Spearman correlation test: $r_s = 0.403$, $S = 99\,460$, $P < 0.001$). In the evening quadrat survey, *S. peetersi* workers were found in 40 and *P. mandibularis* in 12 of the 100 sampled quadrats. Eleven quadrats contained both species, which again led to a positive correlation for forager presence/absence between species ($r_s = 0.390$, $S = 10\,1748$, $P < 0.001$).

We did not observe workers of either species entering or leaving more than one conspecific nest (i.e. neither species is polydomous at this site). Of the 60 *S. peetersi* foragers marked at the beginning of the study, none were observed entering or leaving an alternative nest. Of the 40 marked *P. mandibularis*, five were observed entering heterospecific nests and two entering abandoned nests.

Behaviour Assays

In the field behaviour assays for *S. peetersi*, the number of aggressive events varied greatly according to the type of individual presented (ANOVA square-root-transformed number of aggressive events: $F_{4,145} = 51.7$, $P < 0.001$; Fig. 4a). Individuals were rarely aggressive towards nestmates, intermediately aggressive towards conspecifics from nearby nests (Tukey's multiple comparisons between nestmates and near conspecifics: $P_{\text{adjusted}} = 0.008$) and more aggressive towards conspecifics from distant nests ($P_{\text{adjusted}} < 0.001$ for near compared to far conspecifics). Aggression by *S. peetersi* towards *P. mandibularis* was high, regardless of nest distance ($P_{\text{adjusted}} = 0.999$), and of a similar magnitude towards far conspecifics ($P_{\text{adjusted}} = 0.982$ for near *P. mandibularis* compared to far conspecifics; $P_{\text{adjusted}} = 0.997$ for far *P. mandibularis* compared to far conspecifics).

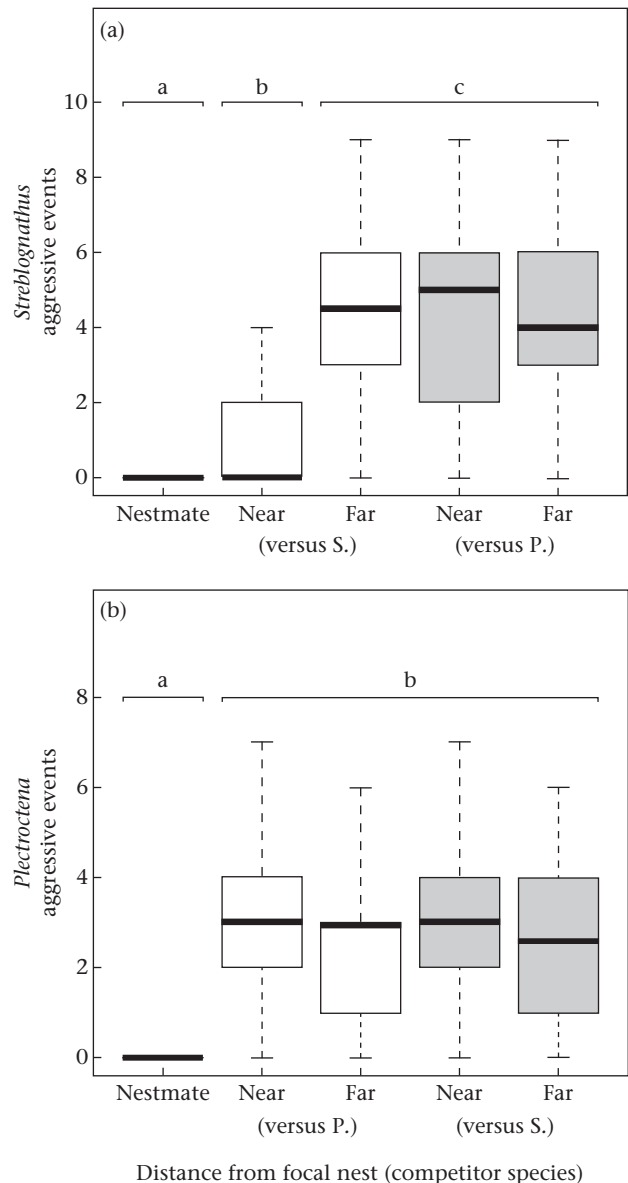


Figure 4. Number (median, quantiles, minimum and maximum values) of aggressive events for (a) *Streblognathus peetersi* (S) and (b) *Plectroctena mandibularis* (P) during field aggression assays ($N = 30$ replicates per group per focal species) with nestmates, conspecifics (near or far from focal nest) and heterospecifics (near and far from focal nest). Letter groupings (a, b and c) reflect significant differences between groups (Tukey's multiple comparisons; $P < 0.01$).

In the field behaviour assays for *P. mandibularis*, there was also an overall significant difference in the number of aggressive events according to the type of individual presented (ANOVA square-root-transformed number of aggressive events: $F_{4,145} = 31.2$, $P < 0.001$; Fig. 4b). While individuals were rarely aggressive towards nestmates, they were more often aggressive towards non-nestmates (Tukey's multiple comparisons: $P_{\text{adjusted}} < 0.001$ for nestmates compared to either near or far conspecifics). In contrast to *S. peetersi*, however, there was no effect of nest distance on the level of intraspecific aggression ($P_{\text{adjusted}} = 0.973$ for near compared to far aggression towards conspecifics). Furthermore, *P. mandibularis* aggression did not differ between intraspecific and interspecific competitors for either nest distance ($P_{\text{adjusted}} = 0.999$ for each comparison, near and far, between aggression towards conspecifics and heterospecifics).

When *S. peetersi* nests that were distant in the field (>100 m) were paired in the laboratory, repeated contact among workers led to a reduction in aggression from 10 min to 1 h after sharing a common foraging area (chi-square tests for eight nest pairs: $P < 0.001$, $P < 0.001$, $P = 0.001$, $P = 0.008$, $P < 0.001$, $P < 0.001$, $P < 0.001$; Fisher's omnibus test for overall significance: $P < 0.001$; Fig. 5). After 24 h of sharing the same foraging area, worker aggression decreased still further in most nest pairs compared to levels after 1 h of sharing (chi-square tests for eight nest pairs: $P = 1$, $P = 0.020$, $P = 0.108$, $P < 0.001$, $P = 0.132$, $P < 0.001$, $P < 0.001$, $P < 0.001$; Fisher's omnibus test for overall significance: $P < 0.001$). This decline in aggression was not due to mortality among the most aggressive individuals, as only two of the 419 individuals used in the experiment died within 24 h of barrier removal.

After the workers had spent 8 weeks in isolation in the laboratory, the correlation between *S. peetersi* aggression and nest distance that was observed in the field assays disappeared. The pair of nests that had been collected near each other in the field and previously exhibited low levels of aggression exhibited similar levels of aggression to the pair of nests that had been collected far away and originally exhibited high levels of aggression ($\chi^2 = 0.433$, $P = 0.835$; Fig. 6). The similarity in aggression between near and far

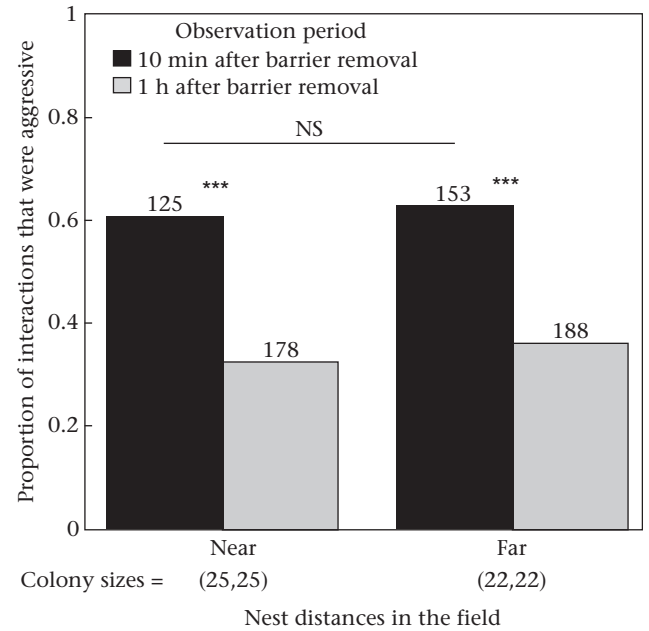


Figure 6. Proportion of interactions observed that were aggressive (numbers at top of each bar show total numbers of interactions during each observation) 10 min and 1 h after the divider was removed from the common foraging area. Near (ca. 10 m) and far (ca. 100 m) refer to nest distances when colony pairs were in the field.

pairs was due to an increase in aggression for the near pair, as levels of aggression for both pairs (ca. 60%) were similar to those of colony pairs that had been distant in the field (Fig. 5).

Although isolation led to an increase in aggression between individuals from nests that had been near each other and nonaggressive in the field, repeated contact among these individuals again reduced worker aggression, regardless of previous nest distance. After 1 h of sharing the foraging area, workers from nests that had been near, and from nests that had been far, both showed

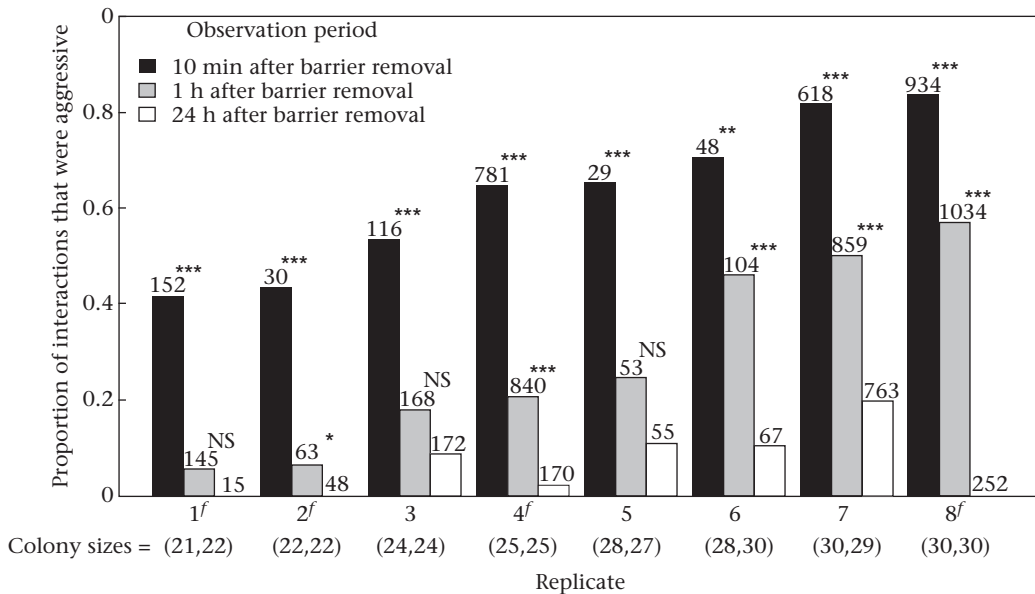


Figure 5. Proportion of interactions that were aggressive (numbers at top of each bar show total numbers of interactions during each observation) 10 min, 1 h and 24 h after the divider was removed from the common foraging area. All colony pairs were collected from far distances (>100 m) in the field. Significance tests reflect decreases in aggression between 10 min and 1 h post barrier removal observation periods, and between 1 h and 24 h post barrier removal observation periods for each replicate (*** $P \leq 0.001$; ** $P \leq 0.01$; * $P < 0.05$). Replicates with superscript *f* represent colonies that fused within 7 days of barrier removal.

a significant reduction in aggression (near pair: $\chi^2 = 22.57$, $P < 0.001$; far pair: $\chi^2 = 22.81$, $P < 0.001$; Fig. 6).

DISCUSSION

Although *S. peetersi* and *P. mandibularis* share many ecological similarities, key differences between these species in dispersal and aggressive behaviour are associated with different spatial distributions. In *S. peetersi*, groups of individuals disperse on foot to form new nests via fission, while in *P. mandibularis*, solitary queens disperse on foot to form new nests alone. Nests of *S. peetersi* were locally aggregated at our study site, while *P. mandibularis* nests were locally overdispersed. Such aggregation among *S. peetersi* nests is in contrast to most ant species' nest distributions. In ants, the high degree of local competitive pressure among nearby nests (Hölldobler & Wilson 1990) generally leads to overdispersion, with the highest levels of competitive overlap and overdispersion occurring among conspecifics (Bernstein & Gobbel 1979; Theunis et al. 2005; Tschinkel 2006; Boulay et al. 2007, 2010).

Our behaviour assay in the field revealed that the extreme level of *S. peetersi* nest aggregation was associated with low aggression between individuals originating from nearby nests. The observation of low aggression between closely located nests makes sense given that intense antagonistic interactions among nearby competitors should lead to local thinning of nests and nest overdispersion (Wiernasz & Cole 1995), as we found in *P. mandibularis*.

Three lines of evidence suggest a correlation between *S. peetersi* nest aggregation and reduced aggression among familiar conspecific foragers. First, workers from nearby *S. peetersi* nests in the field were less aggressive than workers from distant nests, while *P. mandibularis* worker aggression did not change with conspecific nest distance. Second, foragers from distant *S. peetersi* colonies became less aggressive towards each other after repeated contact in the laboratory. Third, following isolation in the laboratory, *S. peetersi* workers from nearby nests that were initially not aggressive became as aggressive towards each other as workers from distant nests, and this aggression also diminished after repeated contact among foragers. Because of the tightly aggregated spatial distribution of *S. peetersi* nests, neighbouring foragers are often likely to encounter each other, and according to our laboratory experiments, repeated encounters among non-nestmate workers can quickly lead to foragers becoming nonaggressive. Although *S. peetersi* is not territorial per se, our field results are consistent with the dear–enemy phenomenon (Ydenberg et al. 1988; Temeles 1994). Furthermore, laboratory experiments revealed that this dear–enemy effect was due to habituation among workers, which is consistent with findings of ant species that are more territorial (e.g. Langen et al. 2000).

Nonaggression towards nearby conspecifics could also result from individual *S. peetersi* not being able to differentiate between nestmates and conspecifics from nearby nests. To the contrary, we found that individual *S. peetersi* can differentiate between nestmates and neighbouring conspecifics, as well as between nearby and distant conspecifics. This differentiation ability is consistent with *S. peetersi*'s social structure, as individuals differentiate between nestmates to maintain multistrata dominance hierarchies (Cuvillier-Hot et al. 2004; Cuvillier-Hot & Lenoir 2006), even within colonies that have multiple matriline and patriline (Schlüns et al. 2006). Furthermore, we observed no *S. peetersi* individuals entering or leaving more than a single nest throughout the study.

The effect of repeated contact on aggression among ant foragers often depends on context such as colony size and competitive strategy. Examples of repeated contact increasing aggression have been mainly reported in species that form large territorial colonies (Thomas et al. 2007; van Wilgenburg et al. 2009; Newey et al.

2010). By contrast, observations of reduced aggression after repeated contact have generally been found in species in which colonies are smaller and do not have well-defined territories (Langen et al. 2000; Zinck et al. 2008). Consistent with this distinction, *S. peetersi* colonies are very small, tightly aggregated, do not defend absolute territories and do not recruit to resources (Ware et al. 1990; Schlüns et al. 2006).

The reduced aggression among nearby *S. peetersi* foragers might be adaptive for two nonmutually exclusive reasons. First, because the costs of defending a two-dimensional territory with temporally and spatially ephemeral food sources generally outweigh the benefits (Hölldobler & Lumsden 1980; Fourcassié et al. 2012), aggressively defending a territory might cost more than it is worth. Colonies in which foragers repeatedly fight with their neighbours would suffer the cost of mortality, thereby reducing the foraging workforce, as well as paying the costs associated with lost foraging opportunities while fighting. *Streblognathus* do not perform trophallaxis (Ware et al. 1990), so foragers returning with and without food could be clearly identified. As only 7–8% of the foragers we observed throughout the study returned to the nest with food items, finding food at this site is not common. Second, reduced aggression towards neighbouring conspecifics may also provide indirect inclusive fitness benefits if geographical proximity is correlated with relatedness (Beye et al. 1998; Langen et al. 2000; Pirk et al. 2001). Social insects that disperse by fission typically exhibit population viscosity (West-Eberhard 1975): nearby colonies are more closely related than distant colonies (Chapuisat et al. 1997; Liautard & Keller 2001; Pirk et al. 2001; Kronauer et al. 2010). The possibility of inclusive fitness benefits from reduced aggression towards neighbours is consistent with our finding that aggression in *S. peetersi* is sensitive to nest distance for conspecifics but not for heterospecifics.

Another potential benefit of reduced aggression among individuals from closely located *S. peetersi* nests is the opportunity for colony fusion. In laboratory *S. peetersi* nest pairs, habituation and reduced aggression were followed by nest fusion within 7 days in four of the eight pairs (Fig. 5). Adams et al. (2007) reported that fusion between termite colonies in the field could be predicted from low aggression levels in laboratory assays. Although ant colony fusion is relatively rare (but see Kronauer et al. 2010 for a discussion of how fusion might be more prominent than previously expected), fusion has the potential to provide benefits in unfavourable conditions (Herbers & Tucker 1986; Buczkowski & Bennett 2008). For example, in dwarf honeybees, *Apis andreniformis* and *Apis florea*, colonies with queens experimentally removed will merge with sympatric conspecific or heterospecific queenright colonies (Wongvilas et al. 2010). Notably, fusion seems to occur predominantly in species that also have a fission stage of dispersal (e.g. Schneirla & Brown 1950; Kellner et al. 2010; Kronauer et al. 2010).

In conclusion, we have shown experimentally that familiarity among *S. peetersi* workers leads to a reduction in conspecific non-nestmate aggression, which is consistent with *S. peetersi* workers in the field exhibiting less aggression towards nearby conspecifics than towards conspecifics from distant nests. This familiarity-based aggression helps to explain the spatial nest aggregation we observed in *S. peetersi*. By contrast, familiarity had no effect on *P. mandibularis* aggression. Workers were equally aggressive towards conspecifics regardless of nest distance, which helps to explain the spatial nest overdispersion we observed in *P. mandibularis*. Although dispersal distance is limited in both species because new colonies are formed without mating flights, *P. mandibularis* queens disperse alone, while *S. peetersi* disperse as a group from the parental nest. The differences in nest distribution and aggressive behaviour between *S. peetersi* and *P. mandibularis*

provide support for a connection between dispersal mechanism, behaviour and spatial distribution for populations.

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