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Research article

How ants find each other; temporal and spatial patterns in nuptial flights

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Abstract. Reproduction is a key factor in understanding population ecology and therefore species occurrence. However, patterns in reproductive behaviour for distinct ant species remain insufficiently known. In this paper strategies in mate finding are studied for six ant species (*Lasius niger*, *Lasius umbratus*, *Temnothorax nylanderi*, *Myrmica rubra*, *Myrmica ruginodis*, *Stenamma debile*) in a forest – forest edge – agricultural field gradient. Using window traps, we studied whether these species had a restricted nuptial flight season, displayed swarming behaviour, and whether the alates aggregated at the forest edge. The flight season was limited to one month or less for *L. niger*, *T. nylanderi*, *M. rubra*, *M. ruginodis* and *S. debile*. Swarming behaviour occurred in all but one (*L. umbratus*) species. Although none of the six species seemed to have highest nest density at the forest edge, three of them, *M. rubra*, *M. ruginodis* and *S. debile*, showed male aggregations there, indicating this to be the main reproduction site. This last finding could be due to a more suitable micro-climate, but most likely, edges are conspicuous land marks which are used by ants to meet mates. The behavioural patterns of ant sexuals at the forest edge can influence dispersal possibilities in fragmented landscapes, reproductive success and nest densities.

Keywords: Edge effects, flight phenology, Formicidae, mate finding, reproduction.

Introduction

Reproduction behaviour and phenology are key factors for any species and need to be recognized to understand species occurrence and population characteristics (Tschinkel, 1991; Kaspari et al., 2001a). For ants, with a relative sessile way of living, flight capable sexuals are of high importance to ensure outbreeding, the founding of new colonies and the colonization of new areas (Kannowski, 1963; Hölldobler and Wilson, 1990; Mabelis, 1994). For this reason, every year much energy is invested in the production of winged sexuals (Brian, 1979). Due to its vital importance, reproductive behaviour is precise and constant in most species. With few exceptions, males and gynes have to rely on meeting each other for mating during nuptial flights. The existence of mechanisms that increase the chance of finding each other is therefore crucial.

Broadly speaking, two types of nuptial flight events can be recognized (Hölldobler and Bartz, 1985; Boomsma et al., 2005): (1) female calling syndrome, where females stay at a certain site and try to attract males, (2) male aggregation syndrome, where males come together at certain sites waiting for and attracting females. Both types can exist in one species (e.g. Franks et al., 1991). The production of pheromones plays an important role to attract each other during these events (Ayasse et al., 2001). Mechanisms to enhance successful mating – especially in the male aggregation syndrome – are the production of large numbers of sexuals (Brian, 1979; Hölldobler and Wilson, 1990) and the synchronous release of winged individuals from the nests (Kannowski, 1963; Hölldobler and Wilson, 1990). A third mechanism is the aggregation of winged ants at certain sites (Chapman, 1954; Marikovski, 1961; Woychiechowski, 1990). During nuptial flights a single or several of these strategies can be exploited and this can vary for different species.

The occurrence of these mechanisms remain fragmentary and poorly known at the species level (Hölldobler and Wilson, 1990). In this paper, the temporal and spatial patterns of nuptial flights of six ant species are

explored at a forest – forest edge – agricultural field transect. We studied whether the alates of these ant species (1) had a restricted flight season (time of year during which alates display nuptial flights), (2) displayed swarming behaviour (many individuals occurring on the same moment), and (3) aggregated at the forest edge. In this way, more insight is obtained in the differences in reproductive behaviour between several co-existing species and a better understanding is gained in the possible effects of landscape features on the occurrence of species.

Material and methods

Study location

At a location near Wageningen (51°58′ N, 5°39′ E, province Gelderland, the Netherlands) a forest, the bordering agricultural grassland and the transition between these habitats were sampled. Each of the three habitats will be referred to as a 'site' during the remainder of this paper.

The tree layer of the forest is approximately 20 m high and is dominated by *Quercus robur*. Other species occurring in the tree and shrub layer are: *Betula pendula, Corylus avellana, Sorbus aucuparia* and *Prunus serotina*. In the herb layer species like *Athyrium filix-femina, Dryopteris dilatata* and *Holcus lanatus* can be found. The forest edge is facing south by southeast and is situated around a ditch and consists of a row of *Alnus glutinosa* trees. This forest edge is sharp and straight and *Rubus caesius, Humulus lupulus, Arrhenatherum elatius* and *Holcus lanatus* are abundant. The agricultural grassland consists of a *Lolium multiflorum* monoculture with sparse occurrence of other plant species. This grassland was mowed three times during the studied period, during two of which the window traps needed to be removed for several days. Manure was injected in early spring before sampling started and after each mowing event.

Measuring ground activity of workers

Ten pitfall traps were used at each of the three sites to measure worker activity. We assume that gradients in worker activity across the sites reflect underlying nest density. The traps were made of a test tube with a diameter of 15 mm and a depth of 120 mm (modified from the description in Majer, 1978), filled with a raspberry/cherry wine (12% alcohol) to attract ants. The traps were placed in the ground at the forest edge (0.1 m into the edge vegetation), 15 m into the field, and 15 m into the forest. Within each site, the traps were spaced 8 m from each other and placed close to the window traps (see below). The test tube traps were open from August the 6th (9:00 AM) until August the 9th (9:00 AM) 2006.

Measuring flight activity of alates

Window traps were used to collect flying ants (Fig. 1, modified from the description in Duelli et al., 1999). The traps were placed with a distance of 8 m from each other in each of the three sites: at the forest edge (0.5 m from the tree branches), 15 m into the field and 15 m into the forest. A trap consists of a wooden framework containing a transparent plexiglass pane of 80 by 60 cm, vertically fixed with its lower side 1 m above ground level. Below each pane, a plastic gutter was placed protruding 8.9 cm on each side. These gutters were half filled with a saturated salt solution. Both in the field and in the forest edge ten window traps were placed, alternately with a parallel and perpendicular orientation towards the forest edge (Fig. 1). In the forest six alternately positioned window traps were operative. This lower number is due to the fact that the setup was initially intended for a study sampling field inhabiting flying ground beetles. In that study the window traps in the forest merely acted as a control to establish whether flying ground beetles entered the forest at all.

Field observations revealed that straight flying small insects were not always effectively intercepted by the window traps. These insects were sometimes able to land on the pane or simply fly off. Probably especially descending insects end up in the gutters, additionally directed by the panes. Males do often not fly away after mating, as gynes do to find possible nesting sites, but 'fall' down (Hölldobler, 1976; Carlton and Goldman, 1984; Hölldobler and Wilson, 1990; P. Boer, pers. obs.). Thus especially when the window trap catches are male

Figure 1. The field location. Some of the window traps in the 'field' and in the 'forest edge' are depicted.

dominated, we expect them to provide a reliable indication of the mating location of ants.

The gutters of the window traps were emptied daily from April the 19th until October the 10th 2006 at approximately 9:00 AM (during the nuptial flight season of the recorded species this coincided with UTC+2 h). After October the 10th, the gutters were occasionally checked until December the 1st, but no more alates were found. Window trap catches from the same site were bulked and treated as one sample. All ants were identified to species level and their sex was noted. If more then 50 % of the total number of collected alates was caught on only one or two days, the species was considered to display a synchronous release of sexuals. Species with an observed flight season of less then one month, are considered as having a restricted flight season (Kannowski, 1963). The period between the first and the last catch of multiple sexuals on one day was considered the flight season, since the catches of single individuals might concern ants from other areas or decision errors of individuals (Kaspari et al., 2001b). From the 10th until the 17th of May and from the 22nd until the 26th of June, the window traps were temporarily removed during agricultural activities in the field.

Micro-climate measurements

To determine differences in micro-climate, six data loggers (Hobo RH/ T. H08-003-02) were attached to window traps; two per site. Every month, the data loggers were randomly redistributed among the traps. The data loggers measured relative humidity and temperature every 15 minutes. The average of both data loggers per site was used to determine temperature and relative humidity.

Statistics

The spatial distribution of ant workers (differences between sites) was analysed using G-tests for goodness of fit (with Williams' correction), assuming an even distribution of workers over the sites. The distribution of flying alates over the sites was tested against the distribution of worker ants (from the test tube traps), using logit analyses of proportions allowing for the difference in window trap number. For species not found in the test tube traps we used goodness of fit tests, assuming an even distribution over the sites and again allowing for the difference in window trap number. Two analyses were performed for species found in both the test tube traps and in the window traps. Firstly it was analysed whether the relative number of alates (compared to worker density) differed between the species' nesting site (either forest or field) and the forest edge. Secondly the same test was done between the nesting site and the remaining opposite site (field or forest). Sex ratios were analysed using goodness of fit tests.

Differences in temperature and relative humidity between the sites were analysed using Wilcoxon signed rank tests. In this analysis, only data from the actual period of nuptial flights were used, i.e. the 29th of May until the 1st of October.

Results

Species composition and sex ratio

A total of nineteen ant species was collected in the window traps (Table 1). Six species were found in sufficiently high numbers in the window traps for analyses: *Lasius niger*, *Lasius umbratus*, *Temnothorax nylanderi*, *Myrmica rubra*, *Myrmica ruginodis* and *Stenamma debile* (Table 1).

For these six species, sex ratios (number of ♂♂ divided by number of ♀♀) were found to significantly

Table 1. All ant species caught using 30 test tube traps and 26 window traps, including the number of worker and alate individuals. The species dealt with in this paper (caught in sufficient numbers by the window traps) are given in bold.

	test tube traps (# workers)	window traps (# alates)
Formica rufa L., 1758	–	1
Lasius brunneus (Latreille, 1798)	–	1
Lasius flavus (Fabricius, 1782)	–	9
Lasius fuliginosus (Latreille, 1798)	–	4
Lasius merdionalis (Bondroit, 1920)	–	7
Lasius mixtus (Nylander, 1846)	–	1
Lasius niger (L., 1758)	**82**	**205**
Lasius platythorax Seifert, 1991	33	5
Lasius umbratus (Nylander, 1846)	**–**	**154**
Myrmecina graminicola (Latreille, 1802)	–	1
Myrmica rubra (L., 1758)	**351**	**33**
Myrmica ruginodis Nylander, 1846	**69**	**209**
Myrmica rugulosa Nylander, 1849	–	1
Myrmica sabuleti Meindert, 1861	8	4
Myrmica scabrinodis Nylander, 1846	–	9
Ponera coarctata (Latreille, 1802)	–	1
Stenamma debile (Förster, 1850)	**–**	**83**
Temnothorax nylanderi (Förster, 1850)	**24**	**53**
Tetramorium caespitum (L., 1758)	–	1

Table 2. Observed sex ratios for alates caught by the window traps.

	♂	♀	sex-ratio (♂/♀)	Significance (d.f. = 1)
L. niger	176	29	6.06	G = 116.79, $P < 0.001$
L. umbratus	29	125	0.23	G = 64.28, $P < 0.001$
T. nylanderi	2	51	0.04	G = 55.91, $P < 0.001$
M. rubra	31	2	15.50	G = 30.20, $P < 0.001$
M. ruginodis	177	32	3.66	G = 51.37, $P < 0.001$
S. debile	65	18	3.61	G = 28.09, $P < 0.001$

deviate from 1, with the catches of *L. umbratus* and *T. nylanderi* dominated by gynes and the catches of the other species dominated by males (Table 2).

Temporal patterns of nuptial flight: Restricted flight season and swarming behaviour

The flight season of the six ant species fell from the end of June until the end of September (Fig. 2, disregarding days on which only one sexual was caught). *Lasius umbratus* had a very long period in which nuptial flights occurred, it might even have been slightly longer, but from the 22nd until the 26th of June no observations could be made. Also *T. nylanderi* had a relatively long flight season. On the other hand, *L. niger* displayed a relatively short flight
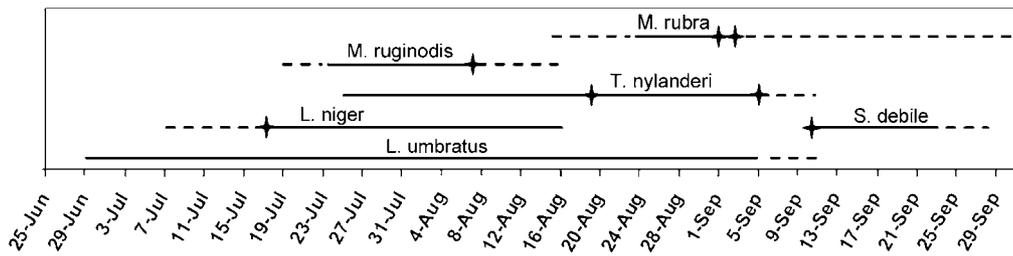
Figure 2. The occurrence of alates of the six ant species at the sampled location in 2006. Dashed lines represent the period in between the first catch of one individual and the first catch of several individuals or between the last catch of several individuals and the last catch of one individual. The solid lines, considered here as the flight season, represent the period between the first and the last catch of several individuals. The vertical marks represent the day on which > 50 % of the alates was found, when two marks are given these days make together > 50 %.

season of exactly one month. *Myrmica rubra*, *M. ruginodis* and *S. debile* showed a short peak, between 1 and 2 weeks, in alate emergence. These results are not caused by sampling artefacts, since *M. ruginodis* (short flight season) was caught with the most individuals and *T. nylanderi* (long flight season) was collected in the lowest abundance. The related *M. rubra* and *M. ruginodis* had a distinct non-overlapping flight season.

Within their flight season, for all species except for *L. umbratus*, more than 50 % of the alates were caught on only one or two days (Fig. 2).

Worker activity

Six ant species were collected in the test tube traps (Table 1). In total, four species were sampled in the forest (352 individuals), four at the forest edge (126 individuals), and three in the field (89 individuals). In the forest *M. rubra* and *M. ruginodis* were the most abundant species. In the edge the samples were dominated by *M. rubra*. In the field *L. niger* was very dominant, with only a few individuals of two other species.

In Figure 3 (grey symbols) the relative amount of collected workers is given across the field – edge – forest transect. Of the six collected species in the test tube traps, four concerned workers of the six studied species: *L. niger*, *T. nylanderi*, *M. rubra* and *M. ruginodis*. Of all four species the occurrence of workers over the sites deviated highly significantly from an even distribution (all d.f. = 2, $P < 0.001$).

Two of the six species were not found in the test tube traps: *S. debile* and *L. umbratus*. In the Netherlands, *S. debile* is a forest species (Van Loon, 2004), so we may assume nests of this species to be most abundant in the forest site. *Lasius umbratus* is a social parasite in nests of *Lasius* s.s. species (Dekoninck et al., 2004). At our location possible hosts are *L. niger* (highest worker activity density in the field) and *L. platythorax* (highest worker activity density in the forest, data not shown). From this, *L. umbratus* might be expected to have the lowest nest abundance in the forest edge.

Spatial pattern of nuptial flights: Aggregation at the forest edge

For four out of the six studied species, highest alate abundance was found at the forest edge (Fig. 3, black symbols). All four species of which workers were caught showed a occurrence of alates over the sites that differed significantly from the worker distribution (d.f. = 2, $P < 0.001$ for all species). Each of these showed a significantly higher alate abundance at the forest edge than would be expected from the occurrence of workers (Fig. 3): *L. niger* (log-odds ratio = 3.052, $P < 0.001$), *T. nylanderi* (log-odds ratio = 3.698, $P < 0.001$), *M. rubra* (log-odds ratio = 3.565, $P < 0.001$) and *M. ruginodis* (log-odds ratio = 3.055, $P < 0.001$). For three of these, alates were also found in significantly higher relative abundances in the habitat 'opposite' to their nesting habitat: *L. niger* in the forest (log-odds ratio = 3.810, $P < 0.001$), and *M. rubra* (log-odds ratio = 3.584, $P = 0.009$) and *M. ruginodis* (log-odds ratio = 4.246, $P < 0.001$) both in the field (Fig. 3). *Temnothorax nylanderi* did not have a high relative alate number in its 'opposite' habitat (log-odds ratio = 0.936, $P = 0.64$).

The alates of the two species of which no workers were caught, *S. debile* (a forest species) and *L. umbratus* (highest nest density most likely not in the forest edge), were not distributed evenly over the sites (G = 63.54 and G = 74.48 resp., both d.f. = 2, $P < 0.001$, Fig. 3). Both species showed a higher abundance of alates at the forest edge when compared to both the forest (*L. umbratus*: G = 61.62; *S. debile*: G = 17.37; both d.f. = 1, $P < 0.001$) and the field (*L. umbratus*: G = 15.03; *S. debile*: G = 71.76; both df = 1, $P < 0.001$) (Fig. 3).

Micro-climatic conditions

As expected, temperature was lower in the forest compared to the edge (Z = – 26.55, $P < 0.0001$) and the field (Z = – 30.16, $P < 0.0001$). Also, temperature at the forest edge was higher then that in the field (Z = – 7.885, $P < 0.0001$). Expected patterns were found for relative humidity as well: in the forest it was higher than at the edge (Z = – 46,49, $P < 0.0001$) and in the field
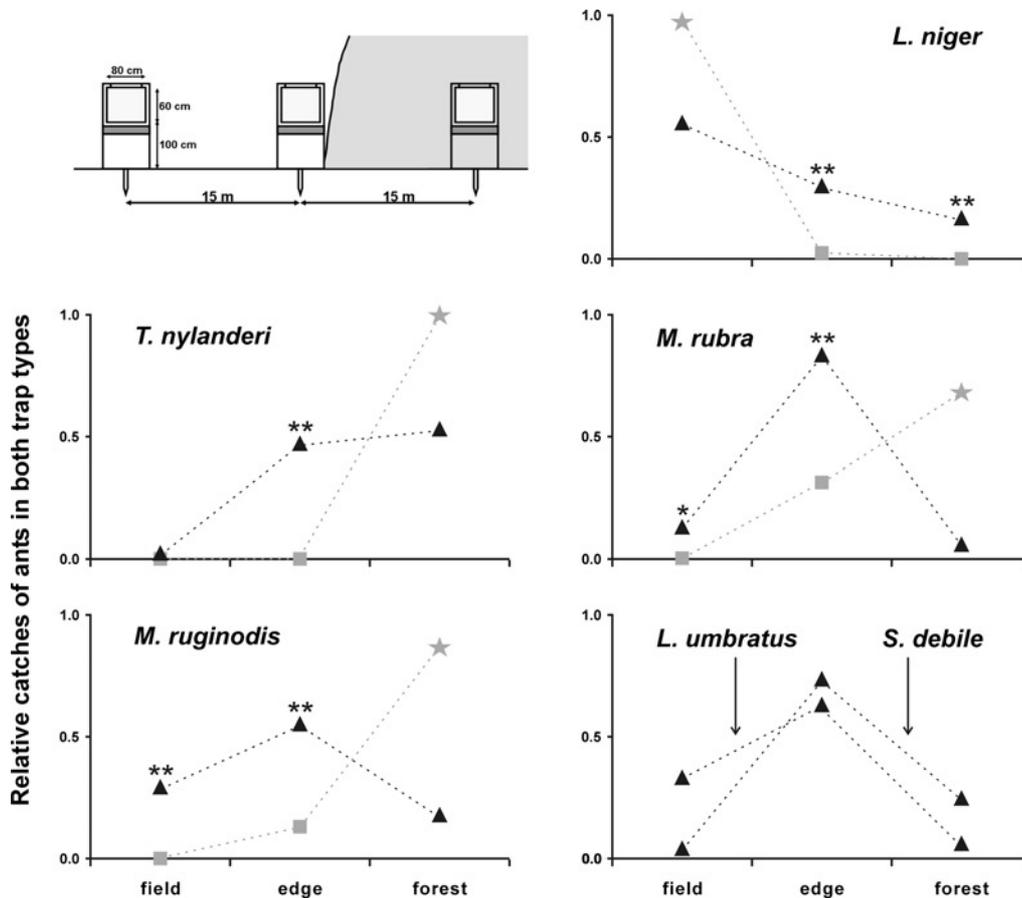
Figure 3. Results from the window trap and test tube trap catches. In the upper left corner a schematically representation of the experimental set-up; the window traps, test tube traps, forest, and relevant distances and sizes are depicted. The other graphs show the relative distribution of the species over the test tube traps (grey symbols) and the window traps (black symbols). The main nesting habitat of the species is indicated by a grey star. Dotted lines between the data points are merely placed to emphasize the patterns. Significance asterisks indicate that in that particular habitat more alates were observed than would be expected from the workers (always tested against the main nesting habitat). *: $P < 0.01$, **: $P < 0.001$.

($Z = -45.20$, $P < 0.0001$). The edge had higher relative humidity than the field ($Z = -2.978$, $P = 0.003$).

Discussion

Sampling methods

Whether test tube traps are appropriate for sampling sufficient numbers of species and individuals, largely depends on the aim of the study. They seem very satisfactory for rapid biodiversity assessments, as they collect all abundant species with ground active workers (Majer, 1997; Borgelt and New, 2006). In our study this proved to be the case: all species with ground active workers that were abundant in the window traps, were also sufficiently caught by the test tube traps. Of the two species that were not collected in the test tubes, the workers of *L. umbratus* live entirely subterranean in symbiosis with root aphids (Czechowski and Rotkiewicz, 1997) and *S. debile* forages mostly underground or in the litter layer with a small home range (Buschinger, 1999).

More intensive sampling with pitfall traps would most likely not have changed the results. In contrast, window traps are suitable to sample abundant species in the airspace around the traps including sexuals of subterranean species.

Types of nuptial flight and sex-ratio

For species with a male aggregation syndrome, the sex ratio is male biased at the reproduction sites. After mating, females fly off to possible nest sites (Seifert, 2007), males however do not move away from these sites (Hölldobler and Wilson, 1990) and therefore have a higher chance of ending up in traps if these are located on the reproduction site (Woyciechowski, 1987, 1990, 1992). Species caught with significantly more males at the study location most likely mate there. The catches of *M. rubra*, *M. ruginodis*, *L. niger* and *S. debile* were all male biased and for the first three species the male aggregation syndrome is known (Brian and Brian, 1955; Boomsma and Leusink, 1981; Woyciechowski, 1990, 1992; Boer,

pers. obs.). For *S. debile* the type of nuptial flight is not easy to describe. Buschinger (1999) found young queens in the nest with their mother; suggesting female calling behaviour, since it is unlikely that a gyne can find her home nest after swarming. Although swarming seems to be uncommon for *S. debile* (Buschinger and Heinze, 2001; Seifert, 2007), on the 10th and the 11th of September 47 and 18 alates respectively were found in the window traps (50 males and 15 females), indicating that the male aggregation syndrome occurs in this species as well.

The catches of *T. nylanderi* and *L. umbratus* were gyne dominated. This could be expected for *T. nylanderi*, since in this genus female calling behaviour is known to occur (Buschinger and Buschinger, 2003). Mating occurs around the nests in the forest, and afterwards only gynes fly off to find suitable nesting places. In other words, there are no 'falling' males to end up in the window traps. However, gyne dominated catches are not expected for *L. umbratus* which typically displays male swarming behaviour, and for which sex ratio's of flying alates are mostly male dominated (Boer, pers. obs.). This species is known to have meeting places high in the air, and possibly only gynes on their way to new nesting sites were intercepted by the window traps.

Temporal patterns in nuptial flight

Four out of six ant species, *L. niger*, *M. rubra*, *M. ruginodis* and *S. debile*, had a short flight season, which is in agreement with the statement of Kannowski (1963) that local populations in temperate regions have flight seasons of approximately one month (but see Dunn et al., 2007). The relatively long flight season of the other two species, *L. umbratus* and *T. nylanderi*, seems to contrast with this. The synchronous flights of *T. nylanderi* alates circumvents the disadvantages of a long flight season and may even turn it into an advantage. The combination of a long possible flight season but a synchronous alate emergence gives the ants a better opportunity to wait for the optimal circumstances for nuptial flights. The alates caught outside the swarming events might have made a decision errors or might originate from other areas and will have a lower possibility to mate (Kaspari et al., 2001b). The length of the flight season of alates appears to be partly determined by geography (latitude: Kaspari et al., 2001b; elevation: Dunn et al., 2007) and further studies of regional effects on flight season and other life-history traits are needed to gain understanding of this pattern. The non-overlapping flight seasons of *M. rubra* and *M. ruginodis* are interesting and might be evolved to avoid hybridisation. Other sites where both species co-exist should be investigated on this phenomenon.

A synchronous release of sexuals from different colonies is a very efficient way to promote outbreeding. Five out of the six species showed this synchronous release pattern, but none of these events coincided for the different species. This means that flight seasons and swarming events are initially dependant on the species in question. The flight season is affected by species' life-history traits and physiology, for example the period of production of sexuals, the moment of alate emergence from pupal cases, the time needed to create nest openings, and the size of the alates (Kannowski, 1963; Boomsma and Leusink, 1981). In the second place, specific meteorological conditions might trigger alate releases from the nest, most likely a combination of high soil temperature and warm and calm above ground conditions (Boomsma and Leusink, 1981; Depa, 2006). Analyses of our data on the occurrence of alates and prevailing meteorological circumstances indicate that most of the here presented species reacted to similar triggers (unpublished data).

Spatial patterns in nuptial flight

Although none of the species seem to have the highest worker activity at the sharp forest edge, four out of the six species showed here the highest abundance of sexuals. Alates of the opportunistic species *L. niger* were found in higher numbers than would be expected from the workers both at the edge and in the forest, so no aggregation at the forest edge could be proven for this species. For *L. umbratus* no swarming events and male aggregations could be found. The higher abundance of this species at the forest edge therefore need not be the result of nuptial flight aggregations. *Lasius* species are known to reach altitudes of 50 m or higher during nuptial flights (Duelli et al., 1989; P. Boer, pers. obs.), so the forest edge is too low to have influence on the nuptial flights of *L. niger* and *L. umbratus*. The observed abundance of *L. umbratus* at the forest edge is possibly caused by gynes on their way to find new nesting places (see Wilson and Hunt, 1966; Goodisman et al., 2000).

Temnothorax nylanderi alates were not found with highest abundance at the edge, but the number of alates was higher there than would be expected from the worker presence. This might be due to an 'indirect' effect: *T. nylanderi* alates were abundant inside the forest (the nesting site), and if these alates simply fly in a random way through the forest, there might be accumulation at the forest edge of individuals that are reluctant to leave their habitat. Alates of the other forest species, *S. debile*, had very low occurrence in the field site as well. This reluctance of gynes to enter non-nesting habitat has also been observed in other species (Wilson and Hunt, 1966).

For the other three species, *M. rubra*, *M. ruginodis* and *S. debile*, the combination of male dominated swarms and the high abundances at the forest edge indicates these species would seem to purposely aggregate here. Mating at aggregation sites is well known for other insects, both for other Hymenoptera (e.g. Alcock and Carey, 1988; Beani and Turillazzi, 2005), as for other insect orders, e.g. Lepidoptera, Ephemeroptera and Diptera (Downes, 1969; Allan and Flecker, 1989; Brown and Alcock, 1990).

There is an obvious reason for aggregation behaviour in ants: it enhances the chance of mate finding and is an appropriate way to avoid kin-mating (Woyciechowski, 1987; Seifert, 2007). Brian and Brian (1955) reported mating of *M. rubra* at the conjunction of an elevated structure and bare ground; males fly towards the structure and wait for females at the ground. All kinds of structures might provide in aggregation sites (e.g. Donisthorpe, 1927; Michener, 1960; Woychiechowski, 1990; Buschinger and Buschinger, 2003). However, it still is unclear how ants 'choose' places for aggregations. Kannowski (1963) observed that alates of day flying species often flew towards places with highest light intensity, and for the forest dwelling species this could explain the establishment of meeting sites at the southerly exposed forest edge. It has also been suggested ants can distinguish prominent features in the landscape and fly towards it (Collingwood, 1958; Seifert, 2007). As the results of the micro-climatologically data have shown, the temperature at the edge was highest and the edge had a higher relative humidity then the field, so this site could also provide more attractive conditions for nuptial flights (Boomsma and Leusink, 1981; Depa, 2006). On the other hand, it is also possible that the observed aggregations are simply directed by accumulations of ants, and consequently pheromones, due to the effects of a physical transition (also influencing wind direction, turbulence, etc.).

Conclusion

With the exception of *L. umbratus*, we could establish at least one behavioural strategy for the species at our study location to increase the chance of finding a mate (Table 3). Especially the behavioural deviations at the forest edge will affect the species. Firstly, this implicates that for ants not only the quality of nesting habitat is important for the completion of life-cycles, but the physical structure of the area as well. Secondly, the reluctance of the sexuals of *S. debile* and *T. nylanderi* to leave their habitat, indicates that habitat fragmentation will lead to dispersal and colonisation limitations for these forest ants. Thirdly, the aggregations at the forest edge might explain differences in nest densities in heterogeneous habitats. The closer a place is to an aggregation site, the higher the chance fertilized females will land here and try to initiate a colony after a nuptial flight. These findings are important for distribution, population and conservation studies on ants.

Acknowledgements

Table 3. Observed strategies in alate nuptial flight for the studied species: restricted flight season (≤ one month), swarming behaviour (synchronous occurrence of > 50 % of the alates during one or two days), and aggregation at the forest edge.

	restricted flight season	swarming behaviour	aggregations
L. niger	+	+	
L. umbratus			
T. nylanderi		+	
M. rubra	+	+	+
M. ruginodis	+	+	+
S. debile	+	+	+

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