

Impacts of red wood ants *Formica polyctena* on the spatial distribution and behavioural patterns of ground beetles (Carabidae)

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Summary

The aim of this study was to examine the effect of red wood ants *Formica polyctena* s.l. Foerst. on the spatial distribution of carabids and describe mechanisms of the ant-beetle interactions at the individual level. Fifteen carabid species were found in the foraging territory of an ant colony. The difference in the numbers of carabids in ant-controlled and ant-free territories was maximal in July, when the ants were most active. Measurements of running speed, duration of stops, and individual trajectories showed significant alterations in the behaviour of beetles in the ant-controlled territory. Experiments with a binary Y-shaped labyrinth showed that different carabid species used species-specific sets of behavioural tactics for avoiding conflict with ants. *Pterostichus magus* and *P. oblongopunctatus*, which are comparable with red wood ants in body length and speed of movement, possess the most effective stereotyped tactics in combination with a flexible behaviour. Such properties allow these species to penetrate ant foraging territory and partly avoid interference competition.

Key words: Red wood ants, carabids, patchy habitats, spatial distribution, interference competition, behavioural tactics

Introduction

A spatial texture of habitats helps to support diverse species assemblages in a landscape. The presence of environmental “grains” generates a patchy habitat structure, increasing regional species richness (Haydon & Pianka 1999). Habitat patches may include mountaintops, areas of forest of certain age, forest gaps, or even individual trees or anthills. Engineering species, such as beavers and ants, can increase landscape-level heterogeneity, creating patches with a peculiar combination of environmental conditions (Laakso & Setälä 1997; Wright et al. 2002). On the other hand, within their large feeding territories the

ants may create “black holes” in the habitat, i.e. areas that are highly dangerous for other species, where intruders can be killed or at least injured.

The settlements of red wood ants may affect the availability of space and resources for many invertebrate species, including litter-dwelling predators like Carabidae, Lycosidae and Staphylinidae. In fact, a significant decrease in dynamic density of spiders was found within the territory of a super-colony of *F. lugubris* Zett. (Cherix & Bourne 1980). Within large settlements of *F. aquilonia* Yarrow, the total density and biomass of litter predators was decreased half as

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great in comparison to control plots (Suvorov 1994). The abundance of Arachnids and Opiliones was reduced in a mesocosm experiment with *F. aquilonia* (Laakso 1999). Ants may act as a factor of disturbance, forcing other litter predators away from their territory. The reduction in predator abundance in the ant territory may therefore be due to interference competition (Halaj et al. 1997; Hawes et al. 2002). There is evidence that ants come into direct collision with other predatory invertebrates dwelling in litter and on the soil surface. Kölbe (1969) demonstrated that a decline in carabid abundance in proximity to a wood ant nest was due to direct attack by worker ants, suggesting that the interaction may be interference rather than exploitation competition. It was also shown that ants of the subgenus *Formica* s.str. were able to distinguish different species of competitors by their walking patterns (Reznikova 1982). Observations of the foraging activity of wood ants in the field and in the laboratory indicated that although adult carabids were attacked, wood ants did not eat them (Hawes 1999). Detailed mechanisms of possible interference interactions between wood ants and carabids are still poorly known.

Carabids seem to be appropriate group for studying the interference competition between ants and other arthropods. Both ants and carabids are generalist predators of comparable size and are very abundant in forest habitats. Habitats with high wood ant density often have low levels of carabid abundance and reduced species richness (Niemelä 1990; Gridina 1990; Rybalov et al. 1998). A decrease in prey abundance or direct predation by ants seems to be insufficient to explain this effect. It was shown that overall abundance of potential prey of carabids (e. g. earthworms) might remain high in the ant territory (Laakso 1999). It is also known that predatory arthropods themselves play a minor role as prey of ants (Cherix & Bourne 1980; Sergeeva 1982; Pollet & Desender 1987; Halaj et al. 1997).

The aim of this study was to examine the effect of red wood ants on the spatial distribution of carabid beetles and to describe mechanisms of their interactions at the individual level.

Materials and Methods

Spatial distribution of carabids on the ant foraging territory

The investigated settlement of *Formica polyctena* s.l. Foerst. was situated in a mixed pine-birch forest and comprised about 100 anthills. The control area was located in the same forest but separated from the settle-

ment by a motorway and therefore almost completely ant-free.

The spatial distribution of carabids in different parts of the ant foraging territory with different levels of ant dynamic density was studied in 1998. Thirty pitfall traps (plastic beakers 7.5 cm in diameter, by the depth of 10 cm) were placed in each of three zones with decreasing levels of ant abundance: immediate vicinity (4–5 m) of an anthill (zone 1); intermediate zone: 10–20 m from the anthill and 0.5–1.5 m from the nearest ant foraging trail (zone 2); periphery of the ant feeding territory: 10–12 m from the nearest foraging trail (zone 3). The traps were exposed from 10 to 20 June and checked every day.

The seasonal dynamics of carabid populations on the periphery of the ant foraging territory (zone 3), in comparison to the control ant-free area, was studied in 2000. Fifteen empty traps were placed at the corresponding sites and exposed for 21 two-day periods between 26 April and 29 July (8 periods in April, May, 8 in June and 5 in July). In order to estimate a seasonal trend in the dynamic density of ants, 15 additional traps containing weak alcohol were exposed at each site for a two-day period in May, June and July. In order to avoid depletion of the beetles during frequent registrations, they were caught alive and released in the same day and at the same place after identification and counting. For short-term registrations of the ants, we used the additional traps with weak alcohol at the bottom because, unlike beetles, ants used to get out of empty traps.

The numbers of beetles collected in the different parts of the ant settlement were compared by means of one-way ANOVA. Dynamic densities of carabids on the periphery of the ant territory and at the ant-free site were compared by *t*-test.

Characteristics of carabids movements in the presence and absence of ants

In order to examine whether predatory carabids change their behavioural patterns in the presence of ants, we recorded quantitative characteristics of movement of 53 individually marked beetles: speed of movement, time spent on stops and crookedness of trajectories.

The first two parameters were compared for beetles placed in the ant territory (close to foraging trails in zone 2) and in ant-free laboratory arenas. We used 30 × 25 × 10 cm plastic arenas covered by litter, which was taken from the immediate vicinity of the field experimental plots. Laboratory observations were conducted by the daylight. It is worth to note that the beetles walking in the arenas and in the ant-free field plots demonstrate the same “walking patterns” (in a sense

of: Lövei & Sunderland 1996). The availability of prey for beetles was null in the arenas and sensibly null in the field plots because of the very high density of ants scaring other invertebrates away. All these allowed us to consider the difference observed in carabid behaviour between the arenas and the ant territory as caused by the presence of ants. Five specimens of *Carabus regalis* F.-W., 5 of *Pterostichus magus* Esch. and 5 of *P. oblongopunctatus* F. were tested. Beetles were collected by manual sampling and kept for one day before experiments in boxes with moist litter. Each beetle was tested five times in the control arena and five times in the ant territory for 5 minutes each time.

The values of the third parameter (trajectory crookedness) were compared in the field. Ten specimens of *C. regalis*, 17 of *P. magus* and 11 of *P. oblongopunctatus* were tested first in the control area and then near ant foraging trails within zone 2. Individual trajectories of the beetle movements were mapped and their behavioural patterns were recorded. Observations were conducted during the time of maximal overlapping of ants' and carabid's diurnal activity, namely, from 8 till 10 a.m. and from 5 till 9 p.m. To facilitate tracking of the beetles, plots with poorly developed grass cover and thin litter layer composed mainly of pine needles were chosen. Each individual was tested 5 times for 5 min with a 30-min rest interval after each test. A quantitative comparison of beetle trajectories was conducted by using an index of crookedness (Reznikova 1983), i.e. the ratio of the shortest distance between initial and final points to the actual length of a crooked path. Thus, highest index values (close to 1) correspond to a trajectory that is close to a straight line. The studied behavioural parameters for each tested species on the control plot and within ant settlement were compared by *t*-test.

The ability of beetles to avoid collision with ants

To examine the ability of carabids to avoid clashes with ants, simple Y-shaped labyrinths were used. One section was empty, while the other contained an active ant tied up by a thin thread. It had been shown in preliminary experiments that tethered ants attack and bite approaching beetles. In the main series of trials a beetle was placed at the entrance of the labyrinth, and subsequent events were recorded. To avoid the possible influence of smell tracking, the paper on the floor of the labyrinths was changed after each test. To exclude possible influence of preference for the left or the right section, control tests for all individuals were conducted in empty labyrinths, lacking any stimuli (30–40 runs per individual). For 145 out of 147 specimens no preference for left or right section was observed and

these beetles were used in the main experiments. In total, 31 specimens of *C. regalis*, 52 *P. magus*, 20 *P. niger* and 42 *P. oblongopunctatus* were used.

The ability of the beetles to avoid collision with ants was estimated as a ratio between errors and 'correct actions'. We defined the 'correct action' as a modification of behaviour that allowed the beetle to avoid a clash successfully. Such modifications included both avoidance of the dangerous section of the labyrinth and use of specific behavioural tactics (see below). Actions that resulted in clashes between insects were considered as errors. The beetles were collected in the forest, therefore some specimens may have had previous experience of contacts with ants, whereas the others may have had none. In order to minimize the influence of preceding experience, we recorded both correct and incorrect actions only since the first successfully avoided conflict with the ant onwards. For a majority of beetles this happened after 1–2 conflicts. The distribution curves for numbers of mistakes were compared by the Kolmogorov-Smirnov test (Polard 1977). In order to estimate species – specificity of sets of behavioural tactics, we compared, by pairs, numbers of cases when beetles of different species used different tactics, applying chi-square test (Stuart et al. 1999).

Results

Spatial distribution of carabids in the ant feeding territory

In 1998, six carabid species were trapped in the ant foraging territory. Only *C. regalis* was more evenly distributed over the ant territory, including zone 1, while the dynamic density of other carabids (*Pterostichus*, *Amara*, *Harpalus*) sharply decreased in the vicinity of the anthill (Table 1).

In 2000, 15 carabid species were collected on the periphery of the settlement and the same species number in the control area. According to the short-term registration, we have got evaluation data on trends of the dynamic density of ants. It increased considerably from May to June and July from 34 to 134 and 157 individuals per 30 trap-days. There was no significant difference in the dynamic density of majority of carabids in the ant foraging territory (zone 3) and ant-free control plot in April – May. At this time, the dynamic density of *A. nitida* was higher in zone 3 than in the control area. By contrast, in June and July a significantly lower ($p = 0.03$) number of carabids was found in the ant territory than in the control plot (Table 2). On average, the dynamic density of carabids in zone 3 was reduced by 39 and 62 % in June and July, respectively,

Table 1. Dynamic density of the carabids within different zones of *Formica polyctena* foraging territory (means±SE, individuals per 30 trap-days) and results of a one-way ANOVA test of the effect of the distance from anthill and foraging trails on carabid distribution: (1) immediate vicinity of the anthill and foraging trails, (2) intermediate zone, (3) periphery of the foraging territory

Carabid species	Zones			F
	1	2	3	
<i>Carabus regalis</i>	0.3±0.6	1.0±0.9	1.5±1.5	1.2 ns
<i>Pterostichus oblongopunctatus</i> and <i>P. magus</i> (together)	0	5.8±2.1	38.0±8.5	66.2***
<i>Amara nitida</i>	0	0.6±0.6	5.0±2.1	18.6***
<i>Harpalus smaragdinus</i> and <i>H. pygmaeus</i> (together)	0	0	2.5±1.6	9.0***

***P<0.001

Table 2. Dynamic density of dominant carabid species (mean±SE, individuals per 30 trap-days) in the peripheral area of the *Formica polyctena* territory (zone 3) and in the control ant – free area

	April–May (n=8)		June (n=8)		July (n=5)	
	Zone 3	Control	Zone 3	Control	Zone 3	Control
<i>Amara nitida</i>	5.5±3.4	1.6±1.3*	1.3±1.3	0.6±0.9	0.2±0.4	0.2±0.4
<i>Pterostichus magus</i>	5.8±2.9	10.5±8.3	16.1±4.8	28.9±9.7*	9.8±6.1	15.8±7.3
<i>P.oblongopunctatus</i>	2.8±1.7	2.5±3.1	6.4±3.6	8.9±6.3	0.2±0.3	0.4±0.8
<i>P. melanarius</i>	1.0±1.3	0.4±0.5	2.1±1.3	4.6±3.4	2.0±2.1	16.6±8.5*
Total Carabidae	17.1±7.4	16.6±11.9	29.0±6.7	7.4±13.9*	13.8±7.2	36.2±8.6*

* significantly different from the respective control, P<0.05, t-test; n, number of samples

as compared to the control plot. The decrease was mainly due to low numbers of *P. magus* and *P. melanarius* in the ant territory (Table 2). These two species dominated in June, July both in the ant territory and control plots. The species with relatively low densities (less than 3.0 individuals per 30 trapping days), for example *C. regalis* and *H. smaragdinus*, had similar densities at both sites.

Changes in carabid behaviour in the vicinity of ant foraging trails

The quantitative characteristics of the beetles' movements, as well as their behavioural patterns, changed considerably in the presence of ants. *C. regalis* did not attempt to avoid encounters with ants and changed the direction of movement only when directly attacked. Instead of manoeuvring, beetles of this species sharply increased speed of movement and shortened the stops (Table 3). Unlike *C. regalis*, *P. magus* and *P. oblongopunctatus* tried to manoeuvre among ants, and that resulted in a significant increase in the crookedness of

their individual trajectories (Table 3). In the presence of ants, the time spent on stops decreased significantly in *P. oblongopunctatus*, but increased in *P. magus* (Table 3). This may be explained by differences in their behavioural tactics: *P. oblongopunctatus* reduced time spent on stops and dodged individual ants, not interrupting its movement, while *P. magus* preferred to stop and wait until the way was clear.

The ability of beetles to avoid collisions with ants

The distribution curve for number of mistakes differed from a Gaussian curve with P<0.01 for *C. regalis*, *P. magus* and *P. oblongopunctatus* and P<0.05 for *P. niger*. In all species the distribution curve was bimodal. Two groups could be distinguished with P=0.05: the beetles that made mistakes in less than 35% of cases (such individuals were considered as effectively avoiding contacts) and in more than 65% of cases. An intermediate group was relatively small in all species (Table 4). One-way ANOVA showed significant differences in the relative importance of these groups in dif-

Table 3. Characteristics of the movement of carabids: speed (cm s⁻¹), length of stops in percent to the duration of observations (100 %, 5 min of observation) and the index of crookedness of trajectories in the vicinity of ant foraging trails and in control ant-free sites. Mean±SE, asterisks indicate significant difference from the respective control, *P<0.05; **P<0.01; ***P<0.001; t-test, n = 25

Carabid species	Site	Speed	Stops	Crookedness index
<i>Carabus regalis</i>	Control	7.1±2.2	20.0±6.5	0.85±0.05
	With ants	16.3±2.5***	5.8±6.3***	0.77±0.07
<i>Pterostichus magus</i>	Control	3.8±1.3	27.5± 8.5	0.87±0.03
	With ants	8.9±2.2***	38.0±10.6*	0.62±0.04***
<i>P. oblongopunctatus</i>	Control	4.8±2.0	11.5±6.8	0.84±0.06
	With ants	1.7±3.0***	5.0±1.5**	0.57±0.07***

Table 4. The proportion of specimens (%), which made less than 35 %, 35–65 % and more than 65 % errors in the labyrinth tests

Species	Number Of beetles tested	% of errors		
		< 35 %	35–65 %	> 65 %
<i>Carabus regalis</i>	31	45 %	16 %	39 %
<i>Pterostichus magus</i>	52	62 %	17 %	21 %
<i>P. niger</i>	20	45 %	20 %	35 %
<i>P. oblongopunctatus</i>	42	72 %	11 %	17 %

Table 5. Numbers of cases when beetles of different species used different tactics (1-5)* for avoidance of conflict with ants in the labyrinth tests.

Species	Behavioural tactics				
	1	2	3	4	5
<i>Carabus regalis</i>	0	1	8	8	4
<i>Pterostichus magus</i>	8	16	18	12	39
<i>P. niger</i>	1	2	5	3	2
<i>P. oblongopunctatus</i>	16	16	18	2	5

* (1) attempted to round the ant; (2) turned away after touching the ant with antennae; (3) turned away at a short distance (but not less than 1 cm) from the ant; (4) avoided the section with the ant; (5) stopped near the ant with legs and antennae hidden

ferent species ($F=2.95$, $P=0.035$). The percentage of the first group was maximal for *P. oblongopunctatus* and minimal for *C. regalis* and *P. magus* (Table 4).

Beetles that successfully avoided conflict with the attached ant demonstrated specific behavioural tactics, i.e.: (1) attempted to round the ant; (2) turned away after touching the ant with antennae; (3) turned away at a short distance (but not less than 1 cm) from the ant; (4) avoided the section with the ant; (5) stopped near the ant with legs and antennae hidden.

Besides these specific tactics, all beetles demonstrated protective behaviour in a case of collision, in particular eructation and/or excretion from pygidial

glands. Some beetles bit the ant, namely, 19.3 % of *C. regalis*, 7.7 % of *P. magus*, 16.6 % of *P. oblongopunctatus* and 30 % of *P. niger*.

Four species tested in the labyrinth seemed to use specific preference for definite sets of tactics, although the simplest tactic 3 was practically universal for all species (Table 5). For *P. oblongopunctatus* tactics 1 and 2 were preferable, i. e. during first tests all individuals of this species tried to round the ant but facing the threat of violence, they began to use tactics 2 and 3 after 3–6 runs. For *P. magus* tactics 2 and 5 were specific. Isolated instances of direct beetle-ant antennal contacts were observed in experiments with *P. magus*

and *P. oblongopunctatus*. *P. niger* and *C. regalis* which are much bigger than the ant, did not try to round it and rarely touched the ant with their antennae. They often turned away at some distance from the ant and avoided the section with the attached ant (the tactic 4). These beetles more frequently attacked and bit the attached ant. Comparing pairwise difference between four beetle species by chi-square test, we found that in all cases, with the exception of one pair (*P. niger* and *C. regalis*), computed statistical values (from 23.8 to 88.0) exceed the tabulated critical number (13.3 at significance level 0.01) and thus frequencies of use of different tactics certainly differ in all species. *P. niger* and *C. regalis* do not differ essentially by the set of tactics for avoidance conflicts with ants (the value of chi-square is 7.48).

Discussion

Comparison of character of spatial distribution of beetles in the ants' territory demonstrated that only *Amara nitida*, which differed significantly from the ants by the seasonal activity in the forest, for a short period had higher density in the ant territory than in the control area. The fact is that *Amara nitida* inhabits open fields, so it is a regular visiting species in the forest in spring, when the birch trees are without leaves. In May 2000, the ants were not fully active (the dynamic density of ants was ca 5 times less in May than in June and July), and *A. nitida* had a peak of seasonal activity in the forest plots. The early activation may permit this species to penetrate and exploit well-drained and heated places of the forest where the studied ant settlement was situated. In June and July all species clearly avoided the central part of the ant territory, and so did *A. nitida*. The significant decrease in dynamic density of carabid beetles in the ant territory during summer months implies the presence of negative interactions between ants and carabids. Though these interactions may include predation, exploitation competition and interference competition, the results of Kölbe (1969), Hawes (1999) and Hawes et al. (2002) suggest that interference competition is of primary importance.

The behavioural experiments and direct observations of ant-carabid interactions at the individual level revealed several tactics used by beetles to avoid direct encounters with ants. The sets of tactics differed in carabid species of different body size. The largest species studied, *C. regalis*, is an agile predator that actively explores large territories (Lövei & Sunderland 1996). *C. regalis* did not avoid individual encounters with ants but increased the speed of movement in sight of them. In combination with robust physical and

chemical defence, this might be enough for avoiding damage from ants. *C. regalis* was the only species tested that showed the ability to penetrate all zones of the ant feeding territory.

All other species attempted to avoid clashes with the ants. Average-sized carabids, *P. magus* and *P. oblongopunctatus*, evaded ant foraging trails, but were able to penetrate patches with low ant density within the ant territory. The main tactics differed in these species. *P. oblongopunctatus* actively manoeuvred between ants, even crossing their routs. Individuals of this species also tried to round the attached ant in the laboratory labyrinth. Individuals of *P. magus* preferred to stop and wait until the ants ran by. In the labyrinth they used mainly tactic 5, i.e. they stopped near the ant. In the control ant-free arenas, freely walking *P. magus* spent twice as much time than *P. oblongopunctatus* on stops. This suggests that the choice of tactic is underlined by certain species – specific behavioural features. It is worth of noting that for *P. oblongopunctatus* there might also exist an additional behavioural tactic, i.e. flight. In publications of European authors this macropteran species is mentioned as capable of using such a way to escape (Pollet & Desender 1987; Lövei & Sunderland 1996; Hawes et al. 2002). But, surprisingly, in the study region we never met it flying being in danger.

The small-bodied *Harpalus* and *Amara* are much more vulnerable to ants because of thin cuticle and sluggishness. On the other hand, these species inhabit deeper litter layers and have a flush streamlined body that provides a good protective shield for legs and antennae. According to our observations, these beetles could fall prey to an ant only if the latter managed to turn them upside down. Therefore, in the case of an encounter with an ant these carabids usually preferred not to move but rather „freeze“ and stow all appendages or hide themselves in litter as soon as possible.

Within each species studied, individual specimens differed in ability to avoid conflicts with ants. The laboratory experiments showed that many specimens were able to avoid conflicts very effectively, after the very first encounter with the tethered ant in the labyrinth. The proportion of such “capable” specimens differed strongly in different species (Table 4). This suggests that the species studied possessed different abilities to avoid collisions with ants.

In conclusion, red wood ants strongly affect the spatial distribution of carabids and change their behavioural patterns at the level of individual direct interaction. The carabids can apply species-specific sets of behavioural tactics for avoiding contact with the ants. The species that are comparable with red wood ants in body size and running speed (such as *P. magus* and *P.*

oblongopunctatus) possess the most effective stereotyped tactics in combination with a flexible behaviour. Such properties allow these species to penetrate ant foraging territory and partly avoid interference competition.

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