

No evidence for a dominance-discovery trade-off among *Formica pratensis* colonies (Hymenoptera: Formicidae)

Raúl JORDAN & Nico BLÜTHGEN

Abstract

The trade-off between behavioural dominance and resource discovery ability is known to be an important consequence of asymmetric interspecific competition in ant communities. This paper tested the hypothesis that such a trade-off occurs between nests from the same species in a population of wood ants, *Formica pratensis* RETZIUS, 1783, specifically between large nests as potential dominants and small nests as potential submissives. This hypothesis was refuted. Workers of smaller nests did not significantly locate baits faster than workers of larger nests when appropriately controlled for prior activity. Different reasons are discussed, and we suggest that the current level of intraspecific competition is too weak and colony density too low to promote the divergence of foraging strategies within this population.

Key words: Behavioural dominance, resource discovery, trade-off, intercolony competition, wood ants.

Myrmecol. News 10: 7-10

Raúl Jordan (contact author), Institut für Ökologie, Friedrich-Schiller-Universität Jena, Dornburger Straße 159, D-07743 Jena, Germany. E-mail: ameisenfuzzi@gmx.de

Dr. Nico Blüthgen, Lehrstuhl für Tierökologie und Tropenbiologie, Universität Würzburg, Biozentrum, Am Hubland, D-97074 Würzburg, Germany. E-mail: bluethgen@biozentrum.uni-wuerzburg.de

Introduction

The composition and the dynamics of local ant communities are shaped by different factors, such as resource size variation and parasitoids facilitating coexistence of ant species (FEENER 2000, LEBRUN 2005, LEBRUN & FEENER 2007), habitat complexity and resource composition (GIBB & HOCHULI 2003, GIBB 2005), and asymmetric interspecific competition (HÖLDOBLER 1986, SAVOLAINEN & VEPSÄLÄINEN 1988, HOLWAY 1999, BLÜTHGEN & FIEDLER 2004). Working with woodland ant communities, FELLERS (1987) postulated an evolutionary trade-off between resource-discovery and behavioural dominance. In a Maryland woodlot she found that the first species emerging at baits, though skilled in finding resources in advance of competitors, were submissive. They avoided encounters with other ants and did not withstand offences. Once the behaviourally dominant species (also termed encounter or extirpator species, WILSON 1971) located the baits, the discoverers vanished. Dominance rankings appeared to be inversely correlated with discovery rankings indicating an evolutionary trade-off between interference and exploitative competitive ability. This mechanism might facilitate the coexistence of species (FELLERS 1987, DAVIDSON 1998, ADLER & al. 2007). In this concept, both dominance and discovery abilities are regarded as intrinsic species-specific characteristics, largely independent of the nest density and proximity. In FELLERS' (1987) study, the speed of bait discovery was found to be independent of the nest distance for six out of seven species.

Behavioural dominance may be largely positively correlated with colony size (DAVIDSON 1998). Therefore, we hypothesized that a similar dominance-discovery trade-off may occur across colonies of different size within a species. A trade-off at the intraspecific level implies that small col-

onies are submissive and detect resources earlier than larger, dominant colonies. Therefore, species conventionally classified as being dominant such as wood ants (*Formica rufa* LINNAEUS, 1761 group), could contain intraspecifically submissive colonies. This study focused on the territorial and dominant wood ant *Formica pratensis* RETZIUS, 1783 and tested for the first time the hypothesis that the speed of resource discovery is inversely correlated with nest size.

Material and methods

Field work was carried out around Jena, Germany (50° 55' N, 11° 35' E, 155 m a.s.l., mean annual precipitation: 587 mm, mean annual temperature: 9.3 °C, Meteorological Station Friedrich-Schiller-Universität Jena). Twenty-seven *Formica pratensis* nests were studied, which belonged to different colonies, suggested by a distance of at least 300 m. Workers transmitted between neighbouring nests were immediately attacked confirming different colony-membership. Five nests were part of polycalic colonies. When they were excluded from the calculations, the conclusions stayed the same. Each nest was investigated once in May, once in June, once in July 2005. All 81 experiments took place during daylight hours (between 6 a.m. and 9 p.m.) and dry weather. When it started raining during an ongoing experiment, the experiment was aborted and repeated on another day of the same month. Each experiment was divided into three parts.

1. Trunk trail measurement: Most of the *F. pratensis* workers do not forage in randomly chosen directions away from their nest, but run along trunk trails (SEIFERT 1996). Twice before placing any bait and twice after the bait trial the number of ants per minute was counted run-

ning to and from the nest along trunk trails about two meters away from the nest-mound before the trunk trails split. These data were used for nest size determination. The temperature was measured 1 m above the nest-mound in shade.

2. Bait placing: The ants were baited with canned tuna fish in brine. Each bait consisted of approximately 4 g tuna served in a lightweight aluminium cup (diameter 3.7 cm). Eight baits were arranged around the *Formica* nest in each compass direction (north, north-east, east, etc.). In 1 m distance of the nest centre towards each direction, a metal ring (diameter 30 cm) was briefly placed on the ground. If a *F. pratensis* worker was already present in the area defined by the metal ring, the metal ring was placed another meter away from the nest in the same compass direction. This was repeated until no single *F. pratensis* worker was present in the area defined by the metal ring. When this condition was fulfilled, a bait was placed into the metal ring's centre and the metal ring was taken away. Thus, before any bait trial started, 8 tuna bait cups stood on the ground in 8 different celestial directions and in different distances from the nest centre with occasional trunk trails in between leading further away to some distant territory border. Every bait was at least 15 cm away from any used trunk trail.

3. Bait trial: Starting immediately after the last bait was placed, we counted the number of ants at every bait every 3 min for a total of 30 min (10 counts per trial per bait). Ants were only counted if they touched the inner side of the bait cup or the tuna. The disturbance of homing ants was minimised by always moving outside the chain of the eight baits and avoiding trunk trails. Three measures were taken from each trial: (a) bait distances from the nest centre, (b) discovered baits, i.e., the number of baits that was attended by at least one *F. pratensis* worker during the trial, and (c) discovery time, i.e., time until the first *F. pratensis* worker was recorded at a bait. The median value was taken for each nest, not considering undiscovered baits.

No nest was excavated to count its population. Relative nest size or activity was firstly given as maximum trunk trail traffic, i.e., the maximum number of workers per minute running towards and away from the nest along one trunk trail before any bait was placed at any time during the study. Secondly, each nest's total number of workers on all trunk trails per minute was recorded and adjusted to a specific temperature (25 °C) incorporating the overall relationship between temperature and traffic. Thirdly, nest-mound diameters were measured.

SPSS 13.0 for Windows was used for statistical analysis. In order to test differences between temperatures across three months ANOVA (ANalysis Of VAriance) was used. Differences between paired samples were analysed with Friedman-ANOVA. Pearson's correlation coefficient was used for linear correlations.

Results

Temperature-adjusted activities were highly correlated with the maximum trunk trail traffic (Pearson's $r = 0.801$, $p < 0.01$, $n = 27$), and with the nest-mound diameters (Pearson's $r = 0.697$, $p < 0.01$, $n = 27$). Likewise the maximum trunk trail traffic was highly correlated with the nest-mound diameters (Pearson's $r = 0.860$, $p < 0.01$, $n = 27$).

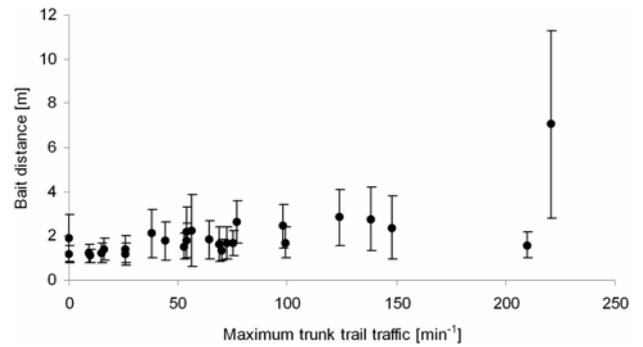


Fig. 1: Relationship between nest size (measured as maximum trunk trail traffic) and mean distance of valid baits from the nest centre among 27 nests of *Formica pratensis*.

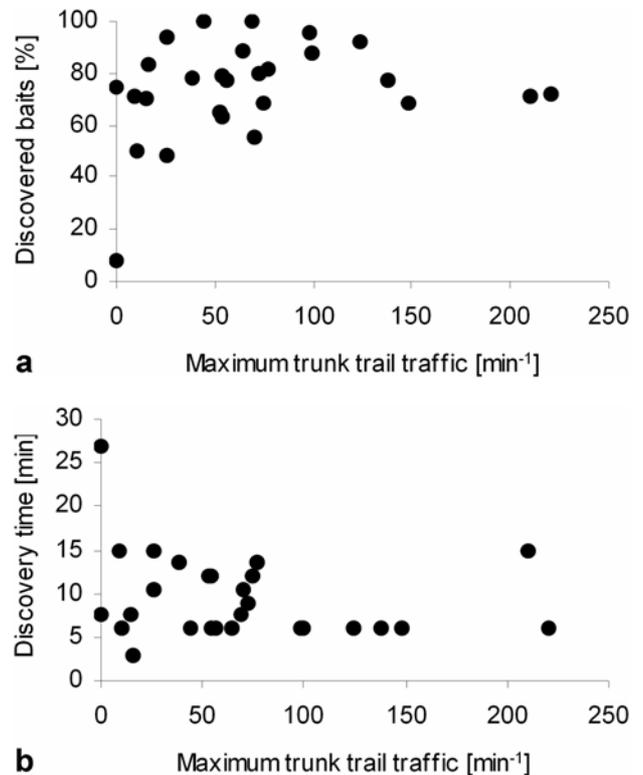


Fig. 2: Relationship between nest size (measured as maximum trunk trail traffic) and median proportion of (a) discovered baits, and (b) median time until first discovery among 27 nests of *Formica pratensis*.

Thus, all three measurements may represent an equally suitable surrogate of nest size. The maximum trunk trail traffic was chosen for subsequent analyses. All analyses were repeated with the two remaining surrogates of nest size, but conclusions were unaffected.

Bait distances from the nest centre were positively correlated with the maximum trunk trail traffic (Fig. 1) (Pearson's $r = 0.674$, $p < 0.01$, $n = 27$). Altogether 648 ($= 3 \times 8 \times 27$) baits were placed of which 97 were declared invalid and barred from further analysis, because 3 min after the bait trial had started already two or more *F. pratensis* ants were present, suggesting that ants may have been overlooked in the area defined by the metal ring during bait placing. In other words, invalid baits were likely placed too close to the nest, where worker density was still too

high and not comparable with the worker density around valid baits.

Of 551 valid baits, 402 were discovered within 30 min. The mean discovery time across colonies was 9.5 min (± 5.0 min s.d.). The number of ants at those baits discovered for the first time varied between 1 and 8 (mean 1.3, median 1), so that recruitment may have already begun at a few baits. Temperatures during bait trials were not significantly different across the three months (ANOVA: $F = 0.11$, $p = 0.89$). The temperature was neither significantly correlated with the percentage of the discovered baits (Pearson's $r = -0.19$, $p = 0.088$, $n = 81$) nor with the discovery time ($r = 0.157$, $p = 0.16$, $n = 80$). The percentage of the discovered baits per colony did not vary significantly across the three months (Friedman ANOVA: $\chi^2_{27} = 1.08$, $p = 0.58$), the same was true for discovery times ($\chi^2_{26} = 1.37$, $p = 0.50$). Hence, the discovery times of the three months could be combined into one value for each nest. The same was done with three proportions of the discovered baits. Across the 27 nests, the maximum trunk trail traffic (representing nest size or activity) did not significantly affect the percentage of baits discovered (Fig. 2a) (Pearson's $r = 0.23$, $p = 0.26$). Moreover, there was no significant effect on median discovery time (Fig. 2b) ($r = -0.22$, $p = 0.27$) or variability of discovery times per nest (quartile range, $r = 0.278$, $p = 0.161$).

Discussion

FELLERS' (1987) dominance-discovery trade-off was not found across colonies of the same species. The prediction that the speed of resource discovery is negatively correlated with the size of *Formica pratensis* nests was refuted. Although colonies differed in resource discovery time, this could not be attributed to colony size. Of course, larger nests covered overall greater foraging areas, confirmed by the positive correlation between trail traffic (surrogate of nest size) and distances of baits. The idea behind the bait arrangement was on the one hand to place the baits in large distances from the nest where the density of the ants was low enough to avoid bait flooding, i.e., the extremely fast discovery of the baits and subsequent worker mass recruitment. On the other hand, the density of the ants needed to be high enough to ensure the discovery of the baits within the trial. Thus, baits were placed further away from a populous nest covering a large foraging area compared to a less populous nest covering a smaller foraging area in order to ensure a comparable ant density. (However, note that distances usually varied within a small range, between 1 - 3 m, Fig. 1).

After controlling for worker activity in the way described above, no difference in bait discovery was found between small and large nests. Moreover, temperature, otherwise a substantive factor for activity in wood ants (HORSTMANN 1970, ROSENGREN 1977, SKINNER 1980, HORSTMANN & SCHMID 1986), provided no explanation for variation in bait discovery: workers of nests surveyed at low temperatures did not locate baits slower or faster than those from nests surveyed at higher temperatures.

Four reasons are suggested to explain why the dominance-discovery trade-off was not detected in *F. pratensis*:

(1) The dominance-discovery trade-off and the related dominance hierarchies may exist within some ant species, but not within *F. pratensis*. For example, ants might

display the trade-off when small colonies do not establish trunk trails at all but distribute their foraging workers evenly in all directions around the nest, while larger colonies establish trunk trails and rather ignore the area between these trails. The large colony may be more efficient in defending a limited number of rich food-sources than constantly patrolling the huge territory. In this case, small colonies may discover many small, ephemeral resources faster than large colonies. However, nearly all *F. pratensis* nests of our study sent out a large number of workers in all directions to maintain both trunk trails as well as sectors between trunk trails.

(2) The range of colony sizes chosen might be too limited to detect the trade-off. An effect may have been better revealed by comparing incipient and mature colonies, since incipient colonies of other ant species are known to compete severely with conspecific mature colonies (OSTER & WILSON 1978). When just founded, a colony's population is midget, rendering any dominance improbable. Whereas a populous colony copes with a possible loss of workers, an incipient colony might be destructed. Thus, a small colony size may require a timid, risk-aversing behaviour compared to mature ones, leading to differential foraging strategies.

(3) The mechanism might not work on an intraspecific level, because ant colonies are largely constrained by a stereotypical species-specific foraging behaviour. However, intercolony differences in foraging strategies have been reported (HÖLLDOBLER & CARLIN 1987). For example, HÖLLDOBLER (1976) discovered that some colonies of *Myrmecocystus* honey-ants were unable to sufficiently recruit workers to tournament areas and were consequently overrun by more populous colonies. Workers of the weak colony retreated to the nest trying to seal the nest-entrance before the stronger colony could start a baneful raid (HÖLLDOBLER 1984). Here, a clear intraspecific dominance hierarchy is demonstrated as well as changing foraging strategies depending on the opponent's size. Analogously, ADAMS (1990) found that the outcome of disputes among *Azteca* colonies depends upon asymmetries in strength between adjacent residents. The decision to attack or to withdraw was found to depend on the ratio of own nest-mates versus intruders. Such species could be more promising to detect intraspecific dominance-discovery trade-offs, especially in areas of high colony-density.

(4) One important difference between FELLERS' (1987) and our experiment was the size of the surveyed area and the density of focal ant colonies. In the interspecific study (FELLERS 1987), ant species were studied in a relatively small habitat where different species nested or at least foraged within the territories of the dominant ant colonies. Therefore, ant species interacted at the baits and were directly competing with each other. Thus, an interspecific dominance hierarchy may be shaped by active competition, forcing submissive colonies to improve their resource discovery abilities in order to coexist with dominants. In contrast, *Formica pratensis* colonies were widely scattered in the region studied here. Workers were never seen foraging within the range of other conspecific colonies. Between colonies a "no ant's land" was common, thus workers monopolised baits once discovered. No interactions with workers of other *F. pratensis* colonies were recorded at the resources. With intraspecific competition being large-

ly relaxed (or if ants occur in low densities as a consequence of past competition), foraging strategies may currently not be under pressure to be adjusted in response to hierarchically superior conspecific colonies.

If intraspecific trade-offs of foraging strategies are indeed uncommon among ant species, this would support an important assumption implied by FELLERS' (1987) interspecific dominance-discovery model: abilities of dominance and discovery are species-specific characteristics and thus more variable across than within species. This pattern should be particularly pronounced in ant communities where interspecific competition is stronger than intraspecific competition.

Acknowledgements

We thank Professor Stefan Halle, Professor Hans Joachim Poethke and especially Doctor Winfried Voigt for supervising this study and for enabling the cooperation between two universities. Two anonymous reviewers and the patient Editors gave important hints improving the manuscript.

Zusammenfassung

In einigen Ameisengemeinschaften wurde nachgewiesen, dass der Dominanzrang von Ameisenarten mit der Schnelligkeit der Entdeckung von Ressourcen in Folge asymmetrischer interspezifischer Konkurrenz negativ korreliert. Diese Studie testete die Hypothese, ob ein derartiger Zusammenhang auch innerhalb einer Ameisenart existiert, zwischen den Nestern einer Population von *Formica pratensis* RETZIUS, 1783. Volkreiche Nester würden den dominanten Ameisen und volkarme Nester den subdominanten entsprechen. Die Hypothese wurde widerlegt. Arbeiterinnen von kleineren Nestern fanden Köder nicht signifikant schneller als Arbeiterinnen von größeren Nestern. Verschiedene Gründe werden diskutiert. Wahrscheinlich ist die momentane intraspezifische Konkurrenz zu schwach und die Koloniedichte zu gering, um eine hierarchische Aufteilung der Fouragiersysteme innerhalb der Population zu erwirken.

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