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The chemistry of competition: exploitation of heterospecific cues depends on the dominance rank in the community

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Interspecific competition is an important ecological mechanism shaping the traits of the interacting species and structuring their communities. Less competitive species benefit from evading direct encounters with aggressive dominants, whereas dominant species could use cues left by subordinates to steal their resources or to chase them off. Here, we studied competitive interactions among five common and syntopic ant species in Central Europe (*Formica polyctena*, *Formica rufibarbis*, *Lasius niger*, *Myrmica rubra* and *Tetramorium caespitum*) and investigated their ability to react to heterospecific chemical cues. Using aggression assays, we established a clear dominance hierarchy of these species, with *L. niger* and *F. polyctena* as the most dominant species. Using Y-mazes, we then tested whether ants avoid or prefer areas with cues of either dominant or subordinate species. These cues included trail pheromones, cuticular hydrocarbons and chemical footprints. Ants of all species ignored heterospecific trail pheromone extracts, but two of the three subordinate species avoided cuticular hydrocarbons of the dominant species. In contrast, dominants either ignored or were attracted to cuticular hydrocarbon extracts of subordinates. The avoidance behaviour of the subordinates might be quantity-dependent, as footprints of the dominant species *L. niger* attracted two subordinates. The lowest ranking species *M. rubra* was unresponsive to cues of heterospecifics but avoided following the traces of their own colony members. Our study shows that ants exploit heterospecific cues either to avoid or to seek competitors and that their reaction depends on their dominance rank in the local community.

Interspecific competition is a widespread phenomenon that influences population dynamics and community structure (Dhondt, 2012; Gibb & Johansson, 2011), thereby exerting selection pressure on many species. This in turn results in the evolution of differentiated niches characterized, for example, by different habitat or diet requirements (Dayan & Simberloff, 2005; Stuart & Losos, 2013). Nevertheless, niches of co-occurring species often partially overlap, leading to competition, which can be indirect or direct. In the former case, a species exploits a shared resource without directly encountering the other species. However, heterospecific competitors often directly face each other in aggressive encounters (Bicca-Marques & Garber, 2003; Vonshak, Dayan, & Hefetz, 2011). The species with the best fighting abilities will dominate the respective resources and aggressively displace subordinate species (Rowland, 1983). To counteract the fitness costs of being outcompeted, subordinates need alternative strategies to be able to co-occur with dominants. Besides niche differentiation, subordinates often exploit visual (Hunter, Durant, & Caro, 2007), acoustic (Durant, 2000) or vibrational (Evans et al., 2009) cues to detect and avoid dominant competitors. However, indirect cues, such as chemical traces unintentionally left behind, have the advantage that they are more persistent than direct cues and can therefore indicate the prior presence of competitors (Kats & Dill, 1998). Such olfactory cues play an important role in antipredator behaviour of prey organisms (Binz, Bucher, Entling, & Menzel, 2014; Caro, 2005; Schmitz, 2008). However, their role in interspecific competition has been addressed by few studies to date, and they involved only two competitors at a time (Baudoin, Haim, & Durand, 2013; Polo-Cavia, López, & Martín, 2009). Like olfactory hunting predators that use chemical cues to detect and locate their prey (Hughes, Price, & Banks, 2010), dominant species could also seek subordinates via olfactory cues either to prey upon them (Carthey, Bytheway, & Banks, 2011; Schatz & Hossaert-McKey, 2010), to steal their food (kleptoparasitism: Creel, Sprong, & Creel, 2001; Nieh, Barreto, Contrera, & Imperatriz-Fonseca, 2004) or to displace them from their territory. Olfactory cues released by subordinates and/or dominant competitors could therefore influence interspecific competition and consequently, as in predator–prey interactions, affect community dynamics.

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In ants, interspecific competition is particularly pronounced (Parr & Gibb, 2012), as 'the worst enemy of an ant is another ant' (Forel, 1874, p. 452). Ant communities are usually structured into dominance hierarchies (Fellers, 1987; Parr & Gibb, 2010), with dominant species aggressively displacing subordinates from resources in direct behavioural interactions (Cerdà, Arnan, & Retana, 2013). Therefore, information on the taxonomic affiliation of an opponent can be of major importance for an ant species. However, interspecific competition in social species and especially in ants may depend not only on the respective species present at a site, but also on their relative abundance (Helfman, 1989). Owing to their diverse chemical communication system, ants are ideal to investigate the role of chemical cues in interspecific competition (Hölldobler & Wilson, 1990). These social insects use cuticular hydrocarbons to distinguish nestmates from non-nestmates, but they can also recognize other species based on their chemical profiles (Drescher, Feldhaar, & Blüthgen, 2011; Lang & Menzel, 2011), which are species-, colony- and often even caste-specific (Bagnères, Rivière, & Clément, 1998; Howard et al., 1982). By walking on receptive surfaces, insects unintentionally leave 'chemical footprints' behind, which are congruent to the individual's cuticular profile (Akino & Yamaoka, 2005; Devigne & De Biseau, 2012) and which can be detected by others (Cárdenas, Jiroš, & Pekár, 2012; Eltz, 2006). These chemical footprints should therefore contain reliable information on the recent presence and workforce of other species. For example, weak cues such as footprints indicate the presence of a few individuals, whereas more intense cues such as the extracts of cuticular hydrocarbons might mimic the presence of multiple individuals. Hence, subordinate species might display different responses to cues of varying intensity. Many ants also deposit pheromone trails to recruit nestmates to food sources, and these pheromones are usually species- or genus-specific (Czaczkes, Grüter, & Ratnieks, 2013). Ant workers of several species have been shown to detect heterospecific trail pheromones and to follow them to food sources (Menzel, Woywod, Blüthgen, & Schmitt, 2010; Morgan, 2009). If subordinate species were similarly able to read the trail pheromones of dominant species, they could use these chemical cues to circumvent competitive encounters.

Here, we studied the interactions among five common and sympatric ant species. We examined whether they react to chemical cues of competing species and whether their response is associated with their dominance rank. First, we determined the dominance hierarchy among the syntopic ant species. Then, Y-maze assays were used to test for the ants' responses to cues by dominants or subordinates. Cuticular hydrocarbon extracts, owing to their similarity to footprints, provide strong evidence for the activity of other species. We thus predicted that subordinate species should avoid cues of dominant species to prevent competitive encounters. Dominant competitors, in contrast, were expected either to ignore subordinates' cues, as they do not pose a threat, or even to be attracted by them in order to exploit the subordinate's food resources, to defend their territory or to prey on them. Our expectations about the response of subordinates to trail pheromones were similar to those for their response to cuticular hydrocarbons, albeit these cues might be less species-specific. Finally, we studied whether the lower quantities of dominants' footprints, in contrast to cuticular hydrocarbon extracts, induce a less pronounced response in subordinates.

METHODS

Study Organisms

We investigated interactions among five common and co-occurring species: *Formica polyctena* (Formicinae), *Formica rufibarbis* (Formicinae), *Lasius niger* (Formicinae), *Myrmica rubra* (Myrmicinae) and *Tetramorium caespitum* (Myrmicinae). All five species can have large colonies with between 1000 and 6 million workers, are widespread throughout Europe with overlapping habitats and food sources (Seifert, 2007) and use trail pheromones for mass food recruiting (Attygalle & Morgan, 1985; Beckers, Deneubourg, & Goss, 1993; Cammaerts-Tricot, Morgan, & Tyler, 1977; Cárdenas et al., 2012; Horstmann, Bitter, & Ulsamer, 1982). On a meadow near Mainz, Germany, we collected 10 colonies each of *F. rufibarbis*, *L. niger* and *T. caespitum*. In addition, 10 colonies each of *F. polyctena* and *M. rubra* were collected in a mixed forest 1.5 km from the first site. As *F. polyctena* is protected by law in Germany (BNatSchG § 41, 42), we could only obtain a permit to collect worker groups (300 ± 80 individuals/mound; Gestattungsvertrag 6./8.3.2012, local nature conservation authority, Mainz-Bingen, Germany). Workers from the mound's surface, which are known to be the older and more experienced workers (so called 'observer workers'; Savolainen, Vepsäläinen, & Wuorenrinne, 1989) were collected a day before the experiments. We dug up entire colonies of the other study species using spades, and transferred them to the laboratory. In some cases, we were only able to obtain the workers but not their queen. Queens were present in four of the 10 *T. caespitum* nests, four of the 10 *F. rufibarbis* nests and none of the 10 *L. niger* nests. For the strongly polygynous *M. rubra*, queen numbers ranged from one to 27 (median 5.5). As brood presence is known to influence activity and stimulate foraging (Ravary, Jahyny, & Jaisson, 2006; Vowles, 1952), all colonies (except of the *F. polyctena* worker groups) contained brood. Colony sizes of *F. polyctena* were calculated using a ground layer formula (provided by B. Seifert, Senckenberg Museum of Natural History Görlitz, Germany):

$$F.\ polyctena\ \text{colony size} = (0.414 \times \text{ground area in m}^2 + 0.119) \times 1\,000\,000 \quad (1)$$

For the other species, we counted all workers in the colonies after the end of the experiments. Colony sizes differed strongly between species and colonies (*F. polyctena*: $2\,602\,586 \pm 421\,782$ SE; *F. rufibarbis*: 1202 ± 240; *L. niger*: 1157 ± 169; *M. rubra*: 276 ± 42; *T. caespitum*: 2969 ± 555). Ant colonies were transferred to and kept in plastic nestboxes (17.5×23.5 cm and 9.5 cm high) with a periodically moistened plaster floor and original nest substrate (soil or plant material) covering half of the floor. Walls were coated with Fluon to prevent ants from escaping. At the side of each nestbox, a plastic tube (10×1 cm) was fixed at ground level which served as a connection to other arenas. All ants that participated in the experiments had deliberately left their nest and walked through the plastic tube. We therefore assumed that all ants we tested were scouting foragers. Ants were kept on a restricted diet (three drops of honey per day) to stimulate scouting activity.

Interspecific Aggression Assays

Aggression between species was measured by confronting the colonies of the different species with colonies of the other species. Each of the five species was confronted with all the other species in a random order, resulting in a total of 10 species combinations. For each species, every colony was confronted once with one of the other species, resulting in 10 replicates per species combination. For such a confrontation, nestboxes of two heterospecific colonies were connected to the same neutral 'arena' (11.5×17.5 cm and 7 cm high plastic box with Fluon-coated walls). The connections consisted of plastic tubes (10×1 cm), which were located at the opposite short sides of the arenas. We placed a bait (four drops of honey mixed with ca. 0.1 g of tuna) in the centre of the arena and