

Reaction of the territorial wood ant *Formica polyctena* Latreille to corpses of its neighbours

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Abstract: In ant colonies, the corpses of dead nestmates can serve multiple functions, including marking territorial boundaries, providing a supplementary protein source during periods of food scarcity, and exerting intimidating effects on potential competitors. To fulfil these functions, ant corpses need to be reliably recognized and discriminated, as different corpses may indicate different types and levels of threat. Corpse discrimination has been investigated in species occupying different positions within the dominance hierarchy, but remains unexplored in territorial species, such as wood ants. To fill this knowledge gap, here we investigated the responses to corpses of different types in the red wood ant *Formica polyctena* Latreille. Five experimental colony fragments were maintained under laboratory conditions and presented with five types of corpses: nestmates, conspecifics, *Formica fusca* Linnaeus, *F. sanguinea* Latreille, and *F. truncorum* Fabricius. Our results suggest that the studied wood ant species readily discriminates among different types of corpses. The most aggressive reactions were induced by the slave-maker *F. sanguinea*, followed by the conspecific, territorial *F. polyctena* corpses. The corpse removal rate of the subordinate *F. fusca* was substantial, suggesting that these corpses may function as prey items for the colonies. Corpses of *F. truncorum* elicited low levels of aggression but high levels of corpse-carrying, whereas responses toward nestmate corpses were minimal. Overall, our results suggest that the territorial and highly dominant wood ant *F. polyctena* is capable of discriminating among corpses of different origins and shows specific responses to them. These responses appear to be context-dependent and are shaped by intra- and interspecific competitive relationships.

Keywords: *Formica fusca*, *Formica sanguinea*, *Formica truncorum*, reaction to corpses, signal of threat, prophylactic behaviour, aggressiveness

INTRODUCTION

Eusocial insects, such as bees, wasps, termites, and ants, form strikingly complex societies, exhibiting sophisticated behaviours that, in many ways, parallel those seen in higher mammals, including humans (Hölldobler & Wilson 1990). Their social lifestyle, much like our own, offers substantial benefits while simultaneously creating challenges that must be addressed for colony survival. A major challenge arises from the spread of pathogens, facilitated by the high density and genetic similarity of colony members (Schmid-Hempel 1998; Cremer et al. 2007). To combat pathogens, social insects have evolved a wide range of behaviours that collectively constitute their “social immunity” (Cremer et al. 2007, 2018). Such behaviours include self- and allogrooming (Hughes et al. 2002; Reber et al. 2011), self-exclusion of infected workers (Heinze & Walter 2010; Bos et al. 2012), selective and risk-adjusted sanitary care (Konrad et al. 2018; Pull et al. 2018; Casillas-Pérez et al. 2023), or pathogen avoidance and dispersal inhibition (Pereira & Detrain 2020; Csata et al. 2026).

In addition to these behaviours, the disposal of dead individuals in insect societies is essential as corpses can

facilitate pathogen transmission (López-Riquelme & Fanjul-Moles 2013). This is particularly important in ants, which typically live in densely populated, enclosed underground nests. Consequently, many ant species engage in necrophoresis, the transport and removal of corpses to refuse piles (“cemeteries”) located either inside or outside the nest (Wilson et al. 1958; Bot et al. 2001). Although the primary function of necrophoresis is prophylaxis (Diez et al. 2012), a growing body of literature suggests that ant corpses may also serve additional roles, thereby providing a final contribution to colony functioning after death. Nestmate corpses can be utilized as supplementary protein sources during periods of food shortage, a behaviour known as cannibalistic necrophagy (Mabelis 1979; Driessen et al. 1984; Lőrincz et al. 2025). Moreover, based on the observations of Dlussky (1965), Gordon (1984) and Czechowski (1990), ant corpses might function as territorial signals, as they are frequently piled up along the boundaries of a colony’s territory. Corpses might also have a signalling function in other conflict situations. The slave-making ant *Formica sanguinea* Linnaeus has been observed transporting corpses to the entrances of nests belonging to its slave species,

F. cinerea Mayr, during raids (Czechowski 1977). Similar behaviours have been reported in other ant species as well, namely in *Lasius niger* Linnaeus (Czechowski 1985) and *F. rufa* Linnaeus (Czechowski et al. 2009). These studies suggest that corpse-carrying during raids or territorial conflicts may function beyond simple disposal, exerting an inhibitory or intimidating effect on opposing colonies and thereby influencing their defensive activity (Maák et al. 2024).

To function as signals during interspecific conflicts, ant corpses need to be reliably recognized and discriminated, as different corpses may indicate different types and levels of threat. The corpses of territorial or slave-making ants, for instance, might signal a serious threat, and thus elicit increased aggression, as was observed for the ant *F. cinerea* (Maák et al. 2014). Slave-making ants, such as *Polyergus rufescens* Latreille or *F. sanguinea* have also been observed to discriminate between corpses of nestmates, non-nestmate conspecifics, heterospecific slave makers, but also corpses of enslaved and non-enslaved hosts (Maák et al. 2016). These results indicate that ant corpses are not meaningless objects but serve as important information carriers during interspecific conflicts, and the ability to discriminate among them likely carries important fitness consequences.

Corpses might also function as information cues for territorial ant species. Red wood ants (*Formica rufa* group), for instance, are fierce competitors that fight extended wars with neighbouring conspecific or heterospecific colonies to establish territorial boundaries and relationships (Mabelis 1979; Czechowski et al. 2013; Adams 2016). The presence of conspecific corpses, or those of heterospecific territorial species, therefore, might indicate a potential threat, against which an increased aggressive response is expected to help protect the integrity of the territory. The corpses of subordinate species, on the other hand, are expected to elicit weaker responses, as the presence of their colonies does not threaten the territorial integrity of wood ants, but their presence can be important as a potential host during colony founding (Seifert 2007; Czechowski et al. 2012). Despite the increasing amount of information on corpse discrimination in ants, no studies have yet formally tested these predictions. In this study, we addressed this knowledge gap by investigating whether the territorial red wood ant species, *F. polyctena* Latreille, discriminates among corpses of different origins and whether these responses vary according to the potential competitive threat posed by the species represented.

MATERIALS AND METHODS

Study species and housing

Formica polyctena builds its large nests deep within temperate submontane coniferous, mixed, and deciduous forests, primarily using fine plant material (Seifert

2007; Czechowski et al. 2012). Its polygynous colonies often consist of several thousand queens and millions of workers. The species readily forms polydomous systems, and through its broad and extensive foraging trails it efficiently covers the forest floor, contributing to the homeostasis of these habitats (Czechowski et al. 2012). As a territorial and dominant ant species, it strongly affects other ant species occurring within its territory and significantly reduces the density of arthropods inhabiting the area. In addition to honeydew obtained through mutualistic relationships with aphids, a substantial part of its diet is acquired through predation and scavenging on animal carcasses (Seifert 2007; Czechowski & Vepsäläinen 2009; Czechowski et al. 2012).

Our five experimental colony fragments, each consisting of approximately 1000 workers and nest material, were collected at least 250 m apart from a planted Scots pine forest near Ásotthalom (southern Hungary) in May 2013. The colonies of the other species used during the experiment also originated from the same habitat. The collected colony fragments were housed in plastic boxes (44 cm × 31 cm × 23 cm). Each box had a circular opening (Ø 15 cm) covered with metal mesh to ensure adequate ventilation and facilitate watering of the colonies. Every experimental colony was connected via a 10 cm plastic tube to an arena made of transparent plexiglass (60 cm × 30 cm × 15 cm). Colonies were maintained under laboratory conditions with a 12-hour light cycle (from 7:00 a.m. to 7:00 p.m.), at a temperature of 22–25°C and relative humidity of 42–43%. Colonies were fed every other day with a commonly used laboratory ant diet (Bhatkar & Whitcomb 1970), which was placed at a fixed location within the arena on a plastic plate reserved exclusively for feeding. Water was supplied by moistening the nests once daily.

Study methodology and design

During our investigations, we used the corpses of nestmates (control), non-nestmates, the slave-maker *F. sanguinea*, the territorial rival *F. truncorum* Fabricius, and the potential slave-species, the submissive *F. fusca* Linnaeus. Corpses were obtained by carefully collecting individuals without injury using an aspirator and immediately placed in a deep freezer (<−18°C), thereby preventing changes in their CHC profile. The corpses were removed from the freezer two hours before the experiments. This time interval has been used in previous studies on *F. polyctena* (Maák et al. 2014, 2020, 2024), which is considered sufficient for the development of the characteristic corpse smell appearing on the cuticle surface (see Howard & Tscinkel 1976; Choe & Rust 2008; Choe et al. 2009). Before the experiments, 10 corpses from the same colony were placed on a plastic disc with a diameter of 10 cm. In each experimental setup, nestmate corpses served as controls.

Corpses of different species were placed on plastic discs positioned 20 cm from the entrance of the arenas. The order of experiments was randomised regarding the corpse type, meaning that every colony received

the corpses in a different order. The twenty 1-minute observation periods were conducted at 3-minute intervals. During the observations, we recorded the number of corpses on the plastic disc both before and after the one-minute observation periods, the number of workers present on the disc, and the behaviour of workers toward the corpses, categorized as follows: neutral behaviour, antennation, mandible opening, biting, carrying, and retreating behaviour (see Martin et al. 2009; Pamminger et al. 2011). Neutral behaviour was defined as a worker appearing on the disc without interacting with the corpses. Antennation was recorded when a worker approaching the disc began to “scan” the corpses with its antennae from a certain distance, without making direct contact. Mandible opening (aggressive behaviour) was recorded when a worker responded to the presence of corpses by opening its mandibles, often followed by flexing the gaster (formic acid spraying posture) and rapid circular running. In these cases, the worker also did not make direct contact with the corpses. Carrying behaviour was defined as a worker biting a corpse and moving it from its original position. Retreating behaviour was recorded when a worker rapidly backed away after antennating a corpse (Maák et al. 2014, 2016).

Statistical analyses

The effects of corpse origin (species) and other variables on the number of ant workers appearing on the plates was analysed using a generalized linear mixed model (GLMM; Poisson error term, maximum likelihood fit). In the full model, corpse origin was included as an explanatory factor, while the number of corpses

present on the plates at the beginning of the one-minute observation period (hereafter: corpse number) was included as a covariate, and colony ID was included as a random factor. Only those one-minute observations were included in the analyses when corpses were still present on the plastic plates.

The effects of corpse origin and other variables on the number of recorded behavioural responses during the one-minute observations was also examined using GLMM (binomial error distribution, maximum likelihood fit). For each one-minute observation period, we calculated an aggression index by dividing the number of aggressive behaviours observed by the total number of recorded behaviours (see Martin et al. 2009; Pamminger et al. 2011). In the full model, corpse origin was included as an explanatory factor, while the number of workers observed on the plates was included as a covariate, and colony ID was included as a random factor. Only those one-minute observations were included in the analyses when corpses were still present on the plastic plates.

Using a GLMM approach similar to the one described above (binomial error distribution, maximum likelihood fit), we investigated the effect of corpse origin on the workers’ decision whether to remove corpses from the plates or not. In this model, corpse origin was included as a categorical explanatory factor, while colony ID was treated as a random factor. The rate of corpse removal was analysed using Cox regression. In this model, corpse origin was included as an explanatory variable, while colonies were treated as a random factor.

All analyses were conducted in the R statistical environment (R Core Team 2026). GLMM analyses

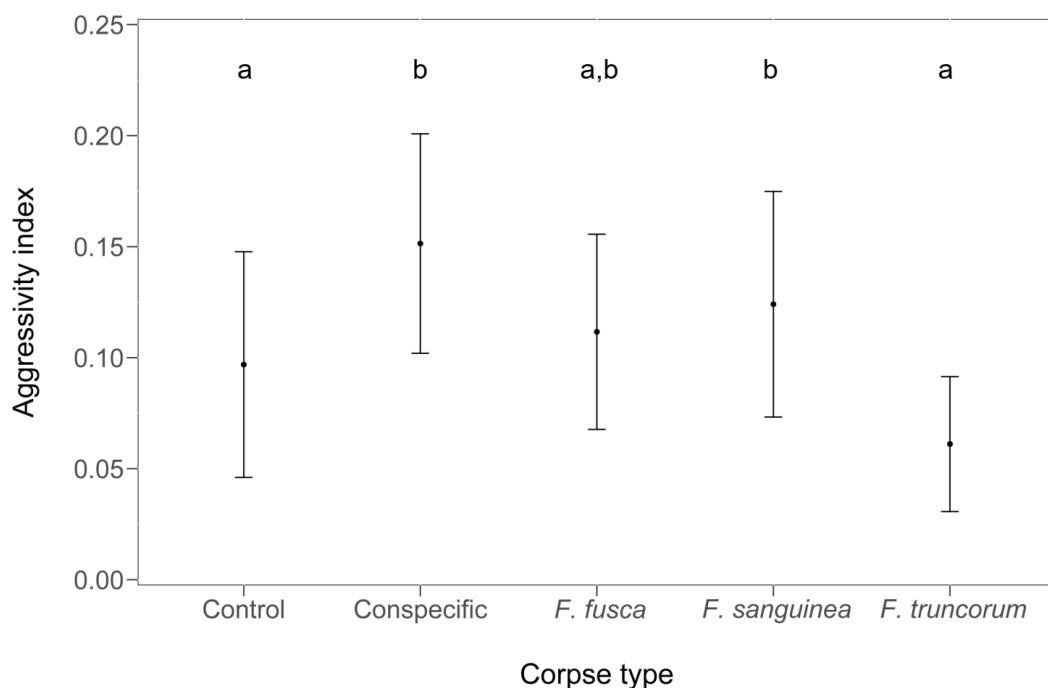


Figure 1. Aggression indices recorded in *F. polyctena* in the presence of corpses of different origin (means and 95% confidence intervals). Control - nestmate *F. polyctena*; Conspecific - non-nestmate *F. polyctena*. Different letters above boxes represent groups that differ significantly from each other.

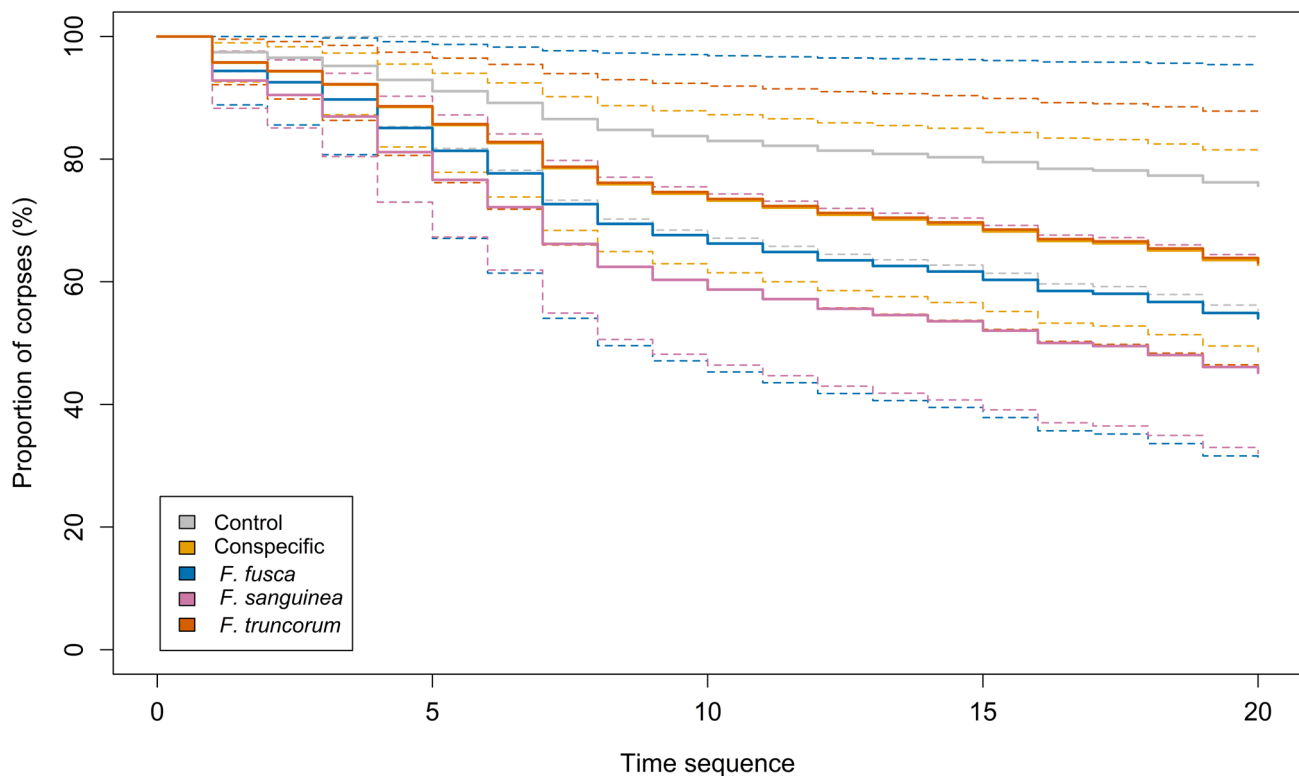


Figure 2. Estimated functions for Cox regression of time to corpse removal based on the origin of corpses in nestmate *F. polyctena* (control) and of other co-occurring *Formica* species. Conspecific – non-nestmate *F. polyctena*. Time sequence – 1-minute observation periods repeated at 3-minute intervals. Kaplan–Meier survival curves were generated for each treatment. Broken lines represent a pointwise 95% confidence interval around the corresponding functions.

were performed using the *glmer* function from the *lme4* package (Bates et al. 2015). Cox regression analyses were carried out using the *coxme* function from the *survival* package (Therneau 2024). To compare the different factor levels of the GLMMs (post-hoc: Tukey HSD), the *emmeans* function (*emmeans* package, Lenth 2026) was used.

RESULTS

The corpse type had a significant effect on the number of individuals that appeared around them ($\text{Chi}^2 = 76.93$, $p < 0.001$). The number of individuals around *F. sanguinea* and *F. truncorum* was higher than around the conspecific *F. polyctena* (*F. sanguinea*: $z = 6.42$, $p < 0.001$; *F. truncorum*: $z = 7.12$, $p < 0.001$) and *F. fusca* (*F. sanguinea*: $z = 5.16$, $p < 0.001$; *F. truncorum*: $z = 5.74$, $p < 0.001$) corpses. Significantly more individuals appeared around the nestmate (control) corpses compared to the conspecific *F. polyctena* ($z = 4.30$, $p < 0.001$) and *F. fusca* ($z = 2.98$, $p = 0.02$) corpses. In the other cases, we did not find any significant difference ($0.25 < z < 2.19$, $p > 0.18$). The number of corpses had a negative effect on the number of individuals appearing around the corpses ($\text{Chi}^2 = 4.78$, $p = 0.03$).

The corpse type also had a significant effect on the number of elicited aggressive responses ($\text{Chi}^2 = 16.36$, $p = 0.002$; Fig. 1). Higher aggressiveness was elicited by

the corpses of *F. sanguinea* compared to the nestmate *F. polyctena* (GLMM $z = 2.89$, $p = 0.03$; Fig. 1) and *F. truncorum* ($z = 3.31$, $p < 0.01$; Fig. 1). On the other hand, the corpses of the conspecific *F. polyctena* elicited a higher aggressiveness than those of *F. truncorum* ($z = 2.67$, $p = 0.05$; Fig. 1), and only a marginally significant compared to the nestmate corpses ($z = 2.52$, $p = 0.09$; Fig. 1). In the other cases, we did not find any significant difference ($0.06 < z < 2.06$, $p > 0.24$; Fig. 1). The number of individuals did not have any effect on the number of aggressive behaviours ($\text{Chi}^2 = 0.02$, $p = 0.89$).

The corpses of *F. sanguinea* were transported at a faster rate compared to the nestmate (Cox $z = 3.30$, $p < 0.01$; Fig. 2) and conspecific *F. polyctena* ($z = 2.85$, $p = 0.03$; Fig. 2) corpses. In the other cases, we did not find any significant difference ($0.38 < z < 2.37$, $p > 0.12$). Significantly more corpses of *F. sanguinea* (GLMM $z = 3.45$, $p < 0.01$) and *F. fusca* ($z = 2.88$, $p = 0.03$) were carried away from the plates compared to the corpses of nestmates. In the other cases, we did not find any significant difference ($0.52 < z < 2.09$, $p > 0.23$).

DISCUSSION

Among organisms living in high densities, such as eusocial insects, the appropriate handling of corpses is crucial, as they can pose a high risk of infection. However, an emerging number of studies suggest the im-

portance of necrophoresis and corpse discrimination beyond prophylaxis (Czechowski 1977; Czechowski et al. 2009; Sun & Zhou 2013; Lőrincz et al. 2025). Studies indicate that the precise recognition of living nestmates, non-nestmate conspecifics and heterospecific individuals functions with corpses as well (Renucci et al. 2011; Diez et al. 2013; Maák et al. 2014). Red wood ants, as territorial and aggressive ant species, play a major role in the dynamics of the ant assemblages incorporating them (Savolainen et al. 1989; Väänänen et al. 2010; Adams 2016). Thus, corpses of co-occurring ant species may serve as information sources also for them. Based on our results, *F. polyctena* workers indeed discriminated among corpses of different origins and showed varying reactions to them. The most aggressive reactions were elicited by the slave-maker *F. sanguinea*, followed by the conspecific *F. polyctena* corpses. The corpses of *F. sanguinea* were transported at the fastest rate away from the plates, and in the highest amount during the time of observations. In general, with time, the majority of the corpses were transported inside the nests, where these could potentially serve as important food sources (Lőrincz et al. 2025) and information carriers for nestmates. However, differences between the corpses of different species cannot be excluded (see Maák et al. 2014; 2016), as we were not able to follow the fate of every corpse in this experiment. Thus, we cannot exclude the possibility that some of the corpses were simply discarded on the waste piles situated in the arenas. Future studies are needed to decipher the exact fate of different corpse types in this territorial wood ant species as well.

As expected, the most aggressive reactions were induced by the slave-maker *F. sanguinea* corpses, as territorial species usually exclude other aggressive species from their area (Cerdá et al. 2013). *F. sanguinea* is a very aggressive and predatory species, which during its raiding season does not respect other species territories (Mori et al. 2000; Czechowski et al. 2012), and also often transports its corpses during raiding (Czechowski 1977). Thus, corpses of this species can indicate potential intruders and threats. Furthermore, the corpse removal rate and recruitment of workers towards *F. sanguinea* corpses indicate that these may be used as information sources for the whole colony. Similar reactions were expected towards the territorial *F. truncorum* corpses as well; however, a more neutral response was observed. Although *F. truncorum* is considered an aggressive species (Savolainen et al. 1989), it is a weaker competitor than representatives of the *F. rufa* group (e.g., due to smaller colony size; Czechowski et al. 2012) and is excluded easily by them (Vepsäläinen & Pisarski 1982). Moreover, in the studied habitat, *F. truncorum* colonies mainly occur along the forest edge, while *F. polyctena* colonies are mainly found in the forest interior (personal observation). Thus, we assume that the low co-occurrence rate and spatial segregation of these two aggressive species result in low numbers of direct confrontations (see also Stockan & Robinson 2016).

The corpse removal rate of *F. fusca* corpses was also substantial, though nestmate recruitment was mini-

mal. *F. fusca* is a submissive ant species (Savolainen & Vepsäläinen 1988), thus, it does not pose any threat to *F. polyctena*, contrary to *F. sanguinea*, which explains the low worker activity around its corpses. Due to their small colony size, opportunistic foraging, and non-aggressive behaviour, they can often be found in large numbers within *F. polyctena* territories (Savolainen & Vepsäläinen 1989), which can be even beneficial for them, as they are protected against other competitors, such as slave-makers (Czechowski & Markó 2006). However, if their colonies are in close proximity to a *F. polyctena* nest, the territorial species can eliminate them. Since a considerable portion of *F. polyctena* foraging (and the *F. rufa* group in general) consists of non-selective predation and scavenging (Czechowski et al. 2012), *F. fusca* can serve as a potential prey and food source, which can clarify the similarly high corpse removal rate to *F. sanguinea* corpses. Similarly, corpses of rival conspecific colonies are substantial protein sources (Mabelis 1979). During food shortages, such as in spring, not only corpses but the predation of rival conspecifics can supply their diet, which is partially the reason behind the aggressive behaviour towards conspecific corpses in addition to intraspecific competition (De Bruyn & Mabelis 1972; Mabelis 1984). Territorial ant species often transport and accumulate waste and corpses at the edges of their territory, where these may function as territorial signals (Gordon 1984; Czechowski 1990). Corpses can therefore provide information about neighbour identity and rival presence (see Maák et al. 2014; 2016), and may influence nest-site selection by inducing avoidance of otherwise suitable nesting locations (Franks et al. 2005; Renucci et al. 2011). Furthermore, corpse-carrying behaviour by competitors may itself have an intimidating effect (Czechowski 1985; Czechowski et al. 2009; Maák et al. 2024). Together, these observations suggest that corpses can convey substantial information even for a territorial species.

Our results indicate that the territorial and highly dominant wood ant *F. polyctena* is capable of discriminating among corpses of different origins and exhibiting specific collective responses to them. These responses appear to be highly context-dependent and are largely shaped by intra- and interspecific competitive relationships. Such context-dependent responses may provide substantial fitness benefits by enhancing pathogen avoidance, facilitating resource acquisition, and reducing encounters with dangerous competitors or slave-making species. Consequently, corpses are not merely regarded as potential sources of infections that require removal, but also as important sources of ecological and social information about conditions within and around the nest and the surrounding territory. Future studies based on larger sample sizes and multiple populations will be important for determining the functional significance of these corpses for a dominant territorial ant species such as *F. polyctena*, including whether corpses contribute to territorial signalling or whether responses differ between neighbouring and more distant colonies.

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STRESZCZENIE

Reakcja terytorialnej mrówki rudnicy (*Formica polyctena* Latreille) na ciała martwych sąsiadów

W koloniach mrówek ciała martwych osobników mogą pełnić wiele funkcji, m.in. wyznaczać granice terytorium, stanowić dodatkowe źródło białka w okresach niedoboru pokarmu oraz działać odstraszająco na potencjalnych konkurentów. Aby mogły spełniać te funkcje, ciała martwych mrówek muszą być niezawodnie rozpoznawane i odróżniane, ponieważ ciała różnych gatunków lub osobników mogą sygnalizować odmienne rodzaje i poziomy zagrożenia. Choć zdolność do rozróżniania martwych osobników badano u gatunków zajmujących różne pozycje w hierarchii dominacji, zagadnienie to pozostawało dotąd niepoznane u gatunków terytorialnych, takich jak mrówki rudnice. Aby uzupełnić tę lukę, zbadaliśmy reakcje mrówki rudnicy (*Formica polyctena* Latreille) na ciała martwych osobników różnego pochodzenia. Pięć eksperymentalnych fragmentów kolonii utrzymywano w warunkach laboratoryjnych i prezentowano im pięć typów martwych osobników: osobników współwystępujących w jednej kolonii, osobników tego samego gatunku pochodzących z innych kolonii, *Formica fusca* Linnaeus, *F. sanguinea* Latreille oraz *F. truncorum* Fabricius. Wyniki wskazują, że badany gatunek skutecznie rozróżnia ciała martwych osobników różnego pochodzenia. Najbardziej agresywne reakcje wywoływały ciała mrówki niewolnicy (*F. sanguinea*), następnie ciała terytorialnego przedstawiciela tego samego gatunku (*F. polyctena*). Wysokie tempo usuwania ciał podporządkowanego gatunku *F. fusca* sugeruje, że mogą one być wykorzystywane przez kolonie jako źródło pokarmu. Ciała *F. truncorum* wywoływały niski poziom agresji, lecz były często przenoszone przez robotnice, natomiast reakcje na ciała osobników były minimalne. Uzyskane wyniki wskazują, że terytorialna i silnie dominująca mrówka rudnica (*F. polyctena*) potrafi rozróżniać ciała martwych osobników różnego pochodzenia i reaguje na nie w sposób specyficzny. Reakcje te wydają się zależeć od kontekstu ekologicznego i być kształtowane przez wewnątrz i międzygatunkowe relacje konkurencyjne.