

The natural history of *Myrmarachne melanotarsa*, a social ant-mimicking jumping spider

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Abstract *Myrmarachne melanotarsa*, an ant-like jumping spider (Salticidae) from East Africa, is an accurate mimic of *Crematogaster* sp. and associates unusually closely with its models. *M. melanotarsa* is remarkable in that it forms dense aggregations and builds large nest complexes (numerous individually-occupied nests connected to each other by silk). Other salticids (*Pseudicius* spp., *Menemerus* spp.) live with *M. melanotarsa* in the same nest complex. These aggregations, which can exceed 50 conspecific individuals per colony, are considerably larger than those few previously described, and seem to have primarily a protective function. We provide baseline information on the natural history of *M. melanotarsa*, paying particular attention to predatory behaviour and association with *Crematogaster* sp., and fit this within current theory on the function of sociality in spiders. Other unusual behaviour of

M. melanotarsa includes “mouthing”, in which the spider opens and closes its chelicerae while pressing its mouthparts against nest silk. We investigated the role of prior presence of *Crematogaster* sp. on nest silk in eliciting this previously unreported behaviour.

Keywords Batesian mimicry; *Crematogaster*; *Myrmarachne*; Salticidae; social spiders

INTRODUCTION

Sociality in spiders is of exceptional interest, because the popular impression is that these predatory arthropods are highly aggressive toward members of their own species and prone to cannibalism, behaviour that would not appear conducive to sociality. Among more than 5000 species in the largest spider family, the Salticidae or jumping spiders, examples of sociality are especially scarce. The better-known examples of sociality come instead from web building species belonging to other families (e.g., Avilés 1997; Avilés et al. 2001; Whitehouse & Lubin 2005).

Although terms such as “eusocial” and “semisocial” have been given strict definitions in the insect literature, we prefer to use the broader, everyday terms “social” and “sociality” without formal definitions, because they are routinely and casually used for species that tend to form groups of conspecific individuals (see Wilson 1975).

Having unique, complex eyes that support exceptional spatial acuity (Land 1985; Land & Nilsson 2002; Harland & Jackson 2004), most salticids are solitary hunters that spend their lives outside webs (Richman & Jackson 1992). Yet there are examples of salticids aggregating into apparently sociable groups. Numerous salticid species from temperate regions occasionally form overwintering aggregations of clustered individual nests under the bark of trees and under stones, which are abandoned at the end of winter (Kaston 1948; Crane 1949; Jennings 1972). With the exception of cohabitation (when an adult male spins a nest alongside a nest of a subadult



Fig. 1 Large colony of *Myrmarachne melanotarsa*. Nest complex in hole in tree caused by limb loss.

(one instar short of maturity) female and mates with her when she matures), which is almost universal in the Salticidae (Jackson 1986a; Jackson & Pollard 1997), the function of aggregating in salticids is poorly understood.

The largest aggregations of salticids are formed by about a half dozen species that live together in nests interconnected by silk (“nest complexes”, Fig. 1, 2) in habitats near the shore of Lake Victoria in Kenya and Uganda (Jackson 1986b,c; Wesolowska & Salm 2002; Wesolowska 2006). More than one salticid species sometimes share the same nest complex. One of the species found in these nest complexes, *Myrmarachne melanotarsa*, is easily mistaken for a social insect, as all species in the genus *Myrmarachne* (Wanless 1978) are ant mimics.

Batesian mimics are palatable individuals that deceive potential predators by resembling unpalatable models to which the predators have an aversion (Wickler 1968; Edmunds 1974, 1978; Vane-Wright 1980; Ruxton et al. 2004) and there is now considerable evidence that *Myrmarachne* is a genus of Batesian ant mimics (Cutler 1991; Cushing 1997; Edmunds 2006; Nelson & Jackson 2006; Nelson et al. 2006). Ants appear to be particularly suitable as models for Batesian mimics because, besides being especially abundant insects in most terrestrial habitats (Hölldobler & Wilson 1990), they are notorious for their defensive adaptations, including powerful mandibles, poison-injecting stings, and ability as social insects to mount communal attacks (Eisner 1970; Blum 1981).

Myrmarachne melanotarsa is normally found in the close company of its model, *Crematogaster* sp. (hereafter *Crematogaster*), and it is an accurate mimic (see Edmunds 2000) of this ant (Fig. 2). Batesian mimics that closely resemble a particular model species might be expected to live near their model, so as to increase the efficacy of the mimic’s protection from predators that are averse to the model (Edmunds 2000). However, it is also typical to find this small (adult body length c. 3 mm) East African salticid in the company of numerous other conspecific individuals. As a social salticid that mimics a social insect, *M. melanotarsa* adds a previously unappreciated perspective to our understanding of *Myrmarachne*-ant relationships.

Crematogaster is an aggressive arboreal ant. A common food source of ants, including *Crematogaster* (Carroll & Janzen 1973), is honeydew, the sugary waste of scale insects (coccids) and other sap-feeding homopterans (Buckley 1987; Völkl et al. 1999). This specialised diet may explain why *Crematogaster* colonies are common in African and Asian arboreal habitats (Room 1971; Carroll & Janzen 1973; Richard et al. 2001). Preying on the homopterans may provide *Crematogaster* with a source of protein and lipids (Carroll & Janzen 1973),

Fig. 2 *Myrmarachne melanotarsa* male (M) and two ants (*Crematogaster* sp.) (C) walking on nest complex.



while the homopterans may gain a sanitation benefit from *Crematogaster*'s active removal of excess honeydew (Flatt & Weisser 2000) and a protective benefit from *Crematogaster* actively driving away not only its own predators but also those of the attended homopterans (Carroll & Janzen 1973).

The present study is an initial step towards understanding the biology of *M. melanotarsa*. Relying on observations from the field and the laboratory, we describe the natural history of *M. melanotarsa*, particularly as it relates to *Crematogaster*. We are especially interested in silk mouthing, a distinctive behaviour performed by *Crematogaster* and *M. melanotarsa* when on nest complexes. Our experimental findings are an initial step toward clarifying the significance of this unusual behaviour.

MATERIALS AND METHODS

Observations in the field and the laboratory

Seventy-five colonies of *M. melanotarsa* (three of which were especially large, containing >50 individuals of *M. melanotarsa*) were observed almost daily over a 4-month period. Observations were made at different times during the day, and each observation period lasted 20–120 min. Additional observations were conducted using colonies that were established in the laboratory in large plastic cages. *Pseudicius* spp. and *Menemerus* spp., the salticids that most often share nest complexes with *M. melanotarsa* in

nature, ants (*Crematogaster*), and a large variety of potential prey were maintained in the same cages. The term “colony” is used for nest complexes occupied by *M. melanotarsa* regardless of whether other salticid species were also present.

Experimental procedure

In order to determine whether the presence of chemical cues left by ants on silk affected *M. melanotarsa*'s propensity for “silk mouthing”, we first established, in the laboratory, nest complexes built by *M. melanotarsa* females. Each nest complex was obtained by putting 20 *M. melanotarsa* females in a cage at 0900 h and ensuring that prey (chironomid midges) were continuously available for the following 10 days. At the end of the 10-day period, preparation was successful only if all spiders were alive and in a single nest complex. At 0900 h on day 10, all individuals of *M. melanotarsa* and all prey remains were removed from these testing cages, leaving the intact nest complex within.

Each testing cage was assigned at random to one of two groups: (1) Experimental group: 10 *Crematogaster* workers were placed in the cage immediately after removing the spiders, and all prey remains. Ants were removed from the cages 24 h later (0900 h on day 11); (2) Control group: no ants were put into the cage. There were 35 replicates of each treatment.

Five *M. melanotarsa* females were placed in testing cages immediately following removal of the ants, and then observed for the following 60 min.



Fig. 3 *Myrmarachne melanotarsa* female feeding on juvenile of *Menemerus* sp.

The outcome of a test was recorded as a “response” whenever at least one of the five spiders mouthed the silk.

RESULTS

Location of nest complexes in nature

Nest complexes were found on tree trunks, especially in the indentations caused by lost limbs (Fig. 1). Nest complexes were also frequently built around and within the existing silk of either abandoned or still occupied eggsacs of *Hersilius caudata*, a bark-dwelling spider (Hersiliidae) that ambushes prey and builds silken eggsacs on tree trunks (Filmer 1991; Metwally 2001).

Observations of silk mouthing

Silk mouthing was the dominant behaviour of *M. melanotarsa* during field observations, and consisted of inserting fangs into the silk, sometimes accompanied by slowly ($1\text{--}2\text{ s}^{-1}$) opening and closing the chelicerae. Immediately before mouthing, the spider usually probed with its forelegs (i.e., its most anterior pair of legs). When probing, it moved these two legs forward and backward so that their

tarsi pushed alternately on the silk (c. 2 cycles s^{-1} ; distance moved $0.5\text{--}1.0\text{ mm}$; phasing of the two legs variable, but primarily alternating). However, when mouthing silk, *M. melanotarsa* stood with forelegs highly flexed, cephalothorax angled $10\text{--}45^\circ$ downward and the front of the cephalothorax (chelicerae and sometimes also the clypeus and anterior medial eyes) pressed against the silk. This posture was usually held for only a few seconds, but there were rare occasions when it was held for more than a minute. The spider finished mouthing by releasing the grip of its fangs on the silk and simply stepping away. However, spiders normally mouthed 10 times or more in one place, then released the silk, stepped about and mouthed again in another location.

Experimental results on silk mouthing

Myrmarachne melanotarsa mouthed significantly more often in the experimental treatment (ants previously present) than in the control (no ants) (13 of 35 in Experimental, 2 of 35 in Control, Fisher exact test, $\chi^2 = 10.266$, $P < 0.01$).

Prey records and predatory behaviour

Except for dipterans (midges and mosquitoes), the prey on which *M. melanotarsa* were found feeding in the field tended to be 1 mm in body length or less,

and *M. melanotarsa* in the laboratory appeared to be reluctant to take prey any larger than this. In most instances, when *M. melanotarsa* was found feeding in the field, the prey was already considerably masticated and could not be identified (Table 1). Salticid eggs and juveniles accounted for the majority of the identifiable prey, followed by hersiliid eggs and juveniles. The remaining prey were insects, especially dipterans (Table 1).

Finding *M. melanotarsa* in the act of feeding on spider eggs and juveniles in the field was difficult, because when feeding on a hersiliid egg or juvenile or on a salticid egg or juvenile, *M. melanotarsa* was under the hersiliid eggsac silk or the nest-complex silk. Laboratory observations confirmed that *M. melanotarsa* readily ate not only representatives of all prey categories recorded from the field, including the eggs and juveniles of hersiliids and of heterospecific salticids (Fig. 3), but also aphids, psyllids, whiteflies, mealy bugs, and other unidentified small, soft-bodied insects.

Predatory sequences with insect prey, and with juvenile salticids that were out of the eggsac, began when *M. melanotarsa* oriented from several body lengths away and approached. When close, *M. melanotarsa* lunged (“lunge” is defined by rear legs remaining on the substrate when the spider suddenly moves its body forward) and grabbed hold of the prey. *M. melanotarsa* never leapt on prey (“leap” is defined by all legs leaving the substrate). *M. melanotarsa* did not lunge at the eggs and juveniles of spiders encountered inside eggsacs but instead simply took hold of an egg or juvenile with its chelicerae and pulled it out of the eggsac to feed. Sometimes eggs, however, were not lifted out, but fed on while

they remained embedded in the silk. *M. melanotarsa* also preyed on recently hatched juveniles by lunging at them as they left their eggsacs.

M. melanotarsa was never seen attacking adult ants, nor was it ever seen attempting to feed on the ants’ eggs, larvae or pupae as long as adult ants were present. However, by simply grabbing hold with its chelicerae, without first lunging, *M. melanotarsa* readily fed on unguarded eggs, larvae, and pupae of *Crematogaster* in the laboratory.

When found in the field, *M. melanotarsa* was usually on the silk of a nest complex (Fig. 2) or at least close by. However, *M. melanotarsa* sometimes commuted alongside columns of *Crematogaster* heading to and fro, and these *M. melanotarsa* individuals were often found 1 m or more from the nearest nest complex. While travelling alongside ant columns, *M. melanotarsa* appeared to react continually to the nearby ants, actively avoiding contact. There were also instances in which *Crematogaster*, as well as coccids or other homopterans that feed on sap, were on leaves with individuals of *M. melanotarsa*. These leaves could be several metres from the nearest nest complex. While on these leaves, *M. melanotarsa* occasionally fed on honeydew from the homopterans (Fig. 4).

Interactions between *Myrmarachne melanotarsa* and *Crematogaster*

When at a nest complex, *M. melanotarsa* routinely oriented toward, and briefly displayed at, conspecific individuals that came close, with males tending to display more persistently than females. Displays included specialised posturing similar to that described for other *Myrmarachne* species (Nelson & Jackson

Table 1 Summary of prey types from observations of *Myrmarachne melanotarsa* feeding in the field.

Prey type	<i>N</i>	Proportion of all prey (<i>N</i> = 113)	Proportion of identifiable prey (<i>N</i> = 48)
Unidentified	65	0.575	—
Salticid juvenile*	16	0.142	0.333
Salticid egg†	13	0.115	0.271
Hersiliid egg	6	0.053	0.125
Hersiliid juvenile	2	0.018	0.042
Diptera‡	7	0.062	0.146
Psocid	3	0.027	0.063
Caterpillar	1	0.009	0.021

*4 *Menemerus*, 3 *Pseudicius*, 9 unidentifiable salticids.

†7 *Pseudicius*, 5 *Menemerus*, 1 conspecific.

‡5 Chironomidae (midge), 2 Culicidae (mosquito).



Fig. 4 Female *Myrmarachne melanotarsa* on leaf with honeydew-producing coccids.

2007). Generally, the conspecific displayed back briefly, and then the two spiders moved apart. When *Crematogaster* came near, *M. melanotarsa* usually oriented without displaying. If the ant approached, *M. melanotarsa* usually moved away, but sometimes *M. melanotarsa* males displayed for a few seconds in much the same way as toward conspecific males, then backed away, avoiding contact with the ant.

Despite *M. melanotarsa*'s apparent efforts to avoid physical contact with *Crematogaster*, there were frequent face-to-face encounters during which *M. melanotarsa* adopted behaviour strikingly similar to how *Crematogaster* reacted to conspecific ants. *M. melanotarsa*, like *Crematogaster*, cocked its abdomen up almost perpendicular to the substrate and then the spider and the ant "antennated" each other, the ant with its real antennae and the spider with its forelegs. These interactions lasted no longer than a few seconds, and usually ended with both individuals departing by moving past each other. Occasionally, when the ant appeared especially agitated and aggressive, with its abdomen pointing almost forward, *M. melanotarsa* turned and moved rapidly away. *M. melanotarsa* never adopted an abdomen-forward posture comparable to that of the ant.

It was routine to see *Crematogaster* on the surface of *M. melanotarsa* nest complexes (Fig. 2) and, as a rule, larger nest complexes harboured more *Crematogaster*. Sometimes other small (unidentified) ants were present as well, but they were almost always a minority when *M. melanotarsa* was present. However, there were a few instances in which ants

other than *Crematogaster* seemed to take over in nest complexes that had formerly been sites of *Crematogaster* activity, and subsequently the numbers of *M. melanotarsa* declined rapidly. Large colonies never persisted in the field for long in the absence of *Crematogaster*.

Individuals of *Crematogaster* seen in nest complexes were usually walking over the silk, frequently stopping and pressing their faces into the silk while opening and closing their mandibles. Sometimes *Crematogaster* removed prey remains, shed salticid and hersiliid exoskeletons and other detritus that they encountered in the nest-complex silk, and took these items to its own nest. We also observed eggs and recently hatched juveniles of *M. melanotarsa* and hersiliids being carried in *Crematogaster*'s mandibles. In these instances, the silk around the nests containing the eggs or juveniles had been torn loose, but ants were never seen tearing the silk and the origin of these tears remains uncertain.

However, we confirmed that ants responded opportunistically to silk being torn by using forceps to pull nest silk away ($N = 10$). In each instance, before tearing the silk, ants were moving in a column adjacent to the nest complex, but the column quickly changed direction and swarmed into the damaged nest complex. *M. melanotarsa* and other salticid species from the damaged and neighbouring parts of the complex stepped aside and remained nearby, all the while keeping away from the ants which carried away the eggs and recently hatched juveniles exposed by the artificial tears in the nest silk.

Interactions with other salticids in nest complexes

The way other salticids reacted to *M. melanotarsa* resembled how they reacted to *Crematogaster*. They oriented towards the ants or the ant mimic and, if they had been walking, they stopped. If the ant or the mimic moved away, the salticid usually watched it and, once the ant or the mimic had moved several body lengths away, the salticid usually walked away in the opposite direction. If approached by an ant, the salticid usually turned and moved quickly away (“ran”) or else first backed away a few millimetres before turning and running.

Crematogaster and *M. melanotarsa* usually showed little response to the other salticids present in the nest complexes, the primary exceptions being instances of close proximity or physical contact. Yet, even when approached by another salticid, *M. melanotarsa* typically showed no reaction until the other salticid came to within a few body lengths, at which point *M. melanotarsa* turned and ran, typically without turning to reorient toward the salticid.

DISCUSSION

Adaptive advantage of proximity to ants

Myrmarachne melanotarsa lives in close proximity to its model, *Crematogaster*, and this is more unusual than it might first appear. The general pattern for species in the genus *Myrmarachne* is to live in the same habitat as the ants they mimic, but not usually side by side with the ants (Edmunds 1978; Jackson & Willey 1994). Species that mimic weaver-ants (Collart 1941; Mathew 1954; Wanless 1978; Nelson & Jackson 2008) are the most comparable to *M. melanotarsa*, but they do not associate with their model ant species as closely as we have found with *M. melanotarsa*. Our research suggests that particularly intricate links have evolved between *M. melanotarsa* and *Crematogaster*. Our objective in ongoing research on *M. melanotarsa* is to clarify the cost-benefit tradeoffs that might apply to living in groups and associating with *Crematogaster*. Here we provide only an overview of this work, and its relationship with the wider literature on spider sociality.

Crematogaster generally moves from place to place in columns and sometimes *M. melanotarsa* joined the marching ants. The *Crematogaster* columns often led to honeydew-producing coccids, and *M. melanotarsa*, along with *Crematogaster*, fed on

honeydew (Fig. 4). Reports of salticids feeding on honeydew are scarce. In fact, other than the present study, we know of only one other report (Collart 1929). However, there might be an important lesson to be found by considering the literature on nectar feeding by salticids and other spiders. Until recently, reports of this were rare in the literature, but recent work suggests that it is probably common for salticids to feed from flowers and extra-floral nectar-ies (Ruhren & Handel 1999; Jackson et al. 2001). Records of nectar feeding might provide a hint that this mode of feeding is particularly prevalent in the genus *Myrmarachne*. Four of the 31 (12.9%) salticid species seen feeding on nectar in the field (Jackson et al. 2001) were from the genus *Myrmarachne*. Yet, out of about 5000 described salticid species, only about 200 (4%) are from the genus *Myrmarachne* (Platnick 2007; Proszynski 2007). It is interesting that the only other report besides ours of a salticid feeding on honeydew came from *M. foenisex*, another species from the genus *Myrmarachne* (Collart 1929). Perhaps feeding on honeydew is disproportionately common in salticids that mimic ants, as honeydew-producing insects tend to attract ants and ants tend to deter most other salticids (Nelson & Jackson 2006).

The silk-mouthing behaviour of *M. melanotarsa* and *Crematogaster* may also be a method by which the ant and the ant mimic can feed on honeydew together. Homopterans make honeydew by excreting only partially digested sap, and possibly ants in turn fail to digest all of the sugar in honeydew before excreting it on nest silk. If so, silk mouthing by *M. melanotarsa* and the ants may be a way of harvesting sugar excreted by the ant as secondary honeydew.

Our observations suggest that, for *M. melanotarsa*, the risk of ant predation on eggs is an important cost of associating with *Crematogaster*. Something similar seems to apply to embiopterans, web-spinning insects that resemble social salticids by using silk to spin communal oviposition and resting shelters (Edgerly et al. 2006). Ants are common in the same environments as embiopterans, often making trails directly across the silk (Edgerly 1988). As long as the embiopterans' silk walls remain intact, the ants remain outside. However, should the silk covering be breached, ants swarm over the embiopteran colony, entering through the breach and attacking the inhabitants (Edgerly 1988). This behaviour is similar to the way *Crematogaster* reacts to nest complexes of *M. melanotarsa* being damaged. When we tore nest-complex silk, *Crematogaster* swarmed over and into

the normally inaccessible interior and, once inside, the ants foraged on eggs and juveniles.

Waste and prey remains inevitably build up with so many salticids living close together in nest complexes, which in turn may encourage deleterious accumulation of parasites and pathogens. For social web-building spiders and other animals that live in large, fixed colonies, waste disposal may be a serious problem, and social web-building spiders are known to devote considerable time to cleaning their communal webs (Ebert 1998). For *M. melanotarsa*, help may be provided by the ants, as *Crematogaster* workers routinely collected and disposed of prey remains, dead spiders, and other detritus that accumulates in the colony silk.

The weighting of these costs and benefits at any one time will determine how we view the relationships between the different participants. Any simple characterisation of how each species is adapted to the other appears unrealistic. However, the conventional Batesian mimicry hypothesis is clearly relevant for understanding the benefits for *M. melanotarsa* of close physical proximity to *Crematogaster* because living in the vicinity of ants might lessen predation by predators that have learned or already have an innate aversion to the model (Nelson et al. 2006).

Associating with other spiders

Myrmarachne melanotarsa is distinctive not only for living in close proximity to ants but also for sharing nest complexes with other salticids, especially *Menemerus* spp. and *Pseudicius* spp., and for building nest complexes on and within the eggsacs of *Hersilius caudata*. In an interesting review, Whitehouse & Lubin (2005) considered the advantages of living in a social group that apply to the individual spider. They argued that, depending on the spider species, these advantages were related to one or more of the following: reproduction, foraging or protection. For *M. melanotarsa*, it is somewhat more complicated because this social salticid has neighbours of the same and of different species, including *Crematogaster*, an ant, *Hersilius*, a non-salticid spider, and other social salticids (from other genera *Menemerus* and *Pseudicius*). For *M. melanotarsa*, foraging advantages are likely, as this ant-mimicking salticid feeds on the juveniles and eggs of the hersiliid and salticid spiders with which it associates. This is an example of brood parasitism, which has been documented in other salticids (Boulton & Polis 2002), including other species of *Myrmarachne* (Jackson & Willey 1994). *M. melanotarsa* puts a different twist on brood parasitism because, as a social

salticid that mimics a social insect (*Crematogaster*) that also preys on eggs and juveniles opportunistically, groups of *M. melanotarsa* might be especially effective at gaining access to eggs and juveniles. We are currently investigating a particular hypothesis: that groups of *M. melanotarsa*, by resembling groups of *Crematogaster*, intimidate other salticids and thereby gain access to the other salticids' eggs and juveniles.

At first sight, it appears maladaptive for *Menemerus* spp. and *Pseudicius* spp. to share nest complexes with *M. melanotarsa*. However, there may be compensating advantages, and these fall, for *Menemerus* and *Pseudicius*, within the protective function of sociality. As many ants are predatory, territorial and highly aggressive (Hölldobler & Wilson 1990), routinely attacking potential predators of salticids that come close, the immediate vicinity of ants and ant mimics could be a safe haven for a salticid. For these salticids, ants and *Myrmarachne* would have a role similar to the role of protector species in mixed-species bird flocks (Pius & Leburg 1998; Richardson & Bolen 1999), where one bird species (the "protector") is more effective at driving predators away and other species in the same flock benefit by associating with the protector species. For the salticids, associating with ants and with *M. melanotarsa* incurs costs (loss of eggs and small juveniles), but these may be compensated for by the protector-species benefits.

Collective mimicry

Batesian mimicry in the genus *Myrmarachne* is typically envisaged as individual ant mimics benefiting from their resemblance to individual ants (Cushing 1997). However, by living in groups, *M. melanotarsa* has taken ant mimicry a step further. Ants are social insects, and potential predators often encounter groups of ants rather than encountering ants one at a time. *Crematogaster*, for example, whether at a nest or travelling along a trail, is seldom alone and, if one ant is attacked, a swarm of conspecific individuals in the vicinity normally come to its defence and ward off the predator. Simply witnessing a large group of ants may be enough to deter many predators. This argument suggests a hypothesis we are currently investigating (the "collective mimicry hypothesis"). We propose that, for some of its predators, a group of *M. melanotarsa* spiders resembles a swarm of *Crematogaster*.

The collective mimicry hypothesis might account for *M. melanotarsa*'s tendency to maintain especially close physical proximity to its model.

For people, and presumably for some of *M. melanotarsa*'s natural predators (see Nelson & Jackson 2006), a mixed-group consisting of *M. melanotarsa* and *Crematogaster* may be hard to distinguish from a pure group of *Crematogaster*, suggesting that, for an individual of *M. melanotarsa*, the prime objective is to be close to other similar individuals. Whether the other individuals are conspecifics or the model may be relatively unimportant.

Collective mimicry appears to be an example of sociality having a role in predator protection as characterised by Whitehouse & Lubin (2005): "the sum of individual behaviours in the group that enhance the survival of the group members... in the presence of predators or parasites". However, *M. melanotarsa* seems to differ from the examples reviewed by Whitehouse & Lubin (2005) because, in the case of *M. melanotarsa*, an anti-predator advantage of sociality seems to have an unusual link to Batesian mimicry. Here we have an example of an ideal convergence between the independent protective functions of social living and of Batesian mimicry of a social model.

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