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SHORT COMMUNICATION

Thievery in rainforest fungus-growing ants: interspecific assault on culturing material at nest entrance

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Abstract

Cleptobiosis in social insects refers to a relationship in which members of a species rob food resources, or other valuable items, from members of the same or a different species. Here, we report and document in field videos the first case of cleptobiosis in fungus-growing ants (*Atta* group) from a coastal, Brazilian Atlantic rainforest. Workers of *Mycetarotes parallelus* roam near the nest and foraging paths of *Mycetophylax morschi* and attack loaded returning foragers of *M. morschi*, from which they rob cultivating material for the fungus garden. Typically, a robbing *Mycetarotes* stops a loaded returning *Mycetophylax*, vigorously pulls away the fecal item from the forager's mandibles, and brings the robbed item to its nearby nest. In our observations, all robbed items consisted of arthropod feces, the most common culturing material used by *M. parallelus*. Robbing behavior is considered a form of interference action to obtain essential resources needed by ant colonies to cultivate the symbiont fungus. Cleptobiosis between fungus-growing ants may increase colony contamination, affect foraging and intracolonial behavior, as well as associated microbiota, with possible effects on the symbiont fungus. The long-term effects of this unusual behavior, and associated costs and benefits for the species involved, clearly deserve further investigation.

Keywords Ant behavior · Fungus-growing ants · Interference competition · Theft · Atlantic rainforest

Introduction

Among social insects, thievery of food items, nesting material, brood, or other valuable items is known as cleptobiosis and can occur among individuals of the same or of different species that do not nest in close association (Breed et al. 2012). This ecological relationship is a form of interference competition, and may be an important strategy for obtaining valuable resources (Hölldobler 1986). Cleptobiosis has been reported in social insects such as ants, bees and wasps, as well as in other arthropod groups such as spiders and thrips (Breed et al. 2012; and included references). Several cases of inter and intraspecific food robbing have been reported among ant species. For instance, Hölldobler (1986) observed that *Myrmecocystus mimicus* robs prey from *Pogonomyrmex desertorum* and *P. maricopa*; Perfecto and Vandermeer (1993) reported *Ectatomma ruidum* stealing food items from *Pheidole radoszkowskii*; Yamaguchi (1995) observed seed stealing between neighboring colonies of *Messor aciculatus*; and Richard et al. (2004) demonstrated for the first time sugary food robbing by *Crematogaster limata* from *Ectatomma tuberculatum*.

Here, we report the first case of thievery of culturing material (cleptobiosis) involving two species of fungus-growing ants, *Mycetophylax morschi* (Emery) and *Mycetarotes parallelus* (Emery), in a coastal, sand-based ("restinga") Atlantic rainforest of Brazil. *Mycetophylax morschi* and *Mycetarotes parallelus* belong to the monophyletic Neotropical Attina subtribe (Formicidae: Myrmicinae: Attini). Both species have obligatory mutualisms with the symbiotic fungi cultivated inside their nests, which serve as food source for the whole colony (Hölldobler and Wilson 2011).

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Mycetarotes parallelus occurs from central and southeast Brazil (Atlantic rainforest, Cerrado savanna, and Amazonia) to northern Argentina (Mayhé-Nunes and Brandão 2006). *Mycetophylax morschi* occurs exclusively along the Atlantic coast of South America (Klingenberg and Brandão 2009). Henceforth, the two ant species are each referred to by the genus only.

Materials and methods

Observations were carried out in October 2016 in Atlantic rainforest at the Parque Estadual Serra do Mar (Núcleo Picinguaba, 23°21′28″S, 44°51′00″W), near Ubatuba, São Paulo, Southeast Brazil. Records of interspecific thievery are based on 8 h of observation involving two neighboring nests of *Mycetarotes* and *Mycetophylax* (55 cm apart). The videos were recorded using Sony Handycam DCR-SR85.

In previous observations in the same area (April–June 2015), we monitored the foraging activity in each of three colonies of *Mycetarotes* and *Mycetophylax*, totaling 30 h of observation for each species. The resources collected by *Mycetarotes* and *Mycetophylax* to cultivate the fungus garden were removed from returning foragers and preserved in 100% ethanol for identification. All observations and interaction events between the two species were made between 09:00 a.m. and 03:00 p.m., at the peak of ant activity.

Results and discussion

Workers of *Mycetarotes* roam near the nest and foraging grounds of *Mycetophylax* and attack returning foragers. Ant robbers intercept laden *Mycetophylax* workers on their way back to the nest, or at the very vicinity (10–20 cm) of the nest entrance (see video ESM1 in supplementary material). We recorded seven attempts by *Mycetarotes* robbers towards *Mycetophylax* foragers bringing in arthropod feces for fungus culturing. Typically, a robbing *Mycetarotes* stops a loaded returning *Mycetophylax*, vigorously pulls away the fecal item from the forager's mandibles (Fig. 1), and brings the robbed item to its nearby nest (see video ESM2 in supplementary material). Upon assault, loaded *Mycetophylax* foragers may grasp the resource tightly and win the item after fighting with robbing ants for up to 10 s (two occasions). Three *Mycetophylax* workers were once seen helping an intercepted nestmate by biting the assaulting *Mycetarotes*, which was chased away without robbing the item. Probably due to their larger size (*Mycetarotes* ≈ 2.8 mm; *Mycetophylax* ≈ 1.8 mm), *Mycetarotes* workers are often successful at pulling the item loose from *Mycetophylax* (four occasions). On one occasion, an approaching *Mycetarotes* walked away after briefly antennating/inspecting a loaded *Mycetophylax* worker.

In all observed theft incidents, the robbed item was taken directly to the nearby *Mycetarotes* nest by the assaulting ant (see video ESM2 in supplementary material). After ca. 5 min, a *Mycetarotes* worker would consistently exit the same nest toward the very location where the robbing event had recently been recorded. Although this observation might suggest persistence of robbing activities by individual workers, as documented in other prey-robbing ants (Hölldobler 1986), further investigation with marked ants is required to confirm this suggestion.

In a field account on the foraging ecology of *Mycetophylax* and *Mycetarotes* in the same area, we observed that both species collect vegetable matter (e.g. leaf and wood fragments), arthropod feces, and arthropod carcass to cultivate the symbiotic fungus. Arthropod feces constitute 35 and 50% of the items collected by *Mycetophylax* and *Mycetarotes*, respectively (Fig. 2a). Data from these three *Mycetarotes* colonies show that, during 8 h of foraging activity, colonies

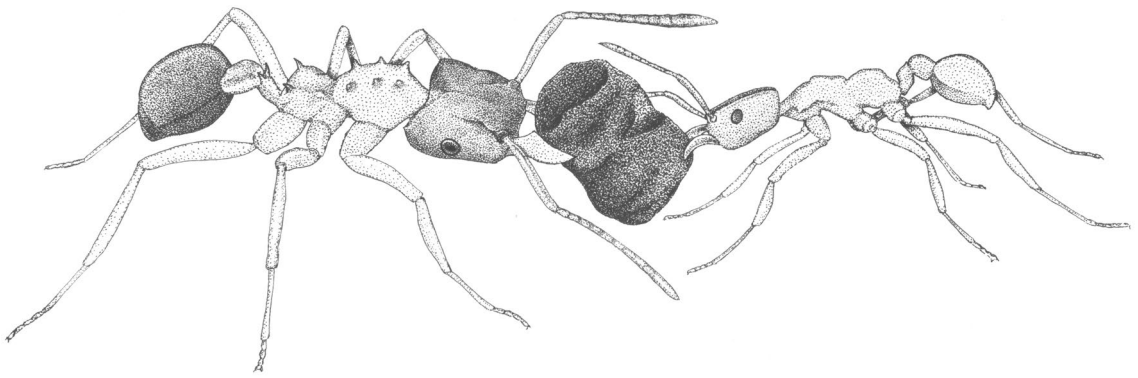

Fig. 1 Schematic drawing of a theft event: a worker of *Mycetarotes parallelus* (left) pulls a recently-collected fecal item from the mandibles of a returning worker of *Mycetophylax morschi*. The robbing ant will take the stolen item to its nearby nest as substrate for the fungus garden (see also Fig. 2). Drawing by Luisa Mota

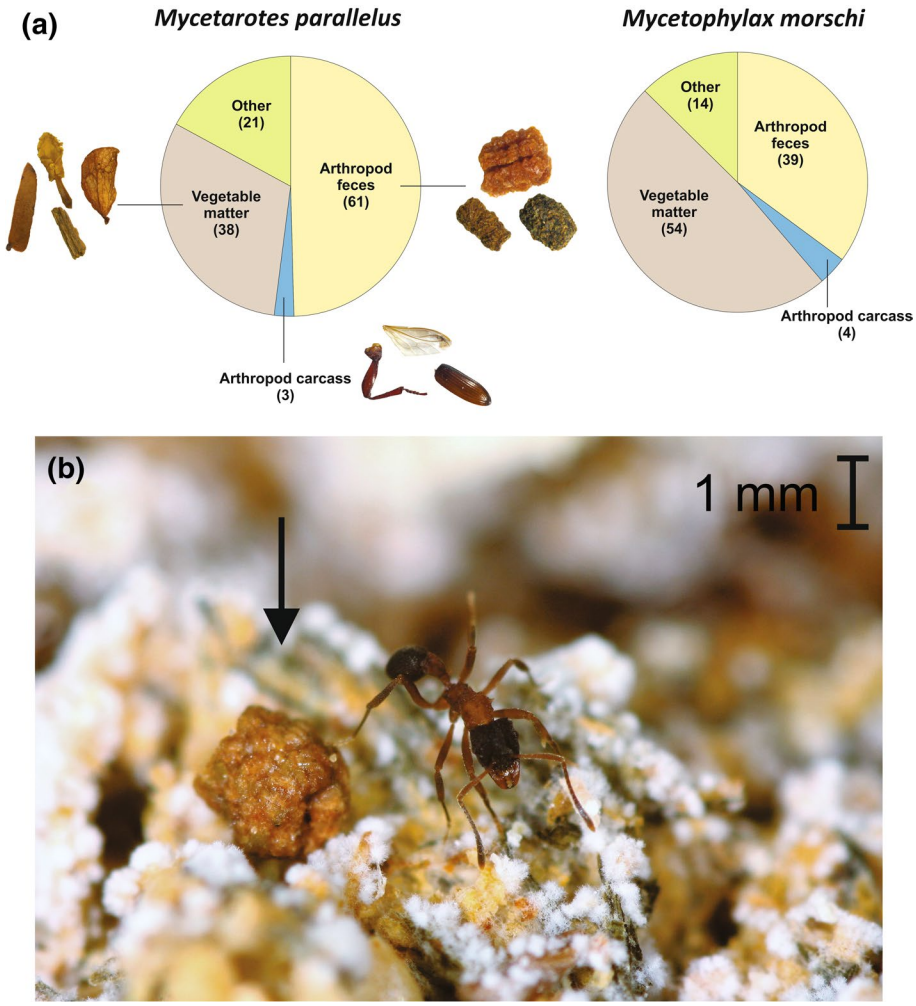

Fig. 2 **a** Culturing substrate for mutualistic fungus collected by *Mycetarotes parallelus* and *Mycetophylax morschi* in coastal Atlantic rainforest, southeast Brazil. Numbers in parentheses designate quantity of items collected during 30 h of observation (three colonies per species). **b** A view of the fungus garden of *Mycetarotes parallelus* showing worker using arthropod feces (arrow) as culturing substrate. The colony was collected in sandy Atlantic rainforest, southeast Brazil

collect on average 16 fecal items (16.26 ± 1.66, mean ± SD, N = 3) for fungus culturing. Our records of robbing involving neighboring *Mycetarotes* and *Mycetophylax* (four stolen items in 8 h) would thus represent nearly 24% of the fecal items normally collected by *Mycetarotes* foragers.

Mycetarotes and *Mycetophylax* are sympatric and have similar preferences for the type of material used for fungus culturing (mainly feces and dead plant fragments, Fig. 2a, b). Although the items stolen by *Mycetarotes* are not for direct ant feeding, they are essential for the cultivation of the symbiont fungus that feeds the colony (Fig. 2b). Unlike leaf-cutter ants of the genera *Acromyrmex* and *Atta* that use fresh plants (fixed and spatially predictable) to cultivate the symbiont fungus, the fecal pellets used by these two non-leaf-cutter attines are scattered in the environment and may be hard to find, analogous to animal prey and seeds (see Hölldobler 1986; Yamaguchi 1995). Robbery by *Mycetarotes* may be advantageous by saving foraging time and reducing predation risk to foragers, thus optimizing fungus and colony growth. The degree to which thievery by *Mycetarotes* can affect foraging activity and fungus growth in *Mycetophylax* colonies await further experimental assessment.

Compared to leaf-cutters, the non-leaf-cutter attine ants are less specialized regarding the material collected for fungus culturing (Wirth et al. 2003; Hölldobler and Wilson 2011). They use arthropod feces and carcass, decaying plant material, fallen fruits and seeds as cultivating material, and can be considered opportunistic (Hölldobler and Wilson 2011). The use of fresh plant material by highly selective *Atta* and *Acromyrmex*, on the other hand, requires several adaptations of the fungus garden for processing the culturing substrate (Khadempour et al. 2016). The low substrate specificity for fungus culturing may thus have favored cleptobiotic behavior in non-leaf-cutter attines, since the fungus garden can develop on variable surfaces and robbed items have good chances of promoting fungus growth. Indeed, two species of non-leaf-cutter attines—*Apterostigma urichii* and *Cyphomyrmex faunulus*—can live in parabiosis and share the same nest and fungus garden without mutual aggression (Sanhudo et al. 2008). This case reinforces the flexibility of the fungus

regarding the culturing substrate, suggesting behavioral plasticity among species of non-leaf-cutter attines.

Cleptobiotic interactions among ants can increase the risk of contamination and pathogenic diseases between cleptobiont colonies due to their frequent and close contact with one another (Breed et al. 2012). Because *Mycetarotes* and *Mycetophylax* workers come in close contact during cleptobiosis, the risk of colony contamination likely increases for both species involved. This could be a critical factor for development of the fungus garden inside their colonies since this symbiosis is susceptible to external contamination, which can lead to death of the fungus and of the entire colony (Currie 2001). Similarly, cases of garden stealing or garden sharing in fungus-growing ants may also result in contamination, leading to pathogen cultivar transfers from one colony to another, as suggested by Adams et al. (2000). Attine ants have diverse bacterial communities associated with their body surface and fungus garden, and some bacteria may protect the ants and the fungus against pathogens (Kost et al. 2007; Mueller et al. 2008). In addition, ant workers of the attine ants keep their fungus free from infection by physically removing invasive microorganisms (Currie 2001). This cleaning behavior is frequently observed in *Mycetarotes* and *Mycetophylax* colonies (MUV Ronque, unpublished data). Grooming is thought to have favored the evolutionary success of fungus-farming ants by decreasing the risk of colony death from infection, thus promoting colony growth (Currie 2001). Grooming behavior may be particularly important for the *Mycetarotes* × *Mycetophylax* cleptobiotic interaction, since microorganisms potentially causing diseases from one species to another can be removed by cleaning workers inside the colonies.

The current field account is the first case of cleptobiosis involving thievery of culturing material between species of fungus-growing ants. The long-term effects of this unusual behavior and the costs and benefits for each species clearly need to be investigated in greater detail, with more quantitative data. This report may stimulate interest in the evolution of foraging and intracolonial behavior, as well as on the microbiology (risk of contamination, associated microbiota) of cleptobiont species in the Attina subtribe, and the possible effect of cleptobiosis on the symbiont fungus.

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