



RESEARCH ARTICLE - ANTS

Evidences of Batesian Mimicry and Parabiosis in Ants of the Brazilian Savanna

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Abstract

Despite the numerous records of ant-mimicking arthropods, reports of ant species that are mimics among themselves are still rare. In the savanna of central Brazil we found two ant species that are remarkably similar in color pattern and body size, *Pseudomyrmex termitarius* and *Camponotus blandus*. Both species are widely distributed in the Neotropical Region, but the cases of mimicry between them are apparently restricted to populations inhabiting nests of the termite *Cornitermes cumulans* in the Brazilian Cerrado. Field observations and excavation of the termitaries revealed that *Camponotus blandus* shares nest chambers and foraging trails with *P. termitarius*, and workers of both species are mutually tolerant. Our observations suggest that the morphological and behavioral similarities between these species represent a Batesian mimicry relationship in which the relatively palatable *Camponotus blandus* mimics the unpalatable *P. termitarius* for predator avoidance. The pacific association between the termitophilous colonies of these species may also suggest some level of parabiotic interaction.

Introduction

Mimicry is considered a conspicuous demonstration of Darwinian selection (Fisher 1930) and can incorporate a wide range of sensory modalities, including visual, auditory, vibrational and chemical (Pasteur 1982). Batesian mimicry has been described as the mechanism by which a palatable species look similar to an unpalatable one to avoid predation. Mimetic systems have been recorded in a vast range of invertebrates and despite the fact that the majority of quantitative studies of Batesian mimicry have examined defensive visual mimicry among lepidopterans (e.g. Joron & Mallet 1998), social insects are one of the most common “models” of Batesian mimics (Hölldobler & Wilson 1990; McIver & Stonedahl 1993; Cushing 1997; Ceccarelli & Crozier 2006). It occurs because social insects may have strong defense mechanisms that are effective against predators. Nevertheless, records of social insects mimicking themselves are relatively rare.

Batesian mimicry has been suggested in few ant species (Ward 1984; Hölldobler & Wilson 1992; Gobin

et al. 1998; Merrill & Elgar 2000; Ito *et al.* 2004), despite the vast diversity of arthropods that mimic ants (e.g. Pie & Del-Claro 2002; Taniguchi *et al.* 2005; Nelson & Jackson 2009). Here we provide a novel account of a remarkable similarity between two species of unrelated ants. We found workers of the formicine ant *Camponotus blandus* (Fr. Smith) reproducing the body coloration and sharing nest chambers and foraging trails of the pseudomyrmecine *Pseudomyrmex termitarius* (Fr. Smith). The two species are exclusively Neotropical, occurring from Central America to northern Argentina. However, the records of Batesian mimicry in these species are apparently restricted to the populations inhabiting termite nests in the savanna of central Brazil.

Like most members of Pseudomyrmecinae, *P. termitarius* is a very aggressive ant with precise mandibles and a painful, venomous sting which serves as a solid deterrent to many potential predators. As its name suggests, *P. termitarius* has a preference for establishing its colonies inside termite nests, although subterranean nests can also be found (Mill 1981; Jaffé *et al.* 1986; Pulgarín 2004). This species is



an opportunistic predator and, when inhabiting termitaries, it can prey upon termite brood or inquiline arthropods that also occupy the termite nests. Populations of *P. termitarius* are widespread in the Brazilian Cerrado, where they can be most commonly found inside nests of the termite *Cornitermes cumulans* (Kollar) (Redford 1984), although colonies can also be found in open soil and in association with other termite species (Kempf 1960).

In contrast, the defense mechanisms of formicine ants are limited to a formic acid spray, since these ants do not possess a functional sting. This is the case with *Camponotus blandus*. The formic acid of these ants renders some of them unpalatable to some predators. However, lacking more substantial defenses, many formicines may be relatively more vulnerable to predation (Lamon & Topoff 1981; Montgomery 1985; Merrill & Elgar 2000). For example, ants of the genus *Camponotus* are among the most commonly preyed upon by Australian birds (Barker & Vestjens 1990). Like many species of this genus, *C. blandus* is a polymorphic, generalist ant (Fernández 2003). The nests are found in the soil, in preexisting cavities under rocks, decaying logs or termite mounts. The foraging is largely arboreal but the workers can be efficient ground predators, preying on terrestrial arthropods and even raiding termite galleries (Fowler & Crestana 1987; Mendonça & Resende 1996).

Morphologically, *Camponotus blandus* can be highly variable regarding the color patterns along its wide geographical distribution, but as far as we know, only in the Brazilian Cerrado this species assumes the reddish and black pattern typical of *P. termitarius*. Both species can share nests of *Cornitermes cumulans* in central Brazil. Our morphological, geographical and behavioral lines of evidence indicate that one species is a visual model of the other. We argue that *C. blandus*, a member of a normally highly predated genus, mimics an aggressive and venomous ant, *P. termitarius*, in order to reduce the risk of predation in the open areas of central Brazil. This is the first formal report of mimicry of an ant by another ant in the Neotropical Region and may also represent a new case of parabiosis between ant species.

Materials and Methods

Collecting and observations on interactions between *Camponotus blandus* and *Pseudomyrmex termitarius* were carried out in two field stations. The first one, Estação Experimental Embrapa Cerrados, is located in the Planaltina municipality, near Brasília, in Brazil's Federal District (15,36'35,5"S; 47,44'09,5"W). It is a 3,500 hectares site with permanent ecological reserves and 10 different Cerrado phytophysiognomies (Embrapa 2010). The second station, Reserva Acangaú, is situated in the Paracatu municipality, State of Minas Gerais (17,12'08,2"S; 47,4'19,6"W). It is classified as a Private Natural Heritage Reserve of 3,000 hectares, where the Cerrado *sensu strictu* is the prevalent physiognomy (INMET 2011).

We made qualitative behavioral observations of workers from five colonies of *Camponotus blandus* and *P. termitarius* cohabiting in termitaries of *Cornitermes cumulans* (Fig. 1a). Termitaries containing colonies of both species were excavated to determine the position of the ant nests and internal organization of the colonies. Then, eight and three additional colonies were collected for *P. termitarius* and *Camponotus blandus*, respectively, from termitaries of both study sites. These additional colonies were found to be isolated, without the presence of the second species. Our observations were made throughout the day, primarily to establish the periods when the ants were most active and abundant above the ground. When possible, all the individuals present in the colonies were collected, including sexuals and brood, and fixed in 70% ethanol. Voucher specimens are deposited at the insect collection of the Instituto de Biologia, Universidade de Brasília (UnB), DF, Brazil.

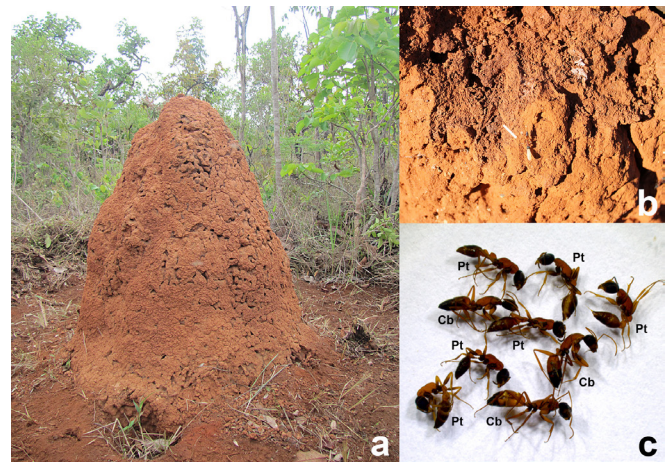


Fig. 1 A typical termitary of *Cornitermes cumulans* in the Brazilian Cerrado (a), worker of *Pseudomyrmex termitarius* foraging solitarily on a termitary (b), mixed sample from a nest chamber containing individuals of *Camponotus blandus* (Cb) and *Pseudomyrmex termitarius* (Pt) (c).

Results

The foraging behavior of *Pseudomyrmex termitarius* is predominantly solitary (Fig. 1b); however, workers may follow disperse trails on the surface of termitaries and in the adjacent areas. We found workers of the mimic *Camponotus blandus* sharing the trails of *P. termitarius* in colonies studied from both study sites, though workers of *Camponotus blandus* could be seen foraging independently.

Termitaries excavation revealed that *P. termitarius* forms polydomous colonies, occupying several chambers inside the termite nests. These chambers were normally found on the hypogaeic portion of the termitaries, from 40 cm high to 15 cm below the soil surface and, in many cases, were shared with colonies of *Camponotus blandus* (Fig. 1c). It was not possible to observe if brood of both species was kept together, but no agonistic interaction was observed between workers of the two species. The presence of the termitary builder

(*Cornitermes cumulans*) is not a requirement for the presence of the ants, since ant nests were found in both abandoned and occupied termite nests. In general, colonies of *P. termitarius* were larger than those of *Camponotus blandus*, with an average number of individuals of 45 and 23, respectively, including brood and sexuals.

Morphologically, the most conspicuous similarity between these two species is their color pattern. Both share the reddish antennae, mesosoma, waist, anterior segments of gaster, and distal portion of legs, and the black head, coxae and apical segments of gaster. Additionally, the total body length is also very similar in both species, about 7 mm (Fig. 2). Extensive collecting was performed in other areas where the species co-occur and the study of specimens of both species deposited in myrmecological collections indicates that the morphological similarity only occurs in populations of termitaries in central Brazil. Most of the *Camponotus blandus* specimens found without the association with *P. termitarius* are predominantly blackish in color. Still, regarding all the species phylogenetically related (subgenus *Myrmaphaenus*) to *Camponotus blandus*, the termitophilous populations of this species are the only ones to exhibit the color pattern observed here.

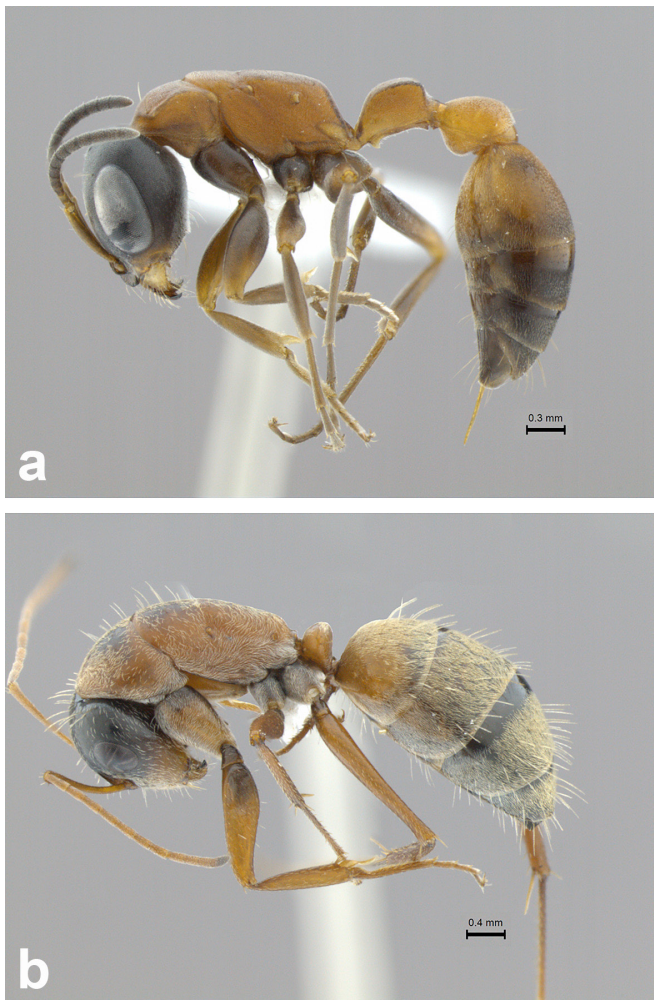


Fig. 2 Lateral view of workers: *Pseudomyrmex termitarius* (a) and *Camponotus blandus* (b).

Discussion

The color combination exhibited by *P. termitarius* and *Camponotus blandus* is most likely aposematic. The black and reddish coloring can frequently be seen as a warning pattern in unpalatable plants and animals of different groups and regions (Lythgoe 1979). Many ichneumonoid wasps and butterflies of the “tiger-complex” combine these colors, apparently to advertise mechanical or chemical defenses to potential predators (Quicke et al. 1992; Beccaloni 1997). Similar reddish and black color patterns can be found within a variety of species in the Australian ant genus *Myrmecia*. Species of these ants are among the most aggressive ants in the World (Haskins & Haskins 1950; Hölldobler & Wilson 1990).

Populations of *Camponotus blandus* occupying termite nests in the Brazilian Cerrado differ in worker caste from the majority of the conspecific populations with arboreal habits and also from those of different biomes and geographic regions. While most species of *Camponotus* have a wide range of size classes, termitophilous *Camponotus blandus* exhibits relatively little variation in the size of the foragers. This conservative caste system helps to create a more consistent congruence in size between *Camponotus blandus* and *P. termitarius* foragers, and thus increases the efficacy of mimicry, given that *P. termitarius* is a monomorphic species.

Mimicry will be most effective when the ranges of the mimic and its model overlap broadly, such that predators encountering the mimic are likely to have had some experience with the model (Pough 1994). The range of *Camponotus blandus* lies entirely within that of *P. termitarius*, although the mimicry cases between both species are apparently restricted to the termitaries in central Brazilian Cerrado. The geographic sympatry of these species is even tighter at the ecological level. Both *Camponotus blandus* and *P. termitarius* share the same nesting and foraging strategies in the open areas of the Cerrado. More significantly, however, is the fact that workers of both species can share nest chambers inside the termitaries, showing an almost complete ecological overlapping.

Theory also predicts that mimicry will be most effective when the model is relatively abundant (Lindström et al. 1997), and in all our observations *P. termitarius* is relatively more common than *Camponotus blandus* within their range, with more individuals per colony. Museum collections corroborate this finding; *P. termitarius* is well represented in the ant collection of the Museu de Zoologia da USP (MZSP), with more specimens than for most of its congeners (RMF, pers. obs.).

The striking similarities between *P. termitarius* and *Camponotus blandus* are obviously unlikely to be derived from a common phylogenetic ancestry given that the formicines and pseudomyrmecines are very divergent phylogenetic lineages (Brady et al. 2006). Instead, our observations suggest that these similarities represent a Batesian mimicry relationship

in which the relatively palatable *Camponotus blandus* mimics the unpalatable *P. termitarius* in order to escape predation.

Batesian mimicry in ants has been reported in *Pheidole nasutooides*, *Camponotus bendigensis*, *Polyrhachis rufipes* and *Camponotus* sp. The major workers of *Pheidole nasutooides* mimic soldiers of nasutitermitinae termites, which have formidable chemical defenses against predation in the Costa Rican tropical forest (Hölldobler & Wilson 1992). *Camponotus bendigensis* shares body size and color patterns with *Myrmecia fulvipes*, a very aggressive Australian ant with a painful venomous sting (Merrill & Elgar 2000). In the Oriental tropics, the species *Polyrhachis rufipes* is often found on trails of *Gnamptogenys menadensis*. Workers of *Polyrhachis rufipes* can follow the trails of *G. menadensis* and thus reach sugar sources (Gobin *et al.* 1998). Finally, workers of an undescribed species of an arboreal *Camponotus* were exclusively observed on foraging trails of the myrmicine ant *Crematogaster inflata* in western Malaysia. The bright yellow and black color pattern, as well as the walking behavior, are very similar in both species (Ito *et al.* 2004).

The most remarkable result of our study is the finding of *Camponotus blandus* sharing nest chambers and foraging trails with *Pseudomyrmex termitarius*, and the mutual tolerance between workers of both species during foraging and intranidal activities. It must be confirmed in the future whether *Camponotus* workers can recognize signals from *Pseudomyrmex termitarius* and *vice versa*, but our observations may suggest some level of parabiogenic interaction between these species. Parabiosis is defined as a particular form of facultative or obligatory symbiosis in which two or more species utilize the same nest structure and sometimes even the same odor trails, but normally keep their broods separate (Hölldobler & Wilson, 1990). It is important to emphasize the facultative nature of this particular association, since neither of the participating species is dependent on the other. Parabiogenic associations have been described for ant species from all over the globe, but most records report facultative relations concentrated in the Neotropics, where several cases, generally involving members of different subfamilies, have been recorded (e.g. Adams 1990; Ipinza-Regla *et al.* 2005; Sanhudo *et al.* 2008).

It remains to be explained why this tight association between the wide distributed *Camponotus blandus* and *Pseudomyrmex termitarius* involves only the termitophilous populations of these species in the Brazilian savanna. The variables favoring this mimetic and probably parabiogenic system may include the predation of *Camponotus blandus* by birds and terrestrial reptiles, both are extremely common in the savanna of central Brazil. It is likely that these predators have sufficient spectral sensitivity to detect the color pattern exhibited by these ants, especially in the open lands of the Cerrado, where foragers are more exposed than in the forests and woodlands where *Camponotus blandus* also occurs.

The efficient defensive mechanisms of *Pseudomyrmex termitarius* and the solid protection of the termitaries of

Cornitermes cumulans have apparently resulted in the evolution of the mimicry and parabiogenic syndromes in *Camponotus blandus*.

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