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Territorial aggressiveness on the arboreal ant *Azteca alfari* by *Camponotus blandus* in French Guiana due to behavioural constraints

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Abstract

This study reports new information on interactions between two sympatric ant species, the plant-ant *Azteca alfari* (Dolichoderinae) living in association with the myrmecophyte *Cecropia obtusa* (Cecropiaceae) and *Camponotus blandus* (Formicinae), a ground-nesting, arboreal-foraging species. Workers of *A. alfari* forage only on the foliage and the upper parts of the trunk of their host *Cecropia*, while *C. blandus* nests in the ground but frequently forages and patrols pioneer tree foliage, including *Cecropia*. The activity pattern of *A. alfari* and the number of *C. blandus* on *Cecropia obtusa* was monitored hourly during a two-day period in a disturbed area in French Guiana. The maximum activity of *C. blandus* occurred between 8:30 and 12:30, at which time *A. alfari* had retreated within the domatia and were least present on the trunks. Even though aggressive confrontations were observed, *C. blandus* workers often initiate confrontations but do not prey on *A. alfari* nor exploit food bodies produced by *Cecropia*, the principal food source of *A. alfari*. Hence hostility appears to be the result of territoriality. Differences in their foraging rhythms are proposed as promoting resource and territory partitioning in this ant assemblage. ***To cite this article: M. McClure et al., C. R. Biologies 331 (2008).***

Résumé

L'agressivité territoriale de *Camponotus blandus* envers la fourmi *Azteca alfari* en Guyane Française. Cette étude apporte de nouvelles informations sur l'interaction entre deux espèces sympatriques, *Azteca alfari* (Dolichoderinae) vivant en association avec la plante myrmécophyte *Cecropia obtusa* (Cecropiaceae) et *Camponotus blandus* (Formicinae), une espèce qui niche dans le sol. Les ouvrières d'*A. alfari* patrouillent uniquement sur le feuillage et la partie supérieure du tronc de leur hôte *Cecropia*, alors que les ouvrières de *C. blandus* ont une nidification terricole, mais explorent fréquemment la végétation basse, dont le feuillage de plantes pionnières tel que *Cecropia*. Le rythme d'activité d'*A. alfari* et le nombre de *C. blandus* présents sur *Cecropia obtusa* ont été observés toutes les heures pendant deux jours. L'activité maximale de *C. blandus* fut observée entre 8:30 et 12:30, période durant laquelle les ouvrières d'*A. alfari* se sont retirées dans les domaties et sont peu présentes sur le tronc. Malgré l'observation de certaines confrontations, les ouvrières de *C. blandus* ne sont pas prédatrices des ouvrières *d'A. alfari* et elles n'exploitent pas non

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plus les corps nourriciers produits par les *Cecropia*, source principale de nourriture pour *A. alfari*. Ainsi l'hostilité de *C. blandus* semble être une conséquence de leur territorialité. Les différences au niveau des rythmes d'activité semblent promouvoir la partition des ressources dans cet assemblage de fourmis. ***Pour citer cet article : M. McClure et al., C. R. Biologies 331 (2008).***

Keywords: *Azteca alfari* (Dolichoderinae); *Camponotus blandus* (Formicinae); Foraging; Rhythm of activity; Territorial aggressiveness

Mots-clés : *Azteca alfari* (Dolichoderinae) ; *Camponotus blandus* (Formicinae) ; Fourragement ; Rythme d'activité ; Agressivité territoriale

1. Introduction

Trees of the genus *Cecropia* (Cecropiaceae) are common pioneer plants in disturbed Neotropical landscapes. Most species of *Cecropia* are myrmecophytes, or plant-ants, that shelter their resident ants in their hollow trunk and branches (domatia) and provide them with food resources in the form of food bodies or Müllerian bodies produced by specialized pads of tissue (trichilia) situated at the base of leaf petioles. The most common resident ants belong to the genus *Azteca* (Dolichoderinae) which exhibit a wide variety of arboreal nesting habits, including being obligate inhabitants of a variety of myrmecophytes. In exchange for the lodging and the food they receive, *Azteca* ants protect their host *Cecropia* against herbivores, remove encroaching vegetation, and provide minerals [1–3].

Myrmecophytic *Cecropia* have long been thought to form associations only with *Azteca* ants, but certain species are associated with ants of the genera *Pachycondyla* (Ponerinae) and *Camponotus* (Formicinae) [3]. For example, 64% of *Cecropia purpurascens* ($n = 50$) were colonized by ants of four species, of which *Azteca alfari* (Dolichoderinae) and *Camponotus balzani* (Formicinae), were found at a higher frequency [4]. However, only one colony of any given species will inhabit the plant at any given time as these ants are highly territorial.

In most ants, including ground nesting, arboreal foraging species, territoriality contributes to the defence of spatiotemporally stable food resources and to the trails towards these sources. Their territory area is often correlated with colony size, a major determinant of competitive ability [5]. This is also true for plant-ants as in the *Azteca-Cecropia* associations, as larger trees can host larger colonies [4] that would be harder to dominate because they have more individuals available to patrol a plant and recruit defenders [1].

Camponotus blandus (Formicinae), like some other species of the genus [6], is a ground nesting-arboreal foraging species not known to colonize *Cecropia obtusa* (Cecropiaceae). Yet, *C. blandus* workers have been observed to patrol *Cecropia* trees during the day and triggering violent conflicts with the resident *A. alfari*. Other *Camponotus* species [7,8] have also been reported to regularly patrol trails and attack alien conspecifics and other ant species, but it is often difficult to distinguish territorial aggressiveness from predation, as the same behaviours can occur in both cases [9].

This study was conducted to determine if the *C. blandus* major workers frequently observed on *Cecropia obtusa* were (1) hunting *A. alfari* workers; (2) exploited Müllerian bodies; or (3) if their presence corresponded to a type of territoriality. We therefore determined the activity rhythms of these species, the frequency of their encounters and the behaviours in which they resulted.

2. Materials and methods

Fieldwork was done in Petit-Saut, French Guiana (5°03′N; 53°02′W), and data were collected in July 2006, at the end of the rainy season. Both species studied appear to be diurnal [10–12], as neither species was present when we sampled before daybreak, and therefore observations were restricted to daylight hours.

Because tree height is suspected to be correlated with *Azteca* colony size, it can be expected that fewer *C. blandus* would be successful in foraging on larger *Cecropia* trees sheltering large colonies [4]. Preliminary observations were therefore done on 51 trees ranging from 0.5 to 6 m in height and sheltering colonies of *A. alfari* to determine if their size was correlated with the presence or absence of *C. blandus* and to select for an intermediate tree height with increased probability of encounters between *A. alfari* and *C. blandus* for further observations. Binoculars were used to scan the trees and the trunks of taller trees were anchored in a bent fashion to enable easy scanning of single foraging ants.

Isolated saplings (ranging from 1 to 1.75 m in height) of *Cecropia* housing colonies of *A. alfari* were tagged. Selected trees were separated by a distance of at least 10 m, ensuring that they were far enough apart to constitute independent samples. An experimental lot corresponded to 30 trees situated on the territory of *C. blandus* colonies, while 20 other trees were not and formed a control lot. For both the experimental and control lot,

series of 2-min scans were conducted by the three authors on each tree over a 4-day-long period until every hour between 5h30 and 19h30 had been covered once for a total of 12 hours. During each shift, each individual stem was searched for ants. The activity level of *A. alfari* workers on trees was estimated on a scale ranging from 0 to 3 (0: total absence of workers; 1: up to ten workers; 2: 10 to 50 workers; 3: more than 50 workers). On experimental trees the number of *C. blandus* individuals was directly recorded in the same scans as with *Azteca*.

3. Results

Although we noted a trend of fewer *C. blandus* workers, none of which were observed walking in a file or marking trails, with increasing height of *Cecropia* trees inhabited by *A. alfari*, the difference was not significant (seven of the 24 sampled trees of less than two meters scored at least one *C. blandus* worker *versus* three of the 27 sampled trees of more than two meters; Statistica software; Fisher's exact-test; $P = 0.09$; Fig. 1). Nevertheless, almost all *C. blandus* major workers were seen trekking up larger trees before turning back at midpoint, without having encountered any *A. alfari* individuals.

The activity pattern for *A. alfari* was initiated abruptly at dawn. It declined on the experimental trees while that of *C. blandus* increased (up to five workers on a tree) at mid-morning; this was not the case on the control trees (Fig. 2). The maximum activity level for *A. alfari* was noted during the afternoon when the production of Müllerian bodies is at its highest [13], but due to the residual activity of *C. blandus* workers, *A. alfari* workers were more active on control trees than on experimental trees.

Although *C. blandus* workers were absent from most trees at any given time, when present (up to five individuals), they appeared to patrol the focal trees and on several occasions one to three workers stood guard in front of the domatia entrances (near the base of the leaf petiole at the top of the tree) where the *A. alfari* workers had retreated, preventing them from exiting. However, colonies of *A. alfari* have a large number of small, aggressive workers which can occasionally bite the legs of the larger *C. blandus* and spray defensive compounds at them. When confrontations did occur ($N = 9$), *C. blandus* workers were sometimes rapidly overcome and were even chased off the tree on two occasions, but never killed. Even when killed, *A. alfari* workers, which outnumbered the *C. blandus* and

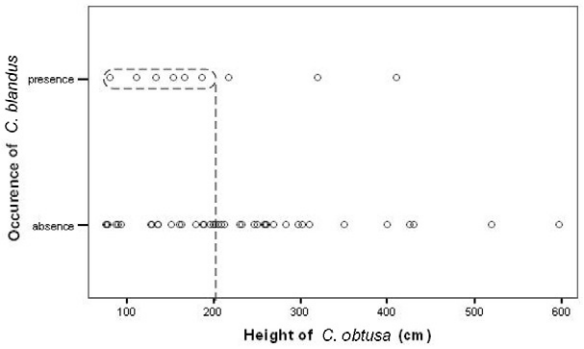

Fig. 1. The presence or absence of *Camponotus blandus* on saplings of *Cecropia obtusa* ($N = 51$) (ranging from 0.5 to 6 m in height) inhabited by *Azteca alfari*.

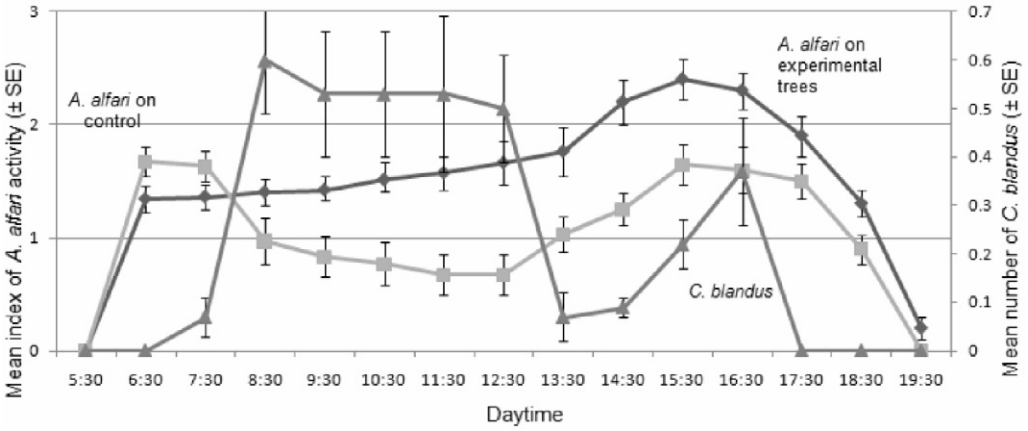

Fig. 2. Mean activity level (±*SE*) of *Azteca alfari* on control (absence of *Camponotus blandus* in the area ($N = 20$)) and on experimental ($N = 30$) *Cecropia obtusa* of the same size (1–1.75 m in height; 20 and 30 trees, respectively) likely to be on the territory of a *Camponotus blandus* colony, with the average number of *C. blandus* major workers per tree on experimental trees (mean activity level of *C. blandus* (±*SE*)) during observations ($N = 700$).

whose corpses littered the trunks, were never retrieved by *C. blandus* (a total of 24 *A. alfari* workers were killed during the nine confrontations).

4. Discussion

Territoriality varies among ants, with some species protecting only their nests or their resources, while others, including plant-ants, establish absolute territories by excluding nearly all other ants ([7,14,15] and references therein). Also, most investigated ant species establish territories that secure access to food resources, and it was suggested that spatial and nychtemeral distributions of the feeding activities among different sympatric species limit competition for resources [16].

Because tall trees can host larger *Azteca* colonies ([4]; pers. obs.) more *A. alfari* workers were observed patrolling their host tree, eventually recruiting numerous nestmates when encountering alien ants [1]. However, although the number of observed *C. blandus* decreased with increasing tree size, the difference was not significant. In fact, the difference is qualitative as when exploring large trees, *C. blandus* workers frequently turned back at mid-point on the trunk without having encountered any *A. alfari* workers. They are likely deterred by the concentration of chemical signals situated at the territorial boundaries of the large *A. alfari* colonies (see also [2]).

The activity pattern described for *A. alfari* is consistent with previous observations, commencing abruptly at dawn with a mid-day plateau or depression and a maximum in the afternoon concomitant with the production of Müllerian bodies [13]. The number of *C. blandus* individuals on the trees increased gradually to a maximum during mid-day (see also [11]). Furthermore, because *C. blandus* is mostly active before *A. alfari* is at its maximum activity level, it is possible that there is a general trade-off between behavioural dominance and thermal preference in these ant species. Indeed, *C. blandus* has been shown to be most active at ambient temperatures of 32–34 °C [17], but it is unclear whether the maximum of activity of *A. alfari* is due to thermal preference, an internal clock related with the production of Müllerian bodies [10,13], or, less likely as the number of cases is reduced, interactions with sympatric ants.

The blocking of the domatia entrances was also noted for certain Neotropical social wasps; while one wasp blocks the domatia entrance of a *Cecropia* to prevent the *Azteca* from leaving, its nestmates gather Müllerian bodies [18]. However, *C. blandus* was never observed collecting Müllerian bodies on *Cecropia* as do other ground-nesting ants, such as *Pheidole fallax* and *Solenopsis saevissima* [18]. Because the blocking of the *Cecropia* domatia entrances by *C. blandus* workers was not related to a strategy permitting to gather Müllerian bodies, nor the predation of *A. alfari* workers, the observed agonistic interactions appear to correspond only to interspecific territoriality.

This territorial response is surprising and this apparent departure from optimal foraging might stem from a behavioural constraint of this species' territorial aggressiveness. Indeed, it seems that *C. blandus* workers are "trapped" by their territoriality because they are not rewarded while blocking *Cecropia* domatia entrances and because *A. alfari* workers never forage on the ground [3] and so never compete with them. It is probable that the perception of *A. alfari* landmarks is at the origin of this behaviour, with a threshold above which *C. blandus* workers do not try to stay on *Cecropia*, such as is the case for tall trees hosting large *A. alfari* colonies. Ants "trapped" by chemical signals were reported for workers of plant-ant species that, although not rewarded, patrol the young leaves of their host myrmecophyte. In this case the most vulnerable parts of the plants are well protected through a "sensory trap", generally a brood odour-mimicking chemical at the origin of this attractiveness [19].

In fact, *C. blandus* are generalists and, when *A. alfari* is absent, may exploit resources (Hemipterans, invertebrate prey) other than Müllerian bodies. A general territorial behaviour may be maintained from benefits related to several other ant species not studied in the present work (i.e., species being important competitors and engaging in frequent encounters with *C. blandus*). That is, realized costs of hostility against *A. alfari* may very well be insignificant compared to benefits from keeping away other species, including *Azteca* species not associated with myrmecophytes. Therefore, aggressive behaviours observed during this study may be a maladaptive consequence of *C. blandus* territoriality on trees occupied by other ant species and warrants further investigation.

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