

Limited Aggressiveness Among African Arboreal Ants (Hymenoptera: Formicidae) Sharing the Same Territories: The Result of a Co-Evolutionary Process

by

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ABSTRACT

In order to understand how the arboreal ant mosaic functions, we hypothesized that dominant, sub-dominant and non-dominant ant species sharing the same trees have evolved behaviors permitting them to limit the cost of interactions during interspecific competition. We chose *Oecophylla longinoda*, the best known "dominant" species and two other Formicinae accepted on its territories: *Polyrhachis laboriosa*, a "sub-dominant" species; and *P. weissi*, a "non-dominant" species. We experimented in nature and on colonies reared on shrubs cultivated in planters. During dyadic encounters, foragers of the three species generally ignored each other. Aggressive interactions were rare and limited to intimidating postures such as opening the mandibles and raising the gaster. However, the need for protein leads arboreal ants sharing territories to prey robbing. The expected dominance hierarchy did not hold true at all levels as both *O. longinoda* and *P. weissi* rob prey from *P. laboriosa*. Also, foragers of *P. weissi* were able to follow the recruitment trails of *P. laboriosa*. As a result, predatory behavior is broken down into two tasks in the latter species: workers carving the prey that tolerate the presence of interspecific intruders, and other workers acting as guards. *P. laboriosa* guards limit the activity of the competitors thanks to allomones released during marking rounds, by drumming the gaster on the substrate, and through dissuasive postures such as opening the mandibles, raising the gaster, bending the gaster and an "outstretched posture" described here for the first time. We concluded that a code containing chemical and behavioral information working at the interspecific level enables ants sharing territories in the arboreal ant mosaic to defuse potentially volatile situations without the loss of individuals. These behaviors can be compared to "true" ritualized displays (i.e. intraspecific), and work here at the interspecific level, implying a co-evolutionary process as selective pressure.

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INTRODUCTION

Among tropical arboreal ants, "dominant" species are characterized by highly developed intra- as well as interspecific territoriality between them. As a result, their territories are distributed in a mosaic pattern in the forest canopy (Majer 1972; Leston 1973; Hölldobler & Wilson 1978). On the contrary, they tolerate on their own territory "non-dominant" species, which are less aggressive and do not defend a territory. Nonetheless, species do exist whose status is intermediary. Generally, they behave like "non-dominant" species, but are capable, under certain conditions, of defending a territory and are, as such, cited as "sub-dominant" (Majer 1976a, b, 1993).

We hypothesized that dominant, sub-dominant and non-dominant ant species sharing the same trees have evolved behaviors permitting them to limit the cost of interactions during interspecific competition. Three kinds of behaviors fulfil these conditions: (1) the complementary nature of the diets; (2) the different rhythms of activity; and (3) behaviors which seem ritualized at the interspecific level (Hölldobler & Wilson 1990; Mercier & Dejean 1996).

Mc Farlans defined "true" ritualized behavior (i.e., at the intraspecific level) as "an evolutionary process by which behavioral patterns become modified to serve communication". Ritualized displays frequently become stereotyped in form and incomplete in their execution, involve a change in function, a change in motivation, and are often accompanied by the evolution of special markings. Such behaviors have been well studied in ants (review in Hölldobler & Wilson 1990; Yamagushi 1995; Mercier *et al.* 1997). The behaviors that we studied here have another origin as they evolved between competing syntopic ant species.

MATERIALS AND METHODS

We chose to work on *Oecophylla longinoda* as the territoriality of this dominant ant species has been thoroughly documented. As sub-dominant, we selected *Polyrhachis laboriosa*, another Formicinae whose biology is beginning to be well known, and as non-dominant, *P. weissi*. The main characteristics of these ants are shown in Appendix 2 and the description of the behavioral displays that we analyzed in Appendix 1.

This study was conducted during four different periods on four colonies of *O. longinoda*, eight colonies of *P. laboriosa* and four colonies of *P. weissi*. These colonies were reared on shrubs cultivated in planters installed on a balcony (13m x 3m) of a building in Yaoundé, Cameroon. Foraging workers were free to explore over the balcony and received honey daily.

Everyday, encounters between species were recorded during 1H-periods at different times of the day. Each time, we placed a prey on a table accessible to all workers. The observers were forced to wait for situations when workers of competing species interacted around the prey. For that reason, each series of experiments between two colonies lasted between two to four months. We used small (< 1 cm) numbered Tettigonidae larvae easily transportable by a worker of both species of *Polyrhachis*, or large (> 4 cm) numbered Tettigonidae not transportable by a single worker.

These experiments were completed with field observations of dyadic encounters by a team of researchers, during more than 200 outings in southern Cameroon.

Statistical comparisons were conducted using the Student t-test (Statistica software) or the Fisher exact test (StatXact software).

RESULTS

Encounters between *O. longinoda* and *P. weissi* foragers

We observed 22 cases when *P. weissi* foragers obviously avoided *O. longinoda* workers out of more than 200 dyadic encounters without noticeable aggressiveness. However, the presence of prey slightly changed the dynamics of these encounters. For example, we noted six cases out of 30 when *P. weissi* foragers obviously avoided an *O. longinoda* worker with its mandibles opened and its gaster raised while defending a group of nestmates occupied in spread-eagling a prey.

Encounters between *O. longinoda* and *P. laboriosa* foragers

During dyadic encounters observed in nature as well as on the balcony, aggressive interactions were limited to opening the mandibles and/or raising the gaster by *O. longinoda* workers that were avoided or ignored by *P. laboriosa* foragers (Table 1). The latter never attempted to rob a prey spread-eagled by a group of *O. longinoda*. They always changed their path and continued to forage.

When transporting a small prey and encountering a group of *O. longinoda*, a *P. laboriosa* forager immediately accelerated its movement and avoided the group. Faced with its agility and swiftness, the *O. longinoda* workers never attempted to rob the prey.

During 147 observations of *P. laboriosa* workers cutting up a large prey (see description in Dejean *et al.* 1994), one to three workers played the role of guard. Each guard moved slowly around the prey along a path that swept in a complete ellipse, without withdrawing from the prey over more than 5 cm. As they moved, they leaned their bodies to one side, stretched out the corresponding hind leg and dragged it as well as the

tip of their gasters, over the substrate. Sometimes, the guards drummed their gasters on the substrate. In the absence of any competitor, one to six ellipsoid trails were laid around the zone where the prey was cut up ($\bar{x} = 2.36 \pm 1.19$ rounds; $n = 25$). In the presence of *O. longinoda* foragers, the guards significantly increased the number of rounds around the prey (one to eight rounds; $\bar{x} = 3.3 \pm 1.92$ rounds; $n = 12$; $t = 3.8$; $df = 11$; $p < 0.010$). In 12 cases out of 13 (92.3%), *O. longinoda* avoided the five to nine workers of *P. laboriosa*. But once (7.7%), the situation differed as only three *P. laboriosa* workers cut up the prey. The *O. longinoda* worker discovering the scene opened its mandibles and raised its gaster, alarming six nestmates situated in the vicinity. Five of them approached while the sixth returned to the nest laying a scent trail, so that numerous recruited nestmates arrived in a few seconds. After about five minutes, an *O. longinoda* worker approached the prey, seized a leg and pulled it back over 2 cm. Others arrived immediately, also seized the leg and pulled it back. The prey was dragged over 5 cm, then surrounded by 10 *O. longinoda* workers that retrieved it whole to their nest. The three *P. laboriosa* workers remained in place mandibles apart, gaster curved and antennae folded backward. They abandoned the spot more than 10 min after the *O. longinoda* had robbed their prey. Note that we did not record direct conflict between workers of the two species.

Encounters between *P. laboriosa* and *P. weissi* foragers

In total, we recorded 264 encounters between *P. laboriosa* and *P. weissi* individuals. No aggressive interactions occurred between single foragers, but *P. weissi* obviously avoided *P. laboriosa* in 12.4% of the cases (Table 2; seq. 1).

A *P. weissi* forager encountering a group of *P. laboriosa* workers

These observations occurred at the end of the evening while workers of *P. laboriosa* were cutting up a prey (Table 2; seq. 2 to 4; 77 cases). In 84.4% of the cases, the *P. weissi* foragers discovered the scene by chance, while for the other cases, they encountered, then obviously followed the recruitment trail of *P. laboriosa*. They walked either toward the prey or toward the *P. laboriosa* nest, so that they turned back when approaching the nest, then went in the correct direction. The comparison of the latter cases with a theoretical random orientation at the point where they crossed the trail of the competing species resulted in a significant difference ($p < 0.01$).

When perceiving *P. weissi* foragers, the *P. laboriosa* guards signifi-

cantly increased the number of rounds around the prey (two to 11 rounds; $\bar{x} = 4.43 \pm 1.99$ rounds; $n = 23$; comparison with absence of competitors: $t = 8.5$; $df = 22$; $p < 0.001$).

The 77 recorded *P. weissi* foragers always attempted to approach the prey in spite of the presence of the guards, so that we recorded the following behavioral sequences, while other *P. laboriosa* workers pursued the cutting up of the prey. (1) The guards undertook new rounds, intensifying chemical trails, and periodically drumming their gasters. In response, 25 intruders abandoned their advance at this point (32.5%). (2) Faced with the 52 intruders that continued their advance toward the prey, the guards placed themselves between the prey and the intruders and took on an intimidating posture (mandibles opened and gaster bent) while they drummed their gasters. Eleven of them also undertook new marking rounds. Faced with these behaviors 28 intruders abandoned (53.8%) while 24 continued to approach the prey. (3) The *P. laboriosa* guards placed themselves in front of the approaching intruders, in an "outstretched posture" and drummed their gasters. Guards and intruders faced each other with mandibles in contact during one to ten seconds. As a result 15 intruders abandoned their attempt to reach the prey (62.5%). (4) The nine remaining intruders faced the guards that attacked them and sprayed venom, ultimately causing them to flee. When out of reach of the guards by 10 to 20 cm, the sprayed *P. weissi* foragers stopped to clean their antennae and different parts of the body during five to 20 minutes.

Several *P. weissi* foragers encountering a group of *P. laboriosa* workers.

During 22 cases out of the 77 previously described, the *P. weissi* foragers that abandoned approaching the prey recruited two to six nestmates. Recruited workers attempted to approach the prey cut up by *P. laboriosa* (66 recruited workers; Table 2; seq. 5). We observed 35 direct confrontations involving one of these recruited *P. weissi* workers and one of the *P. laboriosa* guards resulting in a sequence of behaviors similar to the previous case, but with a higher percentage of full attacks (22 cases out of 35; 62.8% vs. 9 cases out of 77; 11.7%; Fisher exact test: $p = 6 \times 10^{-8}$). During this time, 31 other recruited workers reached the prey (one to three per case). They were never attacked by the *P. laboriosa* that cut up the prey on the spot, permitting them to lick the haemolymph of the prey and in 6 cases to be able to rob a piece of prey.

DISCUSSION

Note that we never observed encounters between an *O. longinoda* or a *P. laboriosa* forager and a *P. weissi* worker retrieving a prey or a group of *P. weissi* capturing a large prey. This is due to the shifting of the peak of activity between these species, to the low density of the workers, and to the very rapid capture and retrieval of small, numbered prey by solitary foragers. Moreover, it seems that large preys were never captured by *P. weissi* due to competition with two well-organized predators (Dejean 1990, 1991; Dejean *et al.* 1994b).

The level of aggressiveness during dyadic encounters between foragers, always very low, was reduced to rare cases of intimidating postures (opening the mandibles and raising the gaster) by workers of the dominant species. These results corroborate field observations that permitted the definition of the status of sub- and non-dominant corresponding to species well tolerated by dominants (Majer 1976 a, b, 1993; Hölldobler & Wilson 1990). The low level of aggressiveness observed on the balcony reflected natural conditions. Note that in nature it is difficult to introduce alien non-dominant ants on a tree occupied by a dominant species. For instance, Hölldobler (1983) noted that introduced workers of the non-dominant *Polyrhachis* sp. on the territory of a *O. smaragdina* colony were attacked although these species can share the same trees. The origin of the tolerance could be due to the capacity of the dominant to learn the colony odor of the associated non-dominant, and vice versa, as noted between parabiotic ant species by Orivel *et al.* (1997).

The need for protein seems to be a limiting factor for arboreal life. For example, it leads *O. longinoda* to hunt on secondary territories situated at soil level, to attack other ants such as *Tetraponera aethiops* and to rob prey, even from Dorylinae (Dejean 1990, 1991; Hölldobler & Wilson 1990). Our experiment on the balcony sought precisely to exploit this phenomenon in order to observe the compared ant species in competition for prey. The expected dominance hierarchy did not hold true at all levels. Indeed, workers of *O. longinoda* were never attacked by nor elicited intimidating postures from either other species, and were able to rob prey from *P. laboriosa*. However, workers of *P. weissi* (non-dominant) regularly tried and succeeded in robbing prey from *P. laboriosa*. Also, foragers of *P. weissi* were able to follow the recruitment trails of *P. laboriosa* (these trails are therefore kairomones for *P. weissi*) as they did with the trails of *Atopomyrmex mocquerysi* (Dejean 1996).

As a result, *P. laboriosa* is at the center of the system in which the predatory behavior is broken down into two tasks with some workers

carving up the prey (they tolerated the presence of interspecific intruders) and the others acting as guards. Thanks to a co-evolutionary process *P. laboriosa* guards limit the activity of the competitors thanks to chemical and semantic communications, permitting the species to coexist.

The allomones released by *P. laboriosa* guards during marking rounds were 100% dissuasive for *O. longinoda* (prey robbing noted only in the absence of guards) and 32.5% for *P. weissi* foragers (they were then reinforced in order to increase their dissuasive effect on foragers that continued to approach the prey).

Among dissuasive semantic postures we recorded previously-known postures such as opening the mandibles, raising the gaster, bending the gaster (see Appendix 2) as well as the "outstretched posture", a new behavior, plus drumming the gaster, rather known as an alarm behavior (Hölldobler & Wilson 1990). Even when present, full attacks by the guards on *P. weissi* intruders never led to death. In other known cases of interspecific competition for food in ants, the time needed by each species for foraging is optimized by the limited simultaneous presence of the antagonists at the source. During hinge periods, conflicts often end up with cases of mutilation or death (review in Hölldobler & Wilson 1990; Savolainen 1991; Retana & Cerdà 1995).

As they provoked the desired reaction from the antagonist and thus permitted direct conflicts to be avoided, the behaviors described in this study can be compared to "true" ritualized displays (i.e., intraspecific). In this case, they work at the interspecific level, implying a co-evolutionary process as selective pressure.

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APPENDIX 1. DESCRIPTION OF THE BEHAVIORAL DISPLAYS

Escape displays.

Fleeing: the ant immediately changed direction and increased its speed when coming into contact with a competitor.

Avoidance: the ant coming into contact with a competitor also changed direction but increased its speed only over 5 to 10 cm, then pursued its foraging.

Non-aggressive displays.

Ignoring: the ant pursued its foraging.

Agonistic displays.

Opening the mandibles: the ant remained immobile, with the mandibles opened, threatening the competitor; this display, considered as a ritualized version of "biting", has a dissuasive function (Hinde, 1970; Hölldobler & Wilson, 1977, 1978, 1990; De Vroey & Pasteels, 1978).

Bending the gaster: when not followed by venom spraying, this display may have a dissuasive function, so that it is considered as a ritualized version of "formic acid spraying" (see Hölldobler & Wilson 1990; Mercier & Dejean, 1996).

Raising the gaster: this display also has a dissuasive function and can be accompanied by opening mandibles (see Hölldobler & Wilson 1978; Mercier & Dejean, 1996).

Drumming: the workers tapped the substrate with their gaster, making a rattling noise.

"Outstretched posture": the worker remained in place, oriented toward the intruder; its body is forward, antennae are tilted back, mandibles apart, and the midlegs and hindlegs are outstretched backward; this posture seems to permit the swift backward movement of the body.

Full attack: one worker violently attacked the competitor, biting and spraying venom. Note that all previous displays have been already noted as "ritualized" in other studies, except for outstretched posture described here for the first time.

Appendix 2: Characteristics of the different species studied.

Worker size	<i>Oecophylla longinoda</i> Triphasic allometry Minor : < 5.0 mm / Major : > 10.0 mm	<i>Polyrhachis laboriosa</i> Monomorphic (Bolton, 1973) 10.2 – 11.6 mm	<i>Polyrhachis sp.</i> Monomorphic (Bolton, 1973) < 6.0 mm
Colony size	Up to 800,000 workers; Polydomous (Hölldobler & Wilson 1990)	1,000 - 10,000 workers; Polydomous (Mercier, 1997)	Small societies < 5,000 workers; Polydomous (Dejean, pers. obs.)
Habitat	Nests in foliage; Leaves bound together with larval silk	Nests in foliage; Vegetable fragments agglomerated with saliva and web silk (Bolton, 1973)	Nests under leaves or in hollow branches; Vegetable fragments larval agglomerated with larval silk (Bolton, 1973)
Dominance status	Dominant; Absolute territories (day and night) (Majer, 1976a, b; Hölldobler & Wilson 1990)	Sub-dominant; Less aggressive than <i>O. longinoda</i> (Leston, 1973; Majer, 1976a, b; Dejean <i>et al.</i> , 1994a; Mercier <i>et al.</i> , 1997)	Non-dominant; Non aggressive
Defense mechanism	Spread-eagling	Venom spraying; Spread-eagling; Ritualized behavior (Mercier & Dejean, 1996; Mercier <i>et al.</i> , 1997)	Venom spraying (Dejean, pers. obs.)
Circadian rhythm	Mainly diurnal (Dejean, 1990a)	Diurnal; Bimodal peak (Mercier & Dejean, 1996)	Diurnal; Crepuscular peak (Dejean, pers. obs.)
Mode of foraging	Permanent Trunk-route (Hölldobler & Wilson, 1978;)	Individual foraging; Group recruitment (Mercier, 1997)	Individual foraging; Trail sharing of other species (Dejean, 1996; pers. obs.)
Diet	Omnivorous; Stalk; tends Homoptera (Hölldobler & Wilson 1990)	Omnivorous; Hunt; Tends Homoptera (Dejean <i>et al.</i> , 1994b)	Omnivorous (Dejean, pers. obs.)