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Ritualised versus aggressive behaviours displayed by *Polyrhachis laboriosa* (F. Smith) during intraspecific competition

J.L. Mercier [a,b,*], A. Lenoir [a], A. Dejean [b]

[a] *Laboratoire d'Ethologie et Pharmacologie du Comportement, Université F. Rabelais, Faculté des Sciences et Techniques, Parc de Grandmont, 37200 Tours, France*

[b] *Laboratoire d'Ethologie Expérimentale et Comparée, URA CNRS No. 2214, Université Paris-Nord, av. J.B. Clément, 93430 Villetaneuse, France*

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Abstract

The intraspecific territoriality of *Polyrhachis laboriosa* was studied thanks to dyadic confrontations between nestmates and alien foragers in chemically marked and unmarked arenas, complementing experiments and observations in nature. When foragers meet, the alien flees while the resident attacks, especially when on a marked area. However, when an alien scout extends its territory, it attacks the resident ant, such confrontation resulting in a high rate of reciprocal full attacks. When surrounded by several residents, the intruder is always spread-eagled if it does not succeed in fleeing. We described ritualised displays, such as threatening (opening mandibles; bending the gaster) or appeasing behaviours (antennal boxing; attempt at trophallaxis; pupal posture; raising the gaster). They occur only when the encounter maintains a low level of aggression, during laboratory experiments, or in nature during encounters involving a queen or an experimentally-introduced intruder. Foraging queens are tolerated on the territories of conspecific mature colonies. When they encounter resident workers, reciprocal avoidance occurs. Nevertheless, the latter perform ritualised displays when the queens approach their nest or attempt to rob their prey. This situation seems to compensate in part the archaic semi-claustral mode of foundation of this species, as the queens are indirectly protected by their conspecifics who do not tolerate other competitors around large food sources. © 1997 Elsevier Science B.V.

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1. Introduction

Aggression and interference competition have been known to play key roles in the organisation

* Corresponding author.

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of ant communities. Intraspecific competition has been studied in several ant species, with acts of aggression between residents and intruders analysed during dyadic or group encounters, in the field or in the laboratory (Le Moli and Parmigiani, 1982; Carlin and Hölldobler, 1986, 1987; review by Wilson, 1990). Recently, Retana and Cerdá (1995) recorded that the level of aggression depends on the species and on the experimental conditions. Furthermore, certain ant species have evolved ritualised aggressive behaviour (Hölldobler, 1971, 1981, 1982; Ettershank and Ettershank, 1982; Le Moli and Parmigiani, 1982; Carlin and Hölldobler, 1983; Yamaguchi, 1995). Ritualisation is frequent in Vertebrates and McFarland (1981) defined it as ''an evolutionary process by which behavioural patterns become modified to serve communication''. Ritualised 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.

Tropical arboreal ants are distributed in a mosaic pattern in the canopy of forests and tree crop plantations. This ant mosaic corresponds to the territories of 'dominant' species characterised by large, polydomous colonies and intra- as well as interspecific territoriality. These ants tolerate on their territories 'non-dominant' and 'sub-dominant' species which have smaller colony sizes (Majer, 1972, 1976a,b, 1993; Leston, 1973; Hölldobler and Wilson, 1978; Majer et al., 1994). Nevertheless, under certain circumstances, subdominants are able to defend territories and are, as such, interesting for the understanding of the establishment of ant mosaics. The goal of this research concerns biological control using ant mosaics that could favour beneficial ant species and exclude others (see Majer, 1976a,b).

The aim of this paper is to study intraspecific aggressiveness in *Polyrhachis laboriosa*, a subdominant species whose status is probably due to its capacity for ritualised behaviour, both at the interspecific level (including the dominant species *Oecophylla longinoda*; see Mercier and Dejean, 1996; Mercier et al., 1996) and the intraspecific level, the present study.

2. Materials and methods

2.1. The ant species

P. laboriosa is a diurnal polydomous ant whose colonies contain from 1000 to 10 000 workers (Mercier et al., 1994). This species, although recorded in the canopy of old tropical forests, lives mostly in forest edges, along the banks of rivers, the sides of paths and in orchards (i.e. citrus, mango, cacao) (Majer, 1972, 1976a,b; Leston, 1973; Dejean et al., 1992). The nests are attached to the undersides of several leaves thanks to a mixture of vegetable fragments held together with saliva and silk (Collart, 1932). Although the species belongs to the Formicinae, colony foundation is semi-claustral (founding queens forage for the first brood), as in the primitive subfamily Ponerinae (Lenoir and Dejean, 1994). Workers forage solitarily, grazing algae and epiphyls on leaf surfaces and exploiting small extrafloral nectaries. Larger sugary food sources can also be exploited and different kinds of prey can be caught, including large, non-transportable items that are cut up on the spot by recruited workers (Bolton, 1973; Leston, 1973; Majer, 1976a,b; Dejean et al., 1994).

2.2. Description of the behavioural displays

During confrontations between workers, or between workers and foraging queens we observed and categorised the following behaviours.

2.2.1. Displays performed by the intruders

2.2.1.1. Escape displays. No aggressive behaviour was performed by the intruders, except during reciprocal full attacks, when they defended themselves against the residents. The following behaviours are not aggressive displays but they arise consequently from the aggression of the resident ant.

Fleeing: When the resident came into contact with the intruder, the latter immediately changed direction, increased its speed and tried to climb up the walls of the arena during dyadic confrontations. In natural situations it swiftly escapes or

jumps from the branch or the leaf where it encountered the resident.

Attempting to escape: When held by a leg by the resident, the intruder tried to escape by walking quickly and sinuously. It was grouped with 'Fleeing' display.

2.2.1.2. Ritualised displays.

Antennal boxing: The resident and the intruder faced each other and moved their antennae very rapidly. The resident tried to bite the intruder, while the latter kept the resident at a distance with its antennal movements. This display was described for the first time by Ward (1986) on *Rhytidoponera metallica*, and can be considered as the ritualisation of the identification of the opponent with the antennae, whose function is modified in an attempt to keep the opponent far away.

Attempt at trophallaxis: The intruder solicited the resident, which responded as for trophallaxis; but the exchange is very brief. Ettershank and Ettershank (1982), who observed the same behaviour in *Iridomyrmex purpureus*, concluded that it is ritualised trophallaxis, incomplete in form and whose function changed in an attempt to appease the resident.

Pupal posture: The ant being attacked folded its antennae and legs in against the body and became motionless. In the Formicinae as well as in *P. laboriosa*, the same position was observed during nest moving in the laboratory and in nature, when the carried nestmate rolled into a backward-facing pupal posture (Hölldobler and Wilson, 1990 and personal observations). In the present study, this ritualised behaviour was not followed by carrying but probably limited aggression by the resident.

2.2.2. Displays performed by the residents

2.2.2.1. Aggressive displays.

Biting: The following types of biting were observed. (1) Mandible bite. The resident bit a mandible of the intruder and pulled it out, or remained immobile. (2) Antenna bite. The resident bit the intruder at the bottom of the funiculus or at the basis of the scape. (3) Leg bite. The resident bit the intruder at the bottom of the tibia or at the tarsus. Any leg could be bitten.

Spread-eagling the intruder: This behaviour happened when the intruder was confronted with several residents and did not succeed in fleeing. Each resident bit a leg or an antenna of the resident and pulled it towards herself.

2.2.2.2. Ritualised displays.

Mandibles opening: The ant remained immobile, with the mandibles opened, threatening the intruder. This display is considered as a ritualised version of 'biting' and has in these situations a dissuasive function. (Hinde, 1970; Hölldobler and Wilson, 1977, 1978; De Vroey and Pasteels, 1978).

Gaster bending: When not followed by venom spraying, this display has a dissuasive function, so that it is considered as a ritualised version of 'formic acid spraying' (Le Moli and Parmigiani, 1982; Carlin and Hölldobler, 1983; Mercier and Dejean as 'Flexing the gaster' in *P. laboriosa*, 1996). This ritualised behaviour was also observed in *Myrmica rubra* (De Vroey and Pasteels, 1978).

Gaster raising: As above, this display has a dissuasive function and was already observed during interspecific competition (Mercier and Dejean, 1996).

2.2.3. Concomitant displays performed by both the intruders and the residents

2.2.3.1. Aggressive displays.

Reciprocal full attack: The resident violently attacked the intruder who defended herself, both ants locking their mandibles on the other's body and appendages while spraying formic acid (Carlin and Hölldobler, 1983, 1986, 1987 in *Camponotus* sp.).

Venom spraying: The worker bent its gaster under the alitrunk and sprayed venom (bubbles could be seen on the other ant). This always occurred when the both workers were gripped together, so we grouped this behaviour with 'reciprocal full attack'.

2.2.3.2. Non-aggressive displays.

Reciprocal avoidance: This behaviour was recorded during encounters in nature between non-nestmates and when alien foraging queens encountered resident workers.

Ignoring each other; **reciprocal antennations**: These behaviours were recorded only during encounters between workers belonging to the same nest or to two different nests of the same colony. Such behaviours were grouped with 'no aggressive display'.

2.3. Experimental device

2.3.1. Provoked encounters under laboratory conditions

In order to test intraspecific aggression, 70 dyadic encounters were provoked between nestmates or conspecific aliens chosen among the foragers. A total of two nests belonging to neighbouring trees (10 m distant; nests A and B) were chosen as well as a third (C) situated 150 m away from the others. For each encounter, two foragers were placed in a cleaned, partitioned neutral arena (8 cm in diameter; 5 cm in height). The partition between the two foragers was removed 10 min later and the timed test (5 min) started when one of the two foragers reacted to the other. A total of six kinds of encounters were tested: (1) Encounters between nestmates from the same nest (A–A; B–B; C–C; 30 tests); (2) encounters between non-nestmates from two neighbouring nests (A–B; 20 tests); (3) encounters between non-nestmates from two distant nests (A–C; B–C; 20 tests).

The influence of territorial landmarks was tested during 40 different dyadic encounters provoked between foragers from two other non-neighbouring nests (D and E). The bottoms of 20 arenas were covered with filter paper which had been previously placed in the foraging arena of colony 'D' over 1 week (tarsal marking with hindlegs; Mercier and Lenoir, in preparation); the bottoms of the 20 others were marked by the workers of nest 'E'.

We worked under double-blind conditions: All the encounters were randomly arranged in chronological order and the observers did not know which kind of encounter they were testing. During each encounter, we recorded the behaviour of each ant every 10 s (instantaneous scan sampling), resulting in 31 behaviours per ant per replicate.

During a third test we introduced alien workers one by one into the foraging arenas (30×30 cm) of five colonies reared in the laboratory, and we observed the behaviour of the intruders and of the residents when they met.

2.3.2. Provoked encounters in nature

We introduced foraging workers previously caught with a forceps onto the territories of different colonies in a zone with several active workers. The introduced workers can originate from: (1) the same nest; (2) another nest belonging to the same colony; (3) another nest belonging to another colony situated in close proximity; or (4) a nest more than 150 m away.

2.3.3. Intercolonial encounters under semi-free conditions

We tested eight colonies of *P. laboriosa* (two at a time), in order to study intraspecific competition during a series of experiments lasting from 2 to 4 months. The nests were installed on shrubs of 1–2 m high (*Alchornea cordifolia*, *Bridelia micrantha*, Euphorbiaceae and *Costus albus*, Zingiberaceae) cultivated in large planters, the workers being free to explore over a balcony (13×3 meters), of a building in Yaoundé, Cameroon. *A. cordifolia* produced abundant extrafloral nectar, while *B. micrantha* and *C. albus* supported Homoptera (depending on the period, Coccidae, Stictococcidae, Membracidae and Tettigometridae), so that a large part of the nutrition required by the colonies was furnished by these plants. In order to facilitate observations, prey and drops of honey were placed on a nearby table that the ants rapidly explored.

Encounters between alien foraging workers were observed for 1-h periods at different times of the day, permitting behavioural sequences to be defined and their frequency noted. We also recorded the behaviour of three founding queens (originating from areas several kilometres away from the places where we obtained the colonies) during their foraging activities on the territories of the colonies.

2.4. Statistical comparisons

For statistical comparisons we used the Student *t*-test for comparisons of displays during dyadic encounters in the arena and the Fisher exact test for comparisons of percentages in the other cases.

3. Results

3.1. Provoked dyadic encounters in arenas (Table 1, experiments 1–5).

During the control encounters between nestmates (exp. 1), only 0.2% of aggressive behaviour was observed. No significant difference was recorded when the tests concerned workers originating from two neighbouring nests (exp. 2; 2.4% of the displays). In both cases, the aggression corresponded to a ritualised display: mandibles opening (only three workers opened their mandibles for a short time in exp. 1). This threatening display was often observed in nature and in the laboratory when the nests were disturbed. First, the guards were very aggressive, running in all directions, trying to bite everything and making a rattling noise with their gaster. After a moment, they stopped and kept their mandibles opened. The two nests could be consequently considered as belonging to the same colony (Mercier et al., 1994).

We recorded significantly more aggressive behaviour during encounters between non-nestmates in a neutral arena (exp. 3; only 61% of non-aggressive behaviour), with the emergence of biting (9.6%) and reciprocal full attack with venom spraying (3%). We observed more cases of ritualised displays, with mandibles opening (11.9%) and pupal posture (1.1%).

When the confrontations occurred on a marked territory (exps. 4 and 5), the ants were more aggressive (only 39.9–43.1% of non-aggressive behaviour); the rate of biting (36.8–38.5%) was significantly superior and three situations occurred: (1) when bitten on its mandible, the intruder was immobilised; (2) when bitten on the antenna, the intruder did not seem able to resist and was at the mercy of the resident ant, who forced the intruder into every part of the arena; (3) when bitten on a leg, the intruder reacted by moving (see 'attempt to escape'), biting or trying to raise up on its legs with the aim of bending the gaster between its legs and spraying venom; in the face of the latter behaviour, the resident laid down, trying to keep the intruder on the ground and prevent it from spraying venom. The rate of reciprocal full attacks with venom spraying (3.1–9%) was not significantly superior to that of encounters in a neutral arena, while the rate of ritualised behaviour decreased to 5.8% ($(1.5 + 0.4 + 3.9) - (0.7 + 1.1 + 4)$%), mandibles opening displays (3.9–4%) being significantly inferior.

We observed that workers were more aggressive in marked arenas than in unmarked ones, the resident biting more frequently in its own arena (36.8–38.5%) than in a neutral one (9.6%). During encounters in marked arenas, the resident became significantly more aggressive than the intruder. It had more tendency to bite (36.8–38.5%), while the latter had more tendency to flee (6.8–11.2%).

We recorded more ritualised displays by workers during experiments in unmarked arenas, when they were not too aggressive, than in marked ones. In our study, antennal boxing was always followed by an attempt at trophallaxis from the intruder. This display had an appeasing role: The resident temporarily lost its aggressiveness and began trophallaxis, then groomed itself and explored the arena. When it met the intruder again, it could be very aggressive.

3.2. Natural encounters between non-nestmates (Table 1, experiments 6 and 7; Table 2, experiment 8).

In nature we observed spontaneous encounters between non-nestmates (exp. 6) resulting in reciprocal avoidance (33.3%); one worker attacked, while the other fled (26.7%); or a reciprocal full attack with venom spraying (40%).

A few days after the colonies were placed on the balcony (see Section 2.3.3) and separated from each other by less than 10 m, two small territories were established, each colony exploiting food sources on its own territory. Encounters between

Table 1
Comparison of the different behavioural phases recorded during provoked or natural dyadic encounters between foraging workers or between foraging workers and queens

Experiments	1	2	3	4	5	6	7
Behavioural phases recorded	Confrontations between workers during dyadic encounters						
	Nestmates	Neighbouring nests	Non-nestmates on neutral arena	Non-nestmates on marked arena		Foragers in nature	Foragers on balcony
	A–A; B–B; C–C	A–B	A–C; B–C	Territory D	Territory E		
Reciprocal avoidance (%)	—[a]	—	—	—	—	33.3[b]	—
No aggressive response (%)	99.8[a]	97.6[a]	61[b]	43.1[c]	39.9[c]	—	—
Reciprocal full attack/venom spraying (%)	—[a]	—	3[a,b]	3.1[b]	9[b]	40.0[c]	96.5[d]
Behaviour of the intruder							
Fleeing (%)	—[a]	—	14.4[b]	11.2[b]	6.8[b]	26.7[c]	3.5[d]
Pupal posture (%)	—[a]	—	1.1[a]	1.5[a]	0.7[a]	—	—
Antennal boxing/attempt at trophallaxis (%)	—[a]	—	—	0.4[a]	1.1[a]	—	—
Behaviour of the resident							
Mandibles opening (%)	0.2[a]	2.4[a,c]	11.9[b]	3.9[c]	4[c]	—	—
Gaster bending (%)	—[a]	—	—	—	—	—	—
Biting (%)	—[a]	—	9.6[b]	36.8[c]	38.5[c]	—	—
No. of encounters	30	20	20	20	20	30	170
No. of acts	1860	1240	1240	1240	1240	—	—
No worker killed (%)	[e]	[e]	[e]	[e]	[e]	60.0	3.5
One worker killed (%)	—	—	—	—	—	6.7	12.9
Two workers killed (%)	—	—	—	—	—	33.3	83.6

All the behaviours in italics correspond to ritualised displays.
[a–d] Indicate significant differences for one line.
[e] The observations finished before the end of the encounter; the percentages were calculated from the number of displays.

Table 2
Comparison of the different behavioural phases recorded during provoked or natural encounters between an alien foraging worker or queen and several residents

Experiments	8	9	10	11	12	13	14
Behavioural phases recorded	Confrontations between one worker and several residents			Confrontations between one queen and one or several resident workers			
	Foragers on balcony	Intruder = worker introduced		1 queen vs 1 worker		Intruder = queen that met	
		In nature	In laboratory	Both forage	Next to the nest	Foragers	Guards
Reciprocal avoidance (%)	—[a]	—	—	100[b]	—	6.7[c]	—
Reciprocal full attack/venom spraying (%)	98.4[a]	31.7[b]	6.5[c]	—	—	—	—
Behaviour of the intruder							
Fleeing (%)	1.6[a]	68.3[b]	72.2[b]	—	—	—	4.4[a]
Avoiding the resident (%)	—[a]	—	21.3[a]	—	100	—	95.6[b]
Ignoring the resident (%)	—[a]	—	—	—	—	93.3[b]	—
Behaviour of the resident							
No aggressive response (%)	—[a]	—	15.2[a]	—	—	93.3[b]	—
Attempting to seize (%)	1.6[a]	35.4[b]	65.8[c]	—	—	—	—
Mandibles opening (%)	—[a]	5[a]	3.9[a]	—	42.8[d]	—	—
Gaster raising (%)	—[a]	—	2.2[a]	—	57.2[b]	—	100[b]
Biting (%)	—[a]	27.9[a]	6.4[b]	—	—	—	—
Spread-eagling (%)	98.4[a]	59.6[b]	12.9[c]	—	—	—	—
No. of acts	—	—	310[e]	44	28	119[e]	68[e]
No. of encounters	62	79	5	—	—	17	17
No individual killed (%)	1.6	35.4	[f]	100	100	100	100
Intruder killed (%)	98.4	64.6	—	—	—	—	—

All the behaviours in italics correspond to ritualised displays.
[a–d] Indicate significant differences for one line.
[e] Percentages were calculated from this value, which corresponds to the number of interactions between the intruder and several residents.
[f] The observations finished frequently before the end of the fight.

non-nestmates were observed when a scout ant explored the other territory and encountered a resident (exp. 7). The intruder fled in only 3.5% of the encounters, the other cases resulting in a reciprocal full attack (96.5%) with the death of one worker (12.9%) or both (83.6% of the cases). Workers were significantly more aggressive in this situation than in experiment 6. This can be explained by the fact that during the observations in nature, we recorded three probable situations. (1) The same as noted above (exp. 7; a scout on the territory of a forager), resulting in reciprocal full attacks. (2) Reciprocal avoidance, frequent but never recorded on the balcony, may correspond to encounters between foragers (or maybe scouts) outside their territories or at the limits of their territories (see the notion of 'no-ant's land' between two territories of a dominant species; Hölldobler and Wilson, 1978). (3) The differences between the rates of fleeing displays by only one worker (26.7 vs. 3.5%) may be due to encounters between foragers, one being on its territory, the other, who flees, outside its territory. This situation was controlled by introducing foragers onto alien territories (see Table 2; exp. 9).

When the intruder met a resident surrounded by nestmates, it avoided combat by swiftly escaping in 1.6% of the cases, while in all others (98.4%) a reciprocal full attack took place, followed by the spread-eagling of the intruder (Table 2; exp. 8). In all these situations, no ritualised behaviour occurred.

3.3. Introduction of a worker on the territory of a colony in nature (Table 2; experiment 9)

Confrontations between non-nestmates resulted in an attempt at biting on the part of the resident, while the intruder fled (68.3%) or counterattacked, so that a reciprocal full attack occurred (31.7%). Intruders that did not succeed in fleeing (27.9%) were spread-eagled as were those who participated in a reciprocal full attack (59.6% of intruders were spread-eagled). Note the difference with the previous case (exp. 8), with a lower rate of reciprocal full attack and a higher rate of fleeing displays. In the previous case, the scouts that extended the territory of their colonies were aggressive (high rate of reciprocal full attacks), while foragers introduced on alien territories had a tendency to flee. Due to the lower level of aggression recorded, ritualised displays such as mandibles openings were recorded in 5% of the cases.

3.4. Introduction of an alien worker into the foraging area of a colony bred in the laboratory (Table 2, experiment 10)

Although presenting similarities with the previous case, this situation had different results as the alien workers showed aggressive behaviour in only 6.5% of the cases. Generally, they fled (72.2%; the resident attempted to seize them in 65.8% of the cases), or avoided the residents (21.3%). Only 6.4% of the intruders ended up by being bitten by a resident, then spread-eagled. When bitten, one of them reacted by counterattacking, so that a reciprocal full attack was recorded before the intruder was spread-eagled. The level of aggression in laboratory experiments was therefore obviously lower than in nature. The residents did not show any aggressive response in 15.2% of the cases, while they opened their mandibles (3.9%) or raised their gaster (2.2%) when the intruder ran in front of them. We suppose that the latter behaviour is accompanied by the emission of chemical compounds (maybe formic acid) as the competitors avoid antennal contact with a raised abdomen. When contact occurred, they cleaned their antennae for a long time.

3.5. Natural dyadic encounters between a worker and an alien found in a queen (Table 2; Experiments 11 and 12)

When a foraging worker and a founding queen met, they always avoided each other and pursued their foraging activity without any modification to their speed (did not increase) or sinuosity (did not decrease as for straight fleeing). Alien founding queens were therefore tolerated on the foraging area of established colonies (exp. 11). In such a situation, resident workers were never aggressive when faced with foraging queens. When an alien

foraging queen approached a nest to less than 20 cm (exp. 12), resident workers presented 100% of the ritualised aggressive postures such as mandibles opening (42.8%) and gaster bending (57.2%). These behaviours were dissuasive enough for the queens who changed direction and were never attacked.

3.6. Foraging queens encountering workers cutting up a large prey on the spot (three queens: 17 cases: Table 2; Experiments 13 and 14)

Hunting workers are able to attack large prey too big to be transported by one worker. The prey are numbed or paralysed by several bites followed by venom spraying. The hunting workers then return to the nest to recruit nestmates that cut up the prey on the spot. The pieces of prey are then transported to the nest by individual workers without any co-operation between them. One of these workers (sometimes two) plays the role of guard (Dejean et al., 1994).

The alien queens avoided direct contact with the workers and were never attacked by the guards who continued to cut up pieces of prey in their vicinity. The guards only raised and oriented their gaster towards the queens in such a manner that their access to the prey became difficult. The queens attempted to pass around the guards who continued to cut up the prey while pivoting laterally thus again hindering access to the prey. The only aggressive behaviour performed by the guards towards the queens was gaster raising (100%), so that the latter always ended up by robbing a piece of prey without being injured. Once, one of them succeeded in successively robbing two pieces of prey. Although the guards perform 100% of the ritualised behaviour in the two situations, they seem to be less aggressive towards the queens when on a food source than when next to their nest.

4. Discussion

The intraspecific aggressiveness of *P. laboriosa* in the laboratory remains low. It is highest during encounters on a marked area. In this case, according to the Bourgeois' strategy (Maynard Smith, 1976), the resident is more aggressive than the intruder. The intraspecific aggressiveness remains also still lower than in nature (see also Wilson, 1971). This could be due to the absence of predators or competitors; it could also be the consequence of handling and of experiments conducted on these colonies (the phenomenon of habituation). In nature, reciprocal full attacks occur in most of the cases and end when the intruder succeeded in fleeing or is spread-eagled. Aggression is highest when two societies compete for a territory, involving the death of at least one ant in 100% of the reciprocal full attacks. Under natural conditions where space is unlimited, two neighbouring societies are more than 10 m distant, each colony defending a large territory. When space is limited, for example on the balcony where the two colonies were less than 10 m distant, the two territories are too small. In this case, intraspecific competition is high, involving violent encounters between scouting intruders and resident workers. Such encounters often end with the spread-eagling of the scouting intruder by several residents. This behaviour is similar to that of *O. longinoda* and *O. smaragdina* and is possibly due to large adhesive pads permitting good adherence to the substrate and as a consequence a good level of effectiveness in stretching other insects (Hölldobler and Wilson, 1978, 1990; Hölldobler, 1979, 1983; Dejean, 1990; Wojtuziak et al., 1995). But, unlike *Oecophylla*, *P. laboriosa* never uses this behaviour for immobilising heterospecific competitors or prey (Dejean et al., 1994; Mercier and Dejean, 1996).

Foraging foundresses are tolerated on the territories of conspecific mature colonies, whereas ants generally have a tendency to eliminate conspecific incipient colonies (Hölldobler and Wilson, 1990). Only the guards are aggressive towards them, avoidance generally disabling the interactions. Although the competition between queens and workers is direct and immediate when the encounter takes place around a food-source, the guards are less aggressive than when they are next to their nest and always perform ritualised behaviour. It is known that the aggressiveness of ants decreases as a function of the distance from

the nest (Wilson, 1971; De Vroey and Pasteels, 1978). The semi-claustral mode of foundation of *P. laboriosa* obliges the queens to forage for food and materials. The level of danger to which this archaic mode exposes the queens depends on the territory on which they forage. The more hostile the territory, the greater the danger. So the queens are less in danger on territories where they are tolerated by the conspecific workers who do not tolerate other competitors on large food-sources. We could suppose that by protecting a non-nestmate queen, the residents increase the genetic fitness of the species to the detriment of their own survival. In fact, they only temporarily protect the foundress, which is vulnerable until the emergence of the first workers. But the presence of such intruding workers triggers a greater number of very aggressive encounters between conspecifics ants competing for territory. The high level of mortality among the intruders prevents the newly-founded colony from developing. To avoid being eliminated, we can suppose that the colony moves according to its natural tendency to build new nests.

Fresneau and Errard (1994) noted that the level of aggression developed by two workers during an encounter depends on each individual chemical template and odours of the substrate. In nature, the level of aggression depends on the context of the encounter and on the functional caste of the workers. According to this, we can classify the following situations recorded in the laboratory with an increasing order in the level of aggression: level 0, dyadic encounter between nestmates (exps. 1 and 2); level 1, encounter between a queen and one or several foragers (exps. 11 and 13); level 2, encounter between a queen and one or several guards (exps. 12 and 14); level 3, dyadic encounter between non-nestmates on a neutral area in the laboratory (exp. 3); level 4, encounter between non-nestmates on a marked area in laboratory (exps. 4 and 5); level 5, encounter between a forager introduced and several residents (exps. 9 and 10); level 6, dyadic encounter between foragers in nature (exp. 6); level 7, encounter between a scout ant and one or several residents (exp. 7 and 8).

Ritualised behaviour occur only when the level of aggression between the ants remains low, from level 0 to 5 (except for level 1, where no interaction occurs, the opponents avoiding or ignoring each other). But we do not know if this is the consequence or the cause of such a low level of aggressiveness. The ritualised displays can be separated in two categories: (1) ritualised threatening or intimidating displays (mandibles opening; gaster bending); and (2) ritualised displays of surrender or appeasement displays (antennal boxing; attempt at trophallaxis; pupal posture; gaster raising). The proportion of ritualised displays remains low, except during encounters involving queens, during which 100% of the displays (except fleeing and avoidance) are ritualised. It is known that queens have a different chemical template than workers (Carlin and Hölldobler, 1986, 1987; Bonavita-Cougourdan et al., 1990); it seems therefore that the odour of alien *P. laboriosa* queens appeases or repels resident workers or else inhibits aggression in workers (see also Francke et al., 1980 in *Formica polyctena*), thus favouring the emergence of ritualised behaviour.

One of the problems posed by the mosaics of arboreal ants concerns the difficulty of manual exploitation of arboreal plantations, due to the existence of very aggressive even dangerous species. Aggression and interference competition play key roles in the organization of ant mosaics. The level of aggression developed by each species depends on its own status, the status of the opponent and environmental factors. The distribution of dominant species in a mosaic pattern interferes in the distribution of sub-dominant and non-dominant ants that they will tolerate on or exclude from their own territory. In this context, the aggressiveness of sub-dominant species like *P. laboriosa* is sufficiently low to permit them to perform ritualised behaviour during their interactions with other species. They can exploit food resources without being strongly attacked (Mercier and Dejean, 1996; Mercier et al., 1996). On the other hand, their aggressiveness is sufficiently high to acquire, under certain conditions, the status of dominant, and thus exclude the other usually aggressive dominant species from their territory. Such species are interesting because they

can help us to understand how a species becomes a dominant and favour the development of such species to the detriment of other more aggressive ones, thus facilitating the task of harvesting.

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