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Agonistic Relationships Among Sympatric Mediterranean Ant Species (Hymenoptera: Formicidae)

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The potential aggressiveness of nine ant species belonging to the same community was estimated by means of two laboratory approaches: individual confrontations and group confrontations. Interspecific aggressiveness was not directly related to size of species in individual tests, although in group tests mortality of smaller ants increased with increasing size difference between the opponents. Tempo was related to the defense strategy of species (low-tempo species used immobility as a mechanism to avoid attacks, while high-tempo species tended to escape when coming into contact with more aggressive ones), but not with their potential aggressiveness: the most aggressive ants in individual and group tests were both low-tempo and high-tempo species when only these two categories were considered. No specific level of aggression was related to the subfamily to which the species belong (both myrmicines and formicines dominated in individual and group tests) or to the degree of taxonomic similarity between species.

KEY WORDS: ant; Formicidae; agonistic relationships; aggressive repertoire; interspecific interactions; Mediterranean community.

INTRODUCTION

Aggression and interference competition have been known to play key roles in the organization of ant communities (Wilson, 1990). Reciprocal conflict both

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within and between species has frequently been observed in neighboring colonies of ants, which compete fiercely for nest site and food (Hölldobler, 1976, 1979; Baroni-Urbani, 1979; Mabelis, 1979; Fellers, 1987). Different competitive strategies, ranging from the use of chemical repellents to the establishment of territories, have been described in ants (reviews by Hölldobler and Michener, 1980; Hölldobler and Wilson, 1990). According to Hinde (1970), aggressive behavior refers to acts directed towards another individual, which could lead to physical injury to the latter and often results in settling status, precedence, or access to some object or space between the two protagonists. This aggressiveness in the strict sense is included in a broader range of behaviors: threat, submission, etc., labeled as agonistic (De Vroey and Pasteels, 1978).

Most studies of aggression in ants have focused on the attack of intruders by residents of a colony (Carlin and Hölldobler, 1986, 1987; Provost, 1985; Crosland, 1990; Jaisson, 1991) and on interspecific fights in natural conditions (Czechowski, 1976, 1985; Hölldobler, 1976; Fowler, 1977; Mabelis, 1984). In some cases, aggressive behavior has been analyzed and quantified (De Vroey and Pasteels, 1978; Jutsum, 1979; Jutsum *et al.*, 1979; De Vroey, 1980; Le Moli and Parmigiani, 1981, 1982; Carlin and Hölldobler, 1986, 1987), both in the laboratory and in the field, although these studies have usually been carried out with individual species or with groups of species which do not necessarily live in the same habitat. However, the potential level of aggression of different species belonging to the same community has not been analyzed independently of the social mechanisms which act in natural conditions.

Laboratory tests have frequently been used to analyze and quantify the aggressive behavior of ants, but since the incidence of fighting has frequently been described as higher in the field than in the laboratory situation (Le Moli and Parmigiani, 1981; Le Moli *et al.*, 1984), wide discussion has occurred as to whether or not potential aggressiveness of ants can be extrapolated from results obtained in laboratory tests. From our point of view, forced, prolonged interactions between ant species are not necessarily the typical interactions occurring in nature, but they do provide useful insight into the methods used and success obtained during interspecific confrontations. With controlled experiments it is possible to analyze the potential level of aggressiveness of ant species in interspecific interactions without taking into account social features which could mask specific aggressiveness.

In this study we analyze the factors conditioning the potential level of aggression of the most abundant species of a Mediterranean ant community, estimated from its agonistic repertoire and its attack and defense mechanisms. Two types of laboratory test have been carried out, individual and group tests; they measure aggression in different ways: according to intensity of behavioral acts and according to numbers of ants killed, respectively.

METHODS

The ant community studied was located in Canet de Mar (Barcelona, Spain) in an area of grassland of *Hypparrhenia hirta* at 50 m above sea level, and 750 m away from the coastline. It was composed of 13 species (Cerdá and Retana, 1988), although only 9 were relatively abundant and considered in this study. The names and main biological characteristics of these species are summarized in Table I.

Two types of aggression test were carried out.

(1) Individual Tests. Confrontation between individual ants was tested by placing a single forager of one colony with that of another, in circular plastic boxes (6-cm diameter) coated on the inner walls with mineral oil in order to prevent escape. During the first 10 min following placement of the two ants in the box, the number of the different types of interaction between them was noted. One hour later, the state of both workers was recorded. All inter- and intraspecific combinations among the nine species were made, each with five replications. Aggression intensity was estimated as the percent of aggressive interactions among all contacts of the five individual tests performed with each pair of species.

(2) Group Tests. Confrontation between groups of workers was tested by placing simultaneously 10 foragers of one species with 10 foragers of another species in a plastic box similar to the one described for individual tests. Following the protocol described by Jones and Phillips (1987), individuals were then left undisturbed for 3 h, after which the numbers of alive and dead ants were recorded. All inter- and intraspecific combinations among the nine species were made, each with 10 replications. Twenty individuals of the same colony of each species were kept in the above-described containers and served as controls.

To compare the level of aggression of the two species in the group tests, the following aggression index (AI) was calculated pooling the 10 replications of each combination of species:

AI = Number of live workers of species 1/Number of live workers of species 2

According to the values of this index, the following types of relationship between species 1 and 2 were defined.

- Total dominance (TD): $AI > 1.50$
- Relative dominance (RD): $1.10 < AI \leq 1.50$
- Counter-balance (CB): $0.90 \leq AI \leq 1.10$
- No aggression (NA): particular case of counterbalance when $AI = 1.00$ and the number of live workers of each species is 100 (10 tests with no injured ant)

Table I. Biological Characteristics of the Studied Ant Species[a]

Species	Type of society	Nest population	Main food resources	Recruitment system	Worker size (length, mm)	Tempo
Dolichoderinae						
Tapinoma nigerrimum	p	c	Honeydew, insects	Mass	2.8–5.1	High
Myrmicinea						
Pheidole pallidula	m	c	Insects, seeds	Mass	3.3–4.9*/1.2–2.6**	High
Tetramorium semilaeve	p	b	Insects, seeds	Mass	2.0–3.2	Low
Aphaenogaster senilis	m	a	Insects, seeds	Group	6.4–7.7	Low
Messor bouvieri	m	b	Seeds	Group	4.0–8.5	Low
Messor capitatus	m	b	Seeds	Group	3.8–13.0	Low
Formicinae						
Camponotus sylvaticus	m	b	Honeydew, nectar	Group	5.3–13.2	High
Camponotus foreli	m	a	Nectar, honeydew	Group	4.0–9.9	High
Cataglyphis cursor	m	a	Insects, nectar	None	4.3–7.2	High

[a] m, monogynous; p, polygynous. Data on nest population (number of workers) are estimated values for the societies found in Canet de Mar: (a) hundreds, (b) thousands, and (c) tens of thousands workers. Main food resources are indicated in order of importance. (*) Major workers; (**) minor workers.

- Relative submission (RS): $0.66 \leq AI < 0.90$
- Total submission (TS): $AI < 0.66$

Samples of workers ($n = 50$) of each species were collected for estimating worker size. The measure of total body length was taken in the laboratory under a stereoscopic microscope, from tip of mandibles to tip of gaster, with the ant in an extended position.

RESULTS

Individual Tests

Considering all the species together, 11 distinct patterns of interaction were recognized in individual confrontations (Table II), and grouped in four types of interaction: aggressive behaviors, nonaggressive behaviors, submissive behaviors, and undergoing aggression.

(i) Aggressive behaviors
  - *Bite (BI).* An ant closes its mandibles on the opponent's appendages, petiole, mandibles or head. It is the only act in which actual physical injury may be inflicted (antennae, legs or even petiole cut off).
  - *Gaster flex (GF).* An aggressive ant stands on its legs II and III and forcibly bends the gaster forward, and squirts formic acid on the enemy. This is found only in the repertoire of *Camponotus sylvaticus*.
  - *Attack (AT).* An ant moves quickly towards an enemy with opened mandibles, threatening it and attempting to bite it. The body is sometimes jerked to and fro.
  - *Mandibles open (MO).* Similar to the previous one, but the ant does not move its body, only directing its head with open mandibles at the opponent.

(ii) Nonaggressive behaviors
  - *Indifference (IN).* After contacting, the ants show neither aggressive nor submissive behavior.
  - *Mutual investigation (MI).* Both ants spend a variable period of time inspecting each other. The subjects perform a rapid antennae inspection which may or may not lead to a prolonged social investigation, either simple antennation or allogrooming.

(iii) Submissive behaviors
  - *Escape (ES).* An ant moves quickly away from the other one after contacting it.
  - *Pupal position (PP).* The ant being attacked folds its antennae and legs in against the body in the pupal position and becomes motionless.

Table II. Aggressive Repertoire of Each Species in All Interspecific Individual Tests[a]

Species	No. acts	BI	GF	AT	MO	IN	MI	ES	PP	BA	BB
Camponotus sylvaticus	239	7.1	0.8	45.6	13.8	18.0		12.6		0.8	1.3
Messor capitatus	200	1.5		43.0	15.5	21.5	3.0	5.5		1.0	9.0
Messor bouvieri	172	1.2		14.0	8.1	30.8	9.9	15.1		2.3	18.6
Pheidole pallidula	135	2.2		8.9	7.4	45.9	11.1	3.7	3.7	4.5	12.6
Tapinoma nigerrimum	129			7.7	7.0	48.0	1.6	24.8			10.9
Aphaenogaster senilis	181			6.6	4.4	30.4	4.4	41.4			12.8
Tetramorium semilaeve	173	0.6		6.3	1.7	45.1	12.7		16.2	0.6	16.8
Camponotus foreli	216			1.4	0.5	27.8	0.9	38.4		0.9	30.1
Cataglyphis cursor	219					25.5	4.6	36.1		4.1	29.7
Total	1664	1.5	0.1	16.0	6.6	30.8	5.0	20.5	2.0	1.5	16.0

[a] Numbers indicate the percentage of each act in the repertoire of the species. Abbreviations of behaviors are as follows: BI, bite; GF, gaster flex; AT, attack; MO, mandibles opening; IN, indifference, MI, mutual investigation; ES, escape; PP, pupal position; BA, being attacked; BB, being bitten.

(iv) Undergoing aggression
  - *Being attacked (BA).* It is the complementary behavior of Attack, when an ant is threatened by an opponent which tries to bite it.
  - *Being bitten (BB).* It is the complementary behavior of Bite, when an ant is attacked by an enemy, that seizes an appendage or part of the body with its mandibles.

More than one-third of all acts were nonaggressive. Indifference was the most common act, while mutual investigation was less frequent. Aggressive behaviors included gaster flex, bite, attack, and open mandibles. *Camponotus sylvaticus* was the only species that performed gaster flexing, and also the most aggressive one, together with *Messor capitatus. Cataglyphis cursor* was the least aggressive species, to the extent that no aggressive act was registered in any of the tests. Submissive behaviors were escape and pupal position. Escape was a very common act, frequent among quick-moving species, and completely absent in a very slow-moving species, *Tetramorium semilaeve*. Pupal position was a typical submissive act, and was observed only in two small Myrmicine species, *T. semilaeve* and *Pheidole pallidula*. The proportion of interactions which involved undergoing aggression reflected the capacity of species to provoke aggression. It was inversely related to their threatening capacity, and highest in nonaggressive ants (*C. cursor* or *Camponotus foreli*) and lowest in the most aggressive ones (*C. sylvaticus* or *M. capitatus*).

Difference in size of the species did not markedly influence the intensity of aggression between them. In Fig. 1, aggression intensity of all pairs of species considered together is graphed against difference in size between them. When fitting linear, exponential, logarithmic and power function regression models to these data, none of them provided a reasonably clear biological interpretation.

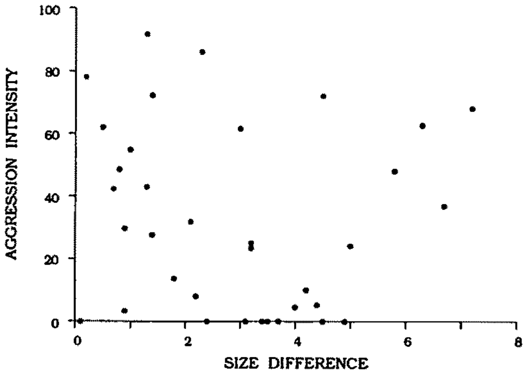

Fig. 1. Aggression intensity (percentage of aggressive interactions among all contacts of the five individual tests performed with each pair of species) graphed against the difference in size (mm) of each pair of species, for all species considered together.

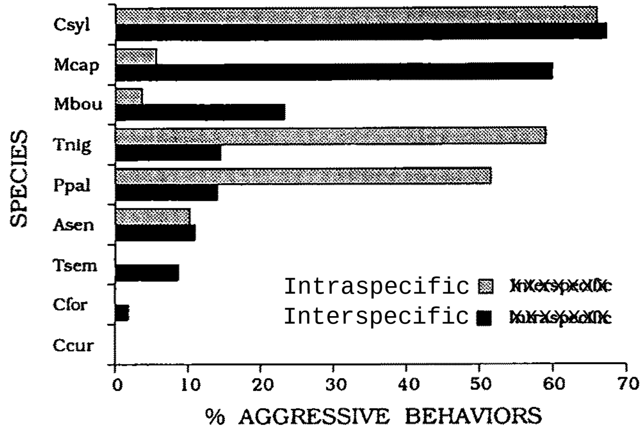

Fig. 2. Percentage of aggressive behaviors for each species in interspecific and intraspecific individual tests. Csyl, *Camponotus sylvaticus*; Mcap, *Messor capitatus*; Mbou, *Messor bouvieri*; Tnig, *Tapinoma nigerrimum*; Ppal, *Pheidole pallidula*; Asen, *Aphaenogaster senilis*; Tsem, *Tetramorium semilaeve*; Cfor, *Camponotus foreli*; Ccur, *Cataglyphis cursor*.

Intraspecific tests were also carried out in order to compare interspecific and intraspecific aggression of each species. In Fig. 2, the percentage of aggressive behaviors in interspecific and intraspecific individual tests is represented for each species. *C. sylvaticus* was the most aggressive species in both interspecific and intraspecific encounters. The two *Messor* species were very aggressive in interspecific interactions, but much less so in intraspecific ones. On the contrary, *P. pallidula* and *T. nigerrimum* were more aggressive in intraspecific encounters. *C. cursor* showed no aggression in either interspecific or intraspecific tests.

Group Tests

In the group tests, size differences of the two species determined the degree of aggression between them. In Fig. 3, difference in mortality between species is graphed against size difference for all pairs of species. This figure shows that there was an increase in mortality when the size difference between workers increased. The best fit of the data was obtained using a second-degree power function (solid line in Fig. 3: $y = 1.97x^2 - 4.73x + 15.32$, $r = 0.72$, $P = 0.01$).

Table III summarizes the aggressive relationships of all pairs of species. As happened in the individual tests, *C. sylvaticus* was again the most aggressive species, but in the group tests the second most aggressive species was *C. foreli*, a nonaggressive species in individual tests. The three smallest species (*P. pallidula*, *T. semilaeve*, and *Tapinoma nigerrimum*) suffered the greatest mortality

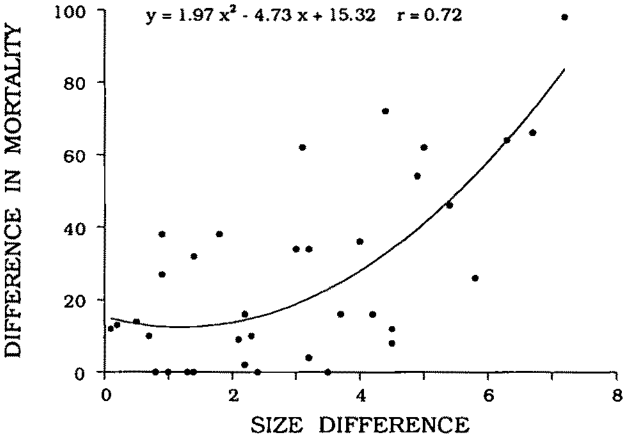

Fig. 3. Difference in mortality between species (difference between the number of live workers of each species in the 10 group tests performed with each pair of species) graphed against the size difference (mm) of each pair of species, for all species considered together. Unbroken line represents the curve of best fit (second-degree power function: $y = 1.97x^2 - 4.73x + 15.32$, $r = 0.72$, $P = 0.01$).

in the group tests. *C. cursor*, a completely nonaggressive species in individual tests (see Table II), was more aggressive in group tests, causing some injuries, especially in small ants such as *P. pallidula* and *T. nigerrimum*. No clear trend of more intense aggression toward taxonomically closely related species than toward distantly related species was found. For example, *P. pallidula* was more frequently killed by formicines such as *C. sylvaticus* and *C. foreli* than by myrmicines such as *M. capitatus*, *M. bouvieri*, and *A. senilis*.

Results of intraspecific group tests are summarized in Table IV. General trends were similar to those found in individual tests, excepting *C. foreli*, which showed a very high intraspecific aggression, with more than 8 dead workers of 20 per box. The high level of aggression of *C. foreli* in intraspecific group tests was similar to that observed in interspecific ones (see Table III). Any aggressive behavior or injured individual was observed in the control tests of the nine species.

DISCUSSION

Important differences have been found when analyzing the behavioral repertoires of the nine species considered. Nonaggressive behavior was observed in one-third of interactions between species, showing a high proportion of agonistic behavior between individuals of different species. Agonistic interactions

Table III. Aggressive Relationships Between Species in Group Tests According to Their Aggression Index (see Methods)[a]

Species	*Csyl*	*Cfor*	*Mcap*	*Asen*	*Mbou*	*Ccur*	*Tnig*	*Tsem*	*Ppal*	AI
Camponotus sylvaticus	*	RD (1.12)	TD(1.83)	CB (1.02)	TD (1.50)	TD (1.57)	TD (1.85)	TD (3.06)	TD (50.0)	62.00
Camponotus foreli	RS (0.89)	*	TD(4.00)	RD (1.14)	RD (1.11)	RD (1.11)	TD (12.5)	TD (3.77)	TD (2.17)	26.69
Messor capitatus	TS (0.55)	TS (0.25)	*	NA (1.00)	RD (1.12)	CB (1.00)	RD (1.14)	RD (1.38)	TD (2.78)	9.20
Aphaenogaster senilis	CB (0.98)	RS (0.88)	NA(1.00)	*	NA (1.00)	NA (1.00)	CB (1.04)	CB (1.09)	TD (1.67)	8.66
Messor bouvieri	TS (0.66)	RS (0.89)	RS (0.89)	NA (1.00)	*	CB (1.09)	NA (1.00)	RD (1.29)	RD (1.35)	8.17
Cataglyphis cursor	TS (0.64)	RS (0.90)	CB (1.00)	NA (1.00)	CB (0.92)	*	RD (1.19)	NA (1.00)	TD (1.50)	8.15
Tapinoma nigerrimum	TS (0.54)	TS (0.08)	RS (0.88)	CB (0.96)	NA (1.00)	RS (0.84)	*	CB (1.00)	TD (1.68)	6.98
Tetramorium semilaeve	TS (0.33)	TS (0.27)	RS (0.72)	CB (0.92)	RS (0.78)	NA (1.00)	CB (1.00)	*	RD (1.17)	6.25
Pheidole pallidula	TS (0.02)	TS (0.46)	TS (0.36)	TS (0.60)	RS (0.84)	TS (0.66)	RS (0.60)	RS (0.85)	*	4.39

[a] In parentheses is the aggression index of each pair of species. Overall aggression index (AI) of each species is obtained by adding together its partial AI values. The types of relationship of species 1 (row) versus species 2 (column) are as follows: TD, total dominance; RD, relative dominance; CB, counterbalance; NA, no aggression; RS, relative submission; TS, total submission. Although the two parts of the table are equivalent, both are represented in order to show the whole interspecific aggressive pattern of each species. For abbreviations of species 2, note that they are in the same order as for species 1.

Table IV. Proportion of Fighting Groups and Mean Number (±SD) of Dead Workers per Box After 3 h in Intraspecific Group Tests (10 vs 10 Workers per Test; 10 Tests per Species)

Species	Proportion of fighting groups	Mean number of dead workers (±SD)
Camponotus foreli	10/10	8.1 ± 2.6
Camponotus sylvaticus	10/10	7.2 ± 0.8
Messor bouvieri	6/10	2.6 ± 2.9
Pheidole pallidula	9/10	2.4 ± 1.4
Tapinoma nigerrimum	3/10	1.2 ± 2.0
Messor capitatus	3/10	1.2 ± 1.8
Tetramorium semilaeve	0/10	0
Aphaenogaster senilis	0/10	0
Cataglyphis cursor	0/10	0

included aggressive and submissive acts, but the level of aggressiveness was not the same in the different species. This was evident not only in the proportion of the different acts, but also in the presence or absence of some of them; e.g., gaster flex, which was observed only in *C. sylvaticus* and served to squirt formic acid on enemies, or pupal position, characteristic of small ants such as *T. semilaeve* and, to a lesser extent, *P. pallidula*. In the two types of laboratory test, *C. sylvaticus* was found to be the most aggressive (Table V), followed by the two *Messor* species in individual tests, and by *C. foreli* and *M. capitatus* in group tests. There was a relative similarity in the behavior of species in the two laboratory tests (Table V), except for *P. pallidula* and *T. nigerrimum*, two small

Table V. Aggressive Rank of Species (1 Being the Most Aggressive Species and 9 the Least Aggressive) in Individual Test and Group Tests[a]

Species	Individual tests	Group tests
Camponotus sylvaticus	1	1
Messor capitatus	2	3
Messor bouvieri	3	5
Pheidole pallidula	4	9
Tapinoma nigerrimum	5	7
Aphaenogaster senilis	6	4
Tetramorium semilaeve	7	8
Camponotus foreli	8	2
Cataglyphis cursor	9	6

[a] Each species was ranked according to its aggression intensity in individual tests and according to its overall aggression index in group tests (see Table III).

species which were found to be aggressive in individual tests, and *C. foreli*, which was very aggressive in group tests and almost nonaggressive in individual tests. In a similar laboratory study performed by Jones and Phillips (1987), a greater similarity was found between individual and group tests: *Solenopsis invicta* and *Pheidole dentata* were the aggressor species, whereas *Forelius foetidus* and *Monomorium minimum* were more defense-oriented.

Brian *et al.* (1976) suggested that the two subfamilies Myrmicinae and Formicinae form two morphologically differentiated guilds, the submissive myrmicines and formicines additionally adapting behaviorally to aggressive formicine ants, and this idea has gained support from later studies [e.g., Fellers (1987) suggested that the most important factor influencing dominance was the subfamily to which the species belonged: the dominant species were formicines, whereas the subordinate species included myrmicines and dolichoderines]. It is obviously not the case of the present study, where one formicine species (*C. sylvaticus*) and three myrmicines (*M. capitatus*, *M. bouvieri*, and *P. pallidula*) dominate in individual tests, while two formicines (*C. sylvaticus* and *C. foreli*) and one myrmicine (*M. capitatus*) dominate in group tests.

A number of authors have reported that larger species are normally socially dominant among vertebrates and frequently so among invertebrates (see reviews by Morse, 1974; Peters, 1983). In ants, worker size difference is considered an important factor determining the interspecific aggressive interactions (Jutsum, 1979), although in natural conditions social mechanisms can alter the outcome of interactions. In the present study, results of the two tests were not concordant: In individual tests, there was no relationship between intensity of aggression and size difference between species, but in group tests, mortality of smaller ants increased with increasing size difference between the opponents. It even led large and usually nonaggressive species such as *C. cursor*, *A. senilis*, or *C. foreli*, to attack and kill workers of small species such as *P. pallidula* or *T. nigerrimum* when they were placed in the same box during group tests. This high level of aggression of nonaggressive species versus small ones was not observed in individual tests. Both experiments were a measure of the inherent fighting ability of ants when removed from their own territory, although according to Wilson's (1971) view, ant workers lose most or all of their hostility when removed from the nest, unless they are defending a food source or are still in the company of large numbers of their nestmates. In individual tests, nonaggressive ants avoided the opponent and their level of aggression remained low. But in group tests, with many ants moving inside the box, avoidance was more difficult and this could lead to fights and eventually the death of some individuals. So *C. cursor*, *A. senilis*, and more obviously *C. foreli*, which were usually nonaggressive species, might become potentially aggressive ones and attack and kill other ants (probably considering them as prey or as undesirable objects in their own vital area).

The tempo or general activity level (Oster and Wilson 1978) was not related to the level of aggression shown by each species, because the most aggressive ants in individual and group tests were both low-tempo and high-tempo species. However, it affected the degree to which the ants underwent aggression: Due to their continuous movements, high-tempo species could disturb the surrounding environment more than low-tempo species and, thus, incite the attack of aggressive species. For example, *C. sylvaticus* attacked the high-tempo *C. cursor* workers much more vigorously than the low-tempo *A. senilis* workers, although both *C. cursor* and *A. senilis* were quite nonaggressive species (see Tables I and II) and similar in size. Tempo also influenced the defense strategy of species. For these low-tempo species, immobility might represent an appeasing tactic to avoid attacks. This was especially evident in the case of *T. semilaeve*, a very low-tempo species in whose repertoire pupal position was quite a characteristic form of behavior. *T. semilaeve* tended to be less aggressive than *P. pallidula* or *T. nigerrimum* (Table II), two higher-tempo species of similar size and level of aggression, which should therefore be attacked with similar intensity. Escape was an alternative avoiding strategy mostly performed by higher-tempo species and less frequent in the repertoire of low-tempo species such as *T. semilaeve*.

Colonies of ants are usually hostile to a degree directly proportional to their degree of similarity to their competitors (Hölldobler and Wilson, 1990). That is, they are more aggressive to other colonies of the same species, somewhat less to other species in the genus, and least of all to forms that not only belong to other genera but differ strongly in size and behavior. De Vroey (1979) tried to lend experimental support to the aforementioned hypothesis by comparing the aggressive responses of workers of a *Myrmica rubra* society confronting them with intruders of species that were taxonomically more and more distantly related to them; she concluded that intraspecific aggression, at least in *M. rubra*, is not necessarily greater than interspecific aggression. Although in the field intraspecific aggression, in general, between workers may sometimes be greater than interspecific aggression (e.g., Hölldobler, 1976; Mabelis, 1979; Czechowski and Pisarski, 1988), most studies show the contrary, interspecific aggression being higher than intraspecific aggression in *Acromyrmex octospinosus* (Jutsum, 1979; Jutsum *et al.*, 1979), *Myrmica rubra* (De Vroey, 1980), *Formica lugubris*, and *Formica rufa* (Le Moli and Parmigiani, 1982; Le Moli *et al.*, 1982, 1984). This seems to be a more general rule among laboratory colonies of ants, and probably results from greater colony odor differences between species than within species (Crosland, 1989). In the present study, no clear differences between intraspecific and interspecific tests were found. Trends were similar in both individual and group tests. Some species had similar high (*C. sylvaticus*) or low levels (*C. cursor* and *C. foreli*) of aggression towards opponents of the same or different species, while in others (the two *Messor* species and *T. semilaeve*) interspecific aggression was higher than intraspecific aggression. Only two species, *Pheidole pallidula* and *Tapinoma nigerrimum*, had higher values of intraspecific than of interspecific aggression; nevertheless, this was more probably due to their inability to attack larger interspecific opponents in the conditions considered than to their low aggressiveness. This was also true when comparing the degree of aggressiveness of species towards more and more taxonomically distant opponents: there was no relationship between the degree of taxonomic similarity and hostility between pairs or groups of ants.

Of course it is clear that aggression is not a unitary phenomenon that can be meaningfully ranked in a linear fashion and that the factors considered could not completely explain the interspecific differences obtained. Nevertheless, several interesting trends can be suggested when summarizing their importance in the present study. Potential aggressiveness between pairs of species was not directly based on size of species, because some small species (*P. pallidula* or *T. nigerrimum*) could show a higher degree of aggressiveness than larger species (e.g., *C. cursor* or *A. senilis*) in individual confrontations. Nor was difference in size of fighting workers a factor that clearly conditioned the aggressive interactions observed, although mortality of smaller ants increased with increasing size difference between the opponents of group tests. Tempo was related to the defense strategy of species (low-tempo species used immobility as a mechanism to avoid attacks, while high-tempo species tended to escape when coming into contact with more aggressive ones), but not with their potential aggressiveness: The most aggressive species in individual and group tests were both low-tempo (*M. capitatus* and *M. bouvieri*) and high-tempo species (*C. sylvaticus*, *C. foreli*, and *P. pallidula*). There was no determined level of aggression related to the subfamily to which the species belonged (both myrmicines and formicines dominated in individual and group tests) or to the degree of taxonomic similarity between species, but there was a certain relationship between the potential level of aggression of each species and the type of food it collected.

It is obvious that any results obtained from individual or group laboratory confrontations may not necessarily reflect those that might be obtained from colony-versus-colony confrontations in the field. In individual or small group interactions, species with large workers are more efficient and mostly dominate interspecific interactions. But when the number of opponents increases, as happens in high-quality food resources such as baits, the probability of escape or avoidance decreases, and overt aggression and fights are a usual outcome of interspecific and intraspecific interactions (Banks and Williams, 1989, Vepsäläinen and Savolainen, 1990). Then, social mechanisms such as methods of fighting and recruitment rates are more important factors than size, and influence the outcome of interactions. Nevertheless, the comprehension of the factors affecting interspecific behavioral interactions of coexisting species is an important starting point for a deeper analysis of the success of each species and the dominance hierarchy in ant communities.

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REFERENCES

Banks, W. A., and Willams, D. F. (1989). Competitive displacement of *Paratrechina longicornis* (Latrelle) (Hymenoptera: Formicidae) from baits by fire ants in Mato Grosso, Brazil. *J. Entomol. Sci.* **24:** 381-391.

Baroni Urbani, C. (1979). Territoriality in social insects. In Hermann, H. R. (ed.), *Social Insects, Vol. I,* Academic Press, New York, pp. 91-120.

Brian, M. V., Mountford, M. D., Abbott, A., and Vincent, S. (1976). The changes in ant species distribution during ten years post-fire regeneration of a heath. *J. Anim. Ecol.* **45:** 115-133.

Carlin, N. F., and Hölldobler, B. (1986). The kin recognition system of carpenter ants (*Camponotus* spp.). I. Hierarchical cues in small colonies. *Behav. Ecol. Sociobiol.* **19:** 123-134.

Carlin, N. F., and Hölldobler, B. (1987). The kin recognition system of carpenter ants (*Camponotus* spp.). II. Large colonies. *Behav. Ecol. Sociobiol.* **20:** 209-217.

Cerdá, X., and Retana, J. (1988). Descripción de la comunidad de hormigas de un prado sabanoide en Canet de Mar (Barcelona). *Ecologia* **2:** 333-341.

Crosland, M. W. J. (1989). Intraspecific aggression in the primitive ant genus *Myrmecia. Insectes Soc.* **36:** 161-172.

Crosland, M. W. J. (1990). The influence of the queen, colony size and worker ovarian development on nestmate recognition in the ant *Rhytidoponera confusa. Anim. Behav.* **39:** 413-425.

Czechowski, W. (1976). Competition between *Formica exsecta* Nyl and *Myrmica rugulosa* Nyl (Hymenoptera, Formicidae). *Ann. Zool.* **33:** 273-285.

Czechowski, W. (1985). Competition between *Myrmica laevinodis* (Nyl.) and *Lasius niger* (L.) (Hymenoptera Formicoidea). *Ann. Zool.* **39:** 153-173.

Czechowski, W., and Pisarski, B. (1988). Inter- and intraspecific competitive relations in *Camponotus ligniperdus* (Latr.) (Hymenoptera, Formicidae). *Ann Zool.* **41:** 355-381.

De Vroey, C. (1979). Aggression and Gause's law in ants. *Physiol. Entomol.* **4:** 217-222.

De Vroey, C. (1980). Relations interspécifiques chez les fourmis. In Cherix, D. (ed.), *Ecologie des insectes sociaux,* C.R.UIEIS sct. française, Lausanne, pp. 107-113.

De Vroey, C., and Pasteels, J. (1978). Agonistic behavior of the ant *Myrmica rubra* L. *Insectes Soc.* **25:** 247-265.

Fellers, J. H. (1987). Interference and exploitation in a guild of woodland ants. *Ecology* **68:** 1466-1478.

Fowler, H. G. (1977). Field response of *Acromyrmex crassispinus* (Forel) to aggression by *Atta sexdens* (L.) and predation by *Labidus praedator* (Fr. Smith). *Aggress. Behav.* **3:** 385-391.

Hinde, R. A. (1970). *Animal Behavior. A Synthesis of Ethology and Comparative Psychology,* MacGraw-Hill, New York.

Hölldobler, B. (1976). Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex. Behav. Ecol. Sociobiol.* **1:** 3-44.

Hölldobler, B. (1979). Territories of the African weaver ant ((*Oecophylla longinoda* (Latreille)). A field study. *Z. Tierpsychol.* **51:** 201-213.

Hölldobler, B., and Michener, C. D. (1980). Mechanisms of identification and discrimination in social Hymenoptera. In Markl, H. (ed.), *Evolution of Social Behavior: Hypotheses and Empirical Tests*, Verlag Chemie, Weinheim, pp. 35–57.

Hölldobler, B., and Wilson, E. O. (1990). *The Ants*, Springer-Verlag, Berlin.

Jaisson, P. (1991). Kinship and fellowship in ants and social wasps. In Hepper, P. G. (ed.), *Kin Recognition*, Cambridge University Press, Cambridge, pp. 60–93.

Jones, S. R., and Phillips, S. A. (1987). Aggressive and defensive propensities of *Solenopsis invicta* (Hymenoptera: Formicidae) and three indigenous ant species in Texas. *Tex. J. Sci.* **39:** 107–115.

Jutsum, A. R. (1979). Interspecific aggression in leaf-cutting ants. *Anim. Behav.* **27:** 833–838.

Jutsum, A. R., Saunders, T. S., and Cherrett, J. M. (1979). Intraspecific aggression in the leaf-cutting ant *Acromyrmex octospinosus. Anim. Behav.* **27:** 839–844.

Le Moli, F., and Parmigiani, S. (1981). Laboratory and field observations of attack by the red wood ant *Formica lugubris* Zett. on *Formica cunicularia* Latr. (Hymenoptera: Formicidae). *Aggress. Behav.* **7:** 341–350.

Le Moli, F., and Parmigiani, S. (1982). Intraspecific combat in the red wood ant (*Formica lugubris* Zett.). *Aggress. Behav.* **8:** 145–148.

Le Moli, F., Mori, A., and Parmigiani, S. (1982). Agonistic behavior of *Formica rufa* L. (Hymenoptera Formicidae). *Monitore Zool. Ital. (N.S.).* **16:** 325–331.

Le Moli, F., Mori, A., and Parmigiani, S. (1984). Studies on interspecific aggression among red wood ant species. *Formica rufa* L. vs *Formica lugubris* Zett (Hymenoptera Formicidae). *Monitore Zool. Ital. (N.S.)* **18:** 41–51.

Mabelis, A. A. (1979). Wood ant wars, the relationship between aggression and predation in the red wood ant (*Formica polyctena* Först.). *Neth. J. Zool.* **29:** 451–620.

Mabelis A. A. (1984). Interference between wood ants and other ant species (Hymenoptera, Formicidae). *Neth. J. Zool.* **34:** 1–20.

Morse, D. H. (1974). Niche breadth as a function of social dominance. *Am. Nat.* **108:** 818–830.

Oster, G., and Wilson, E. O. (1978). *Caste and Ecology in the Social Insects*, Princeton University Press, Princeton, NJ.

Peters, R. H. (1983). *The Ecological Implications of Body Size*, Cambridge University Press, Cambridge.

Provost, E. (1985). Etude de la fermeture de la société chez les fourmis. I. Analyse des interactions entre ouvrières de sociétés differentes, lors de rencontres expérimentales, chez des fourmis du genre *Leptothorax* et chez *Camponotus lateralis* Ol. *Insectes Soc.* **32:** 445–462.

Vepsäläinen, K., and Savolainen, R. (1990). The effect of interference by formicine ants on the foraging of *Myrmica. J. Anim. Ecol.* **59:** 643–654.

Wilson, E. O. (1971). *The Insect Societies*, Harvard University Press, Cambridge, MA.

Wilson, E. O. (1990). *Success and Dominance in Ecosystems: The Case of the Social Insects*, Ecology Institute, Oldendorf/Luhe.