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Social Organization in the Guest-ant *Formicoxenus provancheri*

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Abstract

The results of an investigation on the division of labour in the guest-ant *Formicoxenus provancheri*, conducted by observing colonies containing individually marked adults, are presented. Five colonies of *Formicoxenus* were installed in the laboratory with their hosts, *Myrmica incompleta,* in order to document, over 10 d, the location of individuals as well as individual and interactive types of behaviour. The results show that each colony of *Formicoxenus* consists of three groups: a group of nurses who remain in the *Formicoxenus* nest (some 21% of the colony's members); a group of scouts who spend most of their time in the external area (18%) and a very large group of individuals specialized in licking ('shampooing') the host to obtain regurgitations (61%), who essentially remain in the *Myrmica* nest. Division of labour in *Formicoxenus* appears to be a special adaptation to the xenobiotic way of life. The apparent link between social structure and the probability of profiting from trophallactic exchanges with the host species could lead to interesting predictions on the division of labour in other guest-ants.

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Introduction

Ants of the genus *Formicoxenus* Mayr are guest-ants (xenobionts) in colonies of other ant species (Myrmicinae or Formicinae) (FRANCOEUR et al. 1985). This life history, xenobiosis, is somewhat intermediate between cleptobiosis, where ants steal brood or food from the host, and true social parasitism, where mixed colonies of parasites and hosts are formed (WHEELER 1910; WILSON 1971; BUSCHINGER 1986). *Formicoxenus* are completely dependent on their hosts for feeding but take care of their brood themselves (FRANCOEUR et al. 1985). The nature and the composition of this genus were re-

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examined by FRANCOEUR et al. (1985), who demonstrated the existence of two closely related species, *F. provancheri* and *F. quebecensis* (Francoeur), which are found only in North America and parasitize *Myrmica incompleta* and *M. alaskensis* (Wheeler), respectively. *Formicoxenus provancheri* was long considered a *Leptothorax* (WHEELER 1901) before being classed in the genus *Formicoxenus* (FRANCOEUR et al. 1985).

The principal characteristics of the biology of *F. provancheri* were described by BUSCHINGER et al. (1980), FRANCOEUR et al. (1985) and LENOIR et al. (1992). *Formicoxenus provancheri* forms small societies with relatively autonomous nests in prosperous, polygynous colonies of *Myrmica incompleta*. There is no aggressive behaviour between the members of different nests, but members do not mix, either (LENOIR et al. 1992). *Formicoxenus provancheri* nests may be established at the edge of or in the wall of the nest of their host, but the parasite always rears its brood in chambers separate and isolated from the brood chambers of the host, because it is considered by the latter as prey and eaten. Adult *F. provancheri* are strongly attracted to *M. incompleta* and lick them very frequently. The workers spend much time sitting on top of their hosts (who are 3–5 times larger), whom they lick ('shampoo') and from whom they also obtain food. WHEELER (1901, 1903, 1910) noted that during this licking, the xenobiont receives regurgitated food from its host. Observations made by FRANCOEUR et al. (1985) lead one to believe that this licking of the host might also represent a kind of appeasement behaviour for food solicitation.

Formicoxenus shows a polymorphism of both male and female reproductives. Here we use the terms gynomorph (originally winged, with completely developed ocelli and thoracic structures), intermorph (morphologically intermediate between gynomorph and ergatomorph, wingless and with the ocelli and thoracic sutures more or less greatly reduced) and ergatomorph (thoracic sclerites completely fused, no ocelli) to describe the different female morphs (BUSCHINGER & WINTER 1976; FRANCOEUR et al. 1985; LOISELLE & FRANCOEUR 1988; HEINZE et al. 1993). Regardless of external morphology, all female morphs may have a spermatheca and may thus mate and lay fertilized eggs. However, only one female per nest seems to be fertile and functions as active breeder. In the nests of *Formicoxenus*, supernumerary inseminated females can be found throughout the year. They presumably are daughters of the fertile queen which have returned to the colony after mating (BUSCHINGER & WINTER 1976). Their ovaries remain completely undeveloped and usually show no sign of egg production. Recently, HEINZE et al. (1993) observed that aggressive interactions among queens maintain functional monogyny and may also precede colony fragmentation in this species. *Formicoxenus provancheri* is thus characterized by a functional monogyny and a marked polymorphism in the active breeders (BUSCHINGER 1968; BUSCHINGER et al. 1980).

In the present study, we examine the division of labour in *F. provancheri*. Even though the relationship with the host has been the subject of numerous investigations (LENOIR et al. 1992) which also enabled the establishment of a behavioural repertoire for *Formicoxenus*, no specific study of polyethism has been conducted on this species. The aim of this study was to determine if specialized individuals do exist in the exploitation of the host.

Methods

Five colonies of *Formicoxenus* and their hosts were collected in Quebec, Canada. Studies on behaviour and behavioural interactions were conducted on two colonies from Nantes (Co. Frontenac, Québec, first experiments: colonies B and D), on two colonies from Marlington (Co. Frontenac, Québec, colonies E and M), and on one colony from Mégantic (Co. Frontenac, Québec, colony H).

The ants were bred in Petri dishes (16 cm diameter) according to the method used by FRANCOEUR et al. (1985) at 20°C and subjected to a photoperiod light:dark of 12:12 h. The dishes were equipped with a watering place and two circular nests (4 cm diameter): one for the *Formicoxenus* with an opening which is small in diameter (< 1.2 mm) and impedes the passage of *Myrmica*; and one for the *Myrmica* with a larger opening (> 1.5 mm). The Petri dish itself acted as the external area where food is placed. The colonies were fed with parts of insects (meal worms, flies) associated with an artificial diet to provide a dietary supplement of sugar and vitamins.

As we were interested in a study on the behaviour of the guest-ants and not the hosts, for practical reasons the number of host-ants was reduced. During the observation period, colony B consisted of approximately 20 *Myrmica* host workers and one queen, 15 *Formicoxenus* (including one gynomorph and one male), 10 *Myrmica* larvae and three *Formicoxenus* larvae; colony D consisted of approximately 45 *Myrmica* host workers and one queen, 24 *Formicoxenus* (including one gynomorph and one male), 20 *Myrmica* larvae and seven *Formicoxenus* larvae; colony E consisted of 35 *Myrmica* host workers and one queen, 15 *Formicoxenus* (including one gynomorph and one intermorph), 25 *Myrmica* larvae and six *Formicoxenus* larvae; colony M consisted of about 30 *Myrmica* host workers and one queen, 13 *Formicoxenus* (including one gynomorph and two intermorphs), 15 *Myrmica* larvae and five *Formicoxenus* larvae; and colony H consisted of 40 *Myrmica* host workers and one queen, 18 *Formicoxenus* (eight ergatomorphs), 20 *Myrmica* larvae and five *Formicoxenus* larvae. All gynomorphs were mated egglayers (functional queens).

Adult *Formicoxenus* were individually marked with a coloured dot on the gaster (colonies B, D, E and M) or wires (colony H). In colonies B and D, only *Formicoxenus* present in their nest during the first observations were marked individually, whereas in colonies E, M and H, all *Formicoxenus* individuals were marked. The behavioural data were obtained by observing each marked individual during 10-min sessions per day over a period of 10 d in Aug. (B, D) and 10 d in Sept. (E and M). Individuals from colony H were observed for a total of 32 h in 8 wk.

For each observation, each *Formicoxenus* was associated with an individual location: *Formicoxenus* nest, *Myrmica* nest, or external area (outside the two nests). We then noted the percentage of observation time spent in each of the three locations.

We recorded all behavioural interactions between adult *Formicoxenus* and the duration of each behavioural act through the use of a micro-computer. Activities of all marked individuals were noted under the category 'Total duration'. Data were analyzed through the use of computer software from the laboratory. For the analyses, we combined the results from colonies B and D (pre-experimental colonies) as well as the results from colonies E and M (test colonies), since the analyses conducted on the separate colonies were not different. In the test colonies, the interactions of *Formicoxenus* individuals towards *Formicoxenus* or *Myrmica* individuals (queen or workers) were compared by Wilcoxon matched pairs test (n = 28 for each comparison).

We then used two multivariate analyses in order to estimate the specialization of the ants. The first was factorial correspondence analysis (FCA), a particular form of principal component analysis adapted to frequency analysis (BENZECRI 1973). For example, in the test colonies, the analysis was performed by regrouping the results of all 28 ants from colonies E and M in a frequencies table including 28 lines (individuals) and 18 columns (behaviour and localities variables). For computation, the first 15 columns corresponding to 15 behavioural acts are active data (Table 1) and the 3 last columns corresponding to localities are included in the analyses as non-active data (FN, *Formicoxenus* nest; EX, external area; MN, *Myrmica* nest) as the AFC permits. Secondly a hierarchical cluster analysis (HCA, using Ward's method) was performed with the software package ADDAD, using, for test colonies E and M, all 28 ants and 15 behaviour variables.

Table 1: Behavioural repertoire of *Formicoxenus provancheri* and abbreviations for behavioural categories used in the text

IFN	Immobility in *Formicoxenus* nest
GTF	Active grooming and trophallaxis towards *Formicoxenus*
GFF	Active grooming and trophallaxis from *Formicoxenus*
BTF	Brood care (grooming) towards *Formicoxenus* brood
NA	Nest activity (nest cleaning)
GTM	Active contacts and grooming towards *Myrmica*
EA	External activity
ATF	Agonistic interactions towards *Formicoxenus*
ATM	Agonistic interactions towards *Myrmica*
IG	Individual grooming (self-grooming)
BTM	Brood care towards *Myrmica* brood (grooming)
IMN	Immobility in *Myrmica* nest
GFM	Active contacts and trophallaxis from *Myrmica*
PCF	Passive contacts towards *Formicoxenus* in *Myrmica* nest
Su	Submission

Results

Distribution of Adult *Formicoxenus*

Of the 39 individuals present in the two colonies, B and D, 15 individuals were present in the nest of *Formicoxenus* on the first day of observation (marked individuals). This group of individuals can be broken down in the following manner: seven remained in the nest of *Formicoxenus*; one spent all of its time in the nest of *Myrmica*; one moved between the external area and the nest of *Myrmica* (intermediate between the nest of *Formicoxenus* and the nest of *Myrmica)*; three went rapidly from the nest of *Formicoxenus* to the nest of *Myrmica* (two of which spent more time in the nest of *Formicoxenus* and one which did the opposite); two moved between three locations; and one divided its time between the external area and the nest of *Formicoxenus*.

Of the 28 individual *Formicoxenus* present in colonies E and M, three were constantly in the nest of *Formicoxenus*; three were constantly in the nest of *Myrmica*; 11 moved between the external area and the nest of *Myrmica* (they were never seen in the nest of *Formicoxenus*); four moved rapidly from the nest of *Formicoxenus* to the nest of *Myrmica*; and seven moved between the three locations, but five of those spent more time in the nest of *Myrmica* than in the nest of *Formicoxenus*, whereas two did the opposite.

In each colony, it appears that several ergatomorphs serve as intermediaries between the foragers and the individuals remaining in the nest of *Formicoxenus*. This function was filled by individuals numbered 11 and 12 in colony E, who distributed food to the other members of the nest, and by individuals numbered 23 and 27 in colony M (Table 2). This phenomenon can also be found in colony D where one ant remained in the nest and received trophallaxis from two foragers in order to distribute the food to the adult members of the nest, including the gynomorph. Qualitatively the same results were observed in colony H, where of 18 individuals 17 were occasionally observed either begging food from or sitting on *Myrmica*, but only five individuals interacted regularly with *Myrmica*.

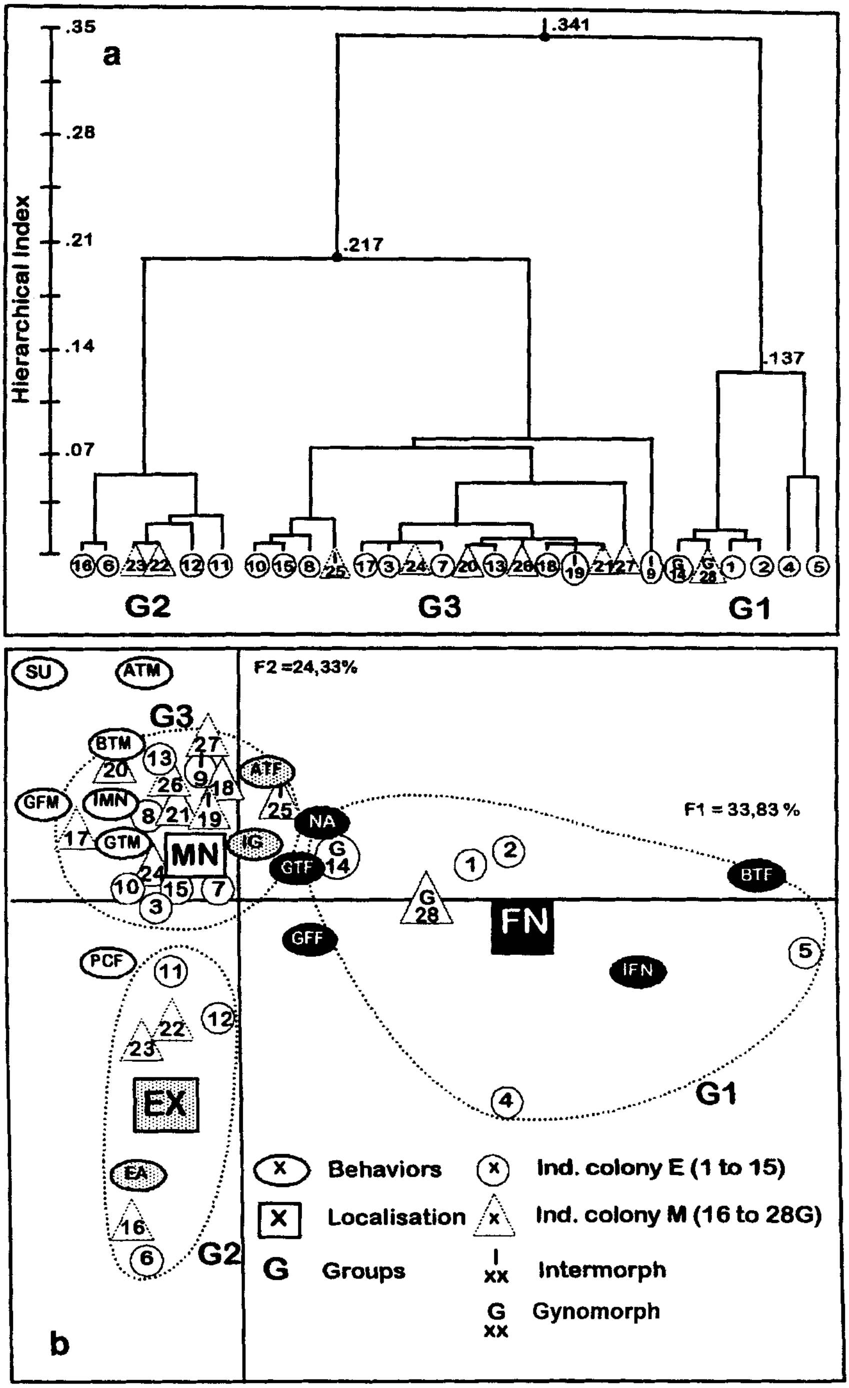
Table 2: Spatial distribution of individual *Formicoxenus* (colonies E and M): percentage of time spent in each of the three possible places (*Formicoxenus* nest, external area, *Myrmica* nest). G = gynomorph; I = intermorph

Individual number	*Formicoxenus* nest	External area	*Myrmica* nest
1	91.6	0	8.3
2	100	0	0
3	0	8.3	91.6
4	60.0	0	40.0
5	87.5	12.5	0
6	0	85.7	14.3
7	0	25.0	75.0
8	0	7.7	92.3
9 I	0	14.3	85.7
10	0	44.4	55.5
11	18.7	37.5	43.7
12	50.0	27.3	22.7
13	0	0	100
14 G	66.6	11.1	22.2
15	0	23.0	77.0
16	0	80.0	10.0
17	0	14.2	85.7
18	33.3	11.1	55.5
19 I	0	0	100
20	18.7	12.5	68.7
21	6.6	33.3	60
22	0	54.5	45.4
23	10	10.0	80.0
24	22.2	0	77.7
25 I	0	0	100
26	0	50.0	50.0
27	30.0	0	70.0
28 G	100	0	0

Sociogram of *Formicoxenus*

We will only present here those results obtained from two *Formicoxenus* colonies, E and M, where all individuals were marked.

Hierarchical cluster analysis (HCA). The schematic representation of the clustering obtained with the HCA algorithm on behavioural data (Fig. 1a) shows the nodes separating three groups to which we assigned a number. The two first nodes (0.341 and 0.217) contribute 44% of the cloud's variance. The separation into three classes is therefore perfectly justified. The two HCAs show clearly that the first node separates group 1 (G1) from groups 2 (G2) and 3 (G3), and the second, which divides groups 2 and 3, is situated at a much less significant level. Groups 2 and 3 are, as such, relatively close to each other whereas group 1, which includes the gynomorphs (numbered 14 and 28), was clearly separate from the two other groups. Group 1 consists of six *Formicoxenus* (four ergatomorphs and two gynomorphs); group 2 of six *Formicoxenus* ergatomorphs;


a
Hierarchical Index
.35
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16 6 23 22 12 11
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PCF
EA
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G3
G2
G1
Behaviors
Localisation
Groups
Ind. colony E (1 to 15)
Ind. colony M (16 to 28G)
Intermorph
Gynomorph

and group 3 of 16 *Formicoxenus* (13 ergatomorphs and three intermorphs, numbered 9, 19 and 25).

As it was not possible to tell which intermorphs and ergatomorphs were mated, there remains the possibility of a certain heterogeneity in the three behavioural groups due to the presence of mated laying or non-laying intermorphs and ergatomorphs. The mated individuals might prefer to stay outside the *Formicoxenus* nest, or with the hosts, after the dominance order has been established in spring, before the experimental period (HEINZE et al. 1993).

Factorial correspondence analysis (FCA with 15 behaviour variables and three localities variables). The two first axes of the FCA are represented. The groups identified by HCA are projected on these two axes. Figure 1b gives a reliable representation since the plane formed by the first two axes alone accounts for 57.9% of the total variance, while the third axis only explains an additional 11.2% of the total variance. The 15 types of behaviour selected for analysis are classified by the plane of the two first axes. The interpretation of their representation depends on two opposing systems, Factor 1 and Factor 2.

The axis called F1 (Factor 1) clearly segregates to the left the behavioural acts (such as GTM, i.e. active contacts with and grooming or 'shampooing' *Myrmica*) related to the workers of *Myrmica* or the external area; and to the right the activities taking place in the nest of *Formicoxenus*, such as IFN (immobility in *Formicoxenus* nest) and BTF (care towards *Formicoxenus* brood). This axis alone includes almost 34% of the total variance and constitutes the first differentiation factor in polyethism.

Axis 2 (Factor 2) fine-tunes our analysis by highlighting a second system of opposition between the movements to the exterior (at the bottom) and the activities in the nest of *Myrmica* (at the top), discriminating between the EA (external activity) and GTM (active contacts and grooming towards *Myrmica*) activities. Even though it comes in the second position, this factor is important because it represents 24% of the total variance.

Outside these two factors, the activities GFF (active grooming and trophallaxis from *Formicoxenus*), GTF (active grooming and trophallaxis towards *Formicoxenus*), and IG (individual grooming) are placed in the centre of Fig. 1b; that is, at the centre of gravity of the two systems of opposition which signifies that they are not discriminant from the point of view of polyethism because they can be achieved indiscriminantly by all of the members of the colony. These activities (GFF, GTF, IG) represent, in fact, the types of behaviour which are typically individual, such as IG or interactive types of behaviour between adult *Formicoxenus*.

The FCA revealed that group G1, which consists of six *Formicoxenus*, is associated with the following types of behaviour: IFN, BTF, NA (nest cleaning activity), GTF and

Fig. 1: Data analysis obtained in individual, 10-min sessions per day over a period of 10 d, in colonies E (individuals 1–15) and M (individuals 16–28) of *Formicoxenus*. a. Hierarchical cluster analysis; and b. Factorial correspondence analysis, on the first two axes. The gynomorphs were G 14 (colony E) and G 28 (colony M); the intermorphs were I 9 (colony E) and I 19, I 25 (colony M). All the other individuals were ergatomorphs

Table 3: Distribution of the interactions of *Formicoxenus* workers (colonies E and M): percentage of the duration of interactions (antennal contacts, grooming and trophallaxis) towards *Myrmica* individuals (workers, queen and brood) and towards conspecifics (workers, queen and brood)

Interactions	Workers	Queen	Brood	Total
Towards *Myrmica* individuals	72.2	8.2	2.7	83.1
Towards *Formicoxenus* individuals	8.6	1.3	7.0	16.9

GFF. This group consists of nurses and gynomorphs, who spend the majority of their time in the *Formicoxenus* nest.

Group 2 also consists of six *Formicoxenus*. The FCA associated this group with the behavioural type EA (external activity). This group represents the scouts who spend the greater part of their time in the external area; in other words, they place themselves in a space intermediate between their nest and that of *Myrmica*.

Group 3 consists of 16 *Formicoxenus*. The FCA associated the following behavioural acts with this group: GTM, GFM (active contacts and trophallaxis towards and from *Myrmica*), IMN (immobility in *Myrmica* nest) and BTM (brood care towards *Myrmica* brood). The individuals of this group spend more time in the nest of the host, since they are specialized in the licking of *Myrmica* (foragers).

Long-term Analysis

Colony H was observed for a much longer period than the other colonies. The results of this study nevertheless were in principle similar to those obtained in the other colonies. Additional 24-h time-lapse video recording did not suggest differences in the overall activity pattern during the day.

In a total of 32 h observation in colony H, 17 ergatomorphs and intermorphs were seen engaging in interactions with *Myrmica* between one and 61 times, but of a total of 320 acts, 226 (71%) were performed by only four *Formicoxenus* (K, I, L and D with 40, 53, 61 and 43 acts, respectively). Trophallaxis from *Myrmica* to *Formicoxenus* was observed 33 times (to C 7, to I 6, and to 10 others in 1–4 acts). Ant R, the individual most specialized on brood care within the *Formicoxenus* nest, was observed interacting with *Myrmica* only once; two intermorphs A and B, which during the observation period engaged in agonistic interactions and later both began to lay eggs in different nests (HEINZE et al. 1993), interacted with *Myrmica* four and six times, respectively. The individuals specialized in grooming adult *Formicoxenus* were not those which specialized in 'shampooing' or begging from *Myrmica* (C, P, H, G and R performed more than 50% of all grooming acts, 106 of 203).

These results corroborate the observations in colonies E and M. It may be seen in Table 3 that, for the colonies of *Formicoxenus* and taking into account the total number of behavioural categories recorded, the types of behaviour directed towards *Myrmica* (83.1%) outweigh behaviour directed towards conspecifics (16.9%). This holds true for behaviour oriented towards workers (72.2% towards *Myrmica*, 8.6% towards *Formicoxenus*, $z = 3.711$, $p = 0.0002$), but not for behaviour directed towards brood

(2.7% towards *Myrmica*, 7.0% towards *Formicoxenus*, z = 0.258, p = 0.79) and queens (8.2% towards *Myrmica,* 1.3% towards *Formicoxenus,* z = 1.095, p = 0.27). *Formicoxenus* foragers therefore interact mostly with adult allospecifics rather than with conspecifics (z = 4.326, p = 0.00001).

Formicoxenus ergatomorphs were highly mobile (34% of their total activity) and frequently moved from one *Myrmica* worker to another, while the *Myrmica* brood seemed unattractive to them (z = 4.457, p = 0.000008). Behaviour directed towards adults was directed more towards queens than towards workers (z = 2.552, p = 0.01), despite a queen to worker ratio of 1:30. The observation that *Formicoxenus* groomed and begged *Myrmica* queens at a higher rate than workers suggests that it might be advantageous for an individual *Formicoxenus* to remain immobile on top of a queen for longer periods of time (LENOIR et al. 1992).

Within *Formicoxenus*, a low proportion of time was devoted to interactions from ergatomorphs towards ergatomorphs and from egg-laying, gynomorphic females to ergatomorphs (5.0 and 7.8%, respectively, of the total number of acts recorded, z = 4.012, p = 0.00006). In colonies B, D, E and M, the nature of the interactions between gynomorphs and ergatomorphs was exclusively non-aggressive. Dominance behaviour such as that seen at the end of hibernation in colony H (HEINZE et al. 1993) was not observed during the experimental period.

Discussion

In several ant species there is a basic division of labour among workers into tasks in the nest, e.g. brood care, in which the majority of the individuals (66–93%) take part, and external service, in which between 7 and 34% of the society's individuals engage. This phenomenon can also be found in species which are considered to be socially primitive, such as *Pachychondyla apicalis*, *P. obscuricornis*, *P. villosa* (70–80% in the nest and 20–30% outside, FRESNEAU 1984; PEREZ-BAUTISTA et al. 1985; FRESNEAU & DUPUY 1988), *Ectatomma ruidum* (88% in the nest and 12% outside, CORBARA et al. 1989) and *Nothomyrmecia macrops* (93 and 7%, respectively, JAISSON et al. 1992), and in more advanced species such as *Myrmecina graminicola* (88 and 12%, FRESNEAU et al. 1982), *Lasius niger* (76 and 24%, LENOIR & ATAYA 1983), and *Tapinoma erraticum* (85–90% in the nest and 10–15% outside, LENOIR 1979).

In *Formicoxenus*, we see evidence of a similar dichotomy, but the percentages of individuals engaged in internal activities and external activities (21.4 and 78.6%, respectively) are in marked contrast to the relation in other species. In *Formicoxenus provancheri*, the largest group consists of the individuals interacting with *Myrmica* queens and workers in the host nest (57%). This social organization differs from that of non-parasitic species. The division of labour observed in *Formicoxenus* appears to be a consequence of their xenobiotic way of resource exploitation. The brood of *Formicoxenus* is low in number and well-protected from the host species in a separate nest with smaller galleries, which prevents invasion by *Myrmica.* Only a few *Formicoxenus* workers remain in their nest in order to defend and take care of the brood. On the other hand, *Formicoxenus* do not forage for their own food but entirely depend on trophallactic exchanges with their *Myrmica* hosts, from whom food is obtained through movements inducing the host to regurgitate (FRANCOEUR et al. 1985). Nonetheless, according to our observations, these trophallactic exchanges are infrequent, and numerous *Formicoxenus* need to spend a lot of time in order to receive sufficient quantities of regurgitated food for the development of the brood. It is interesting to notice that *Myrmica* queens are more attractive to *Formicoxenus*, probably as they receive more trophallaxis than *Myrmica* workers (see Table 2). 'Shampooing', i.e. licking the hosts, could also be a way to obtain *Myrmica* colony odour. It is well known that the different individuals of a colony share a common odour which is mixed during trophallaxis (SOROKER et al. 1994). Furthermore, competition between *Formicoxenus* colonies within the same *Myrmica* nest (LENOIR et al. 1992) obliges *Formicoxenus* to have a greater number of individuals supplying food than providing care. These results are consistent with observations conducted in the field where one finds many adult *Formicoxenus* in the nests of *Myrmica* and few in the small chambers corresponding to the nests of *Formicoxenus*.

The apparent link between social structure and the probability of profiting from trophallactic exchanges with the host species provides a basis for predictions on the division of labour in other guest-ants. Four species of *Formicoxenus*, which all show more advanced characteristics than *F. provancheri* (FRANCOEUR et al. 1985), exploit formicine ants as host species, in which the importance of trophallaxis appears to be higher than in myrmicines (VIENNE 1993). *Formicoxenus nitidulus*, parasitizing several *Formica* species, might thus have a social structure with a lower percentage of individuals engaged in contacts to the hosts.

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