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**Research article**

# Does group closure exist in the social spider *Anelosimus eximius*? Behavioural and chemical approach

A. Pasquet[1], M. Trabalon[1], A.G. Bagnères[2] and R. Leborgne[1]

[1] *Laboratoire de Biologie et Physiologie du Comportement, U.R.A. C.N.R.S. n° 1293, Université H. Poincaré Nancy, 1, B.P. 239, F-54506 Vandoeuvre les Nancy cedex, France e-mail: pasquet@scbiol.u-nancy.fr*

[2] *Laboratoire de Neurobiologie, Communication Chimique, U.P.R. C.N.R.S. n° 9024, F-13402 Marseille cedex 20, France*

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## Summary

The exclusion of a conspecific intruder by the members of a colony is a well-known phenomenon in social insects. This phenomenon is called group closure. It may exist in social spiders as well.

Experiments were conducted to test inter-colony tolerance in *Anelosimus eximius*, a social spider of South America. Two types of information were taken into account: the behavior of the intruder introduced in a group of 10 individuals from same colony and the chemical characteristics of the cuticular products of the spiders.

Spiders were collected from four natural colonies in French Guyana; two colonies were less than 5 km apart, while the others were separated by more than 40 km. Two weeks after collection, an intruder (from the same colony or from another colony) was introduced into the box. In all cases, the intruder was accepted by the members of the group after a minimum of 24 h. Thus, in *Anelosimus eximius*, the aggressive behavior necessary for group closure is nonexistent.

The presence of an intruder (of the same colony or a different one) temporarily affected the structure of the group. Twenty-four hours after the introduction, there was an increase in the nearest neighbor distances between members of the group.

The analysis of the chemical products of the cuticle showed volatile and non-volatile products. There was no qualitative difference between the spiders of the different colonies, only quantitative differences. These differences were not correlated with the distance between colonies. Close colonies had greater differences in the ratios of several chemical cuticular products than did distant colonies.

We conclude that there is no active group closure in *Anelosimus eximius*, although there may be differences in the "odors" of the individuals.

## Introduction

Only 15 species of spiders that use a trap to catch their prey can be considered social (Kullmann, 1972; Burgess, 1978; Buskirk, 1981; Krafft, 1982). In these social species, individuals live in large colonies, share the same web, cooperate in prey capture,

and take care of the egg-sacs and the juveniles. Although individuals from different colonies may accept one another (Darchen and Darchen-Delage, 1986; Roeloffs and Riechert, 1993) and seem to be tolerant of members of other groups, this has not been conclusively demonstrated. All spiders are predators and social individuals must be tolerant of each other and able to make a difference between prey and a conspecific; therefore, tolerance is an important mechanism involved in the sociality of spiders.

Group closure, lack of tolerance towards individuals from other colonies, is well-known in social insects (Wilson, 1971). In this group, it is not yet known whether genetic similarity between individuals is insufficient to isolate colonies or whether it is a consequence of group closure. In some cases, strong genetic links between individuals within the colonies have been established for species that show a high group closure (Getz and Smith, 1983; Breed et al., 1985; Stuart, 1987). On the other hand, some data show that groups with a high degree of inbreeding are tolerant towards intruders (Errard, 1986; Stuart, 1991; Vander Meer et al., 1990). Thus, we can conclude that there are different ways in the evolution to sociality in insects. We know that inbreeding exists in social spiders; it was demonstrated in three species that genetic similarity between individuals is greater for individuals of a colony than between individuals of two different colonies (Lubin et al, 1985; Roeloffs and Riechert, 1988; Smith, 1986).

Tolerance between individuals can be observed by studying mechanisms of communication. In social insects, individuals recognize members of their group through chemical information found on the cuticle (Bonavita-Cougourdan et al., 1987; Howard et al., 1982). Individuals of the same species but of different colonies also show differences in their chemical cuticular products. There is little information, however, on the cuticular products of spiders. Some behavioral tests have shown that such products should exist in social spiders (Krafft, 1971) and the composition of the cuticular products is known in a solitary species, *Tegenaria atrica* (Agelenidae) (Trabalon et al., 1996).

Knowledge of the spider's evolution to sociality can be improved by comparing both inbreeding and group closure of social spiders with that of social insects. To do this, we need to know whether or not group closure exists in social spiders. This article discusses experiments that were carried out in the laboratory on a tropical social spider of South America, *Anelosimus eximius* (Theridiidae) a species with a high degree of inbreeding within the colonies (Smith, 1986). Data are also provided on the different cuticular products of these spiders and comparisons are made between colonies. We used individuals of the same colonies to test group closure and to analyze cuticular products. The aim of this paper is to look for a link between the structure of the group (the presence or absence of group closure) and physical features (chemical communication) that may be used in interindividual relationships.

## Material and methods

Spiders came from French Guyana and were kept in the laboratory (in Nancy) under standardized conditions (temperature 24 °C, humidity 60% to 80%, and a nycthemeral cycle of 12 h; light during the period 9 p.m. to 9 a.m.). Since the spiders

in the field were the most active at the beginning of the nocturnal period, tests were performed during this period. Spiders were collected from different colonies. Two colonies (FRG 29 and FRG 70) were chosen along the same road in a secondary forest; the distance between these two colonies was 5 km. A third colony (R 143) was chosen along another road about 40 km west of the first road in a secondary forest, and a fourth colony (Ste) was from a primary forest 60 km north of the other colonies.

## Behavioral tests

### *Methods*

In these trials, an individual was introduced in a box with ten individuals (marked individually with a dot of paint) coming from a single colony. All the individuals used in these trials were adult females. We chose four possibilities, among all offered, by crossing the four colonies and comparing close colonies (FRG 29 and FRG 70), very distant colonies (Ste and R 143), and intermediate distant colonies (FRG 29 and R 143). We compared the behavior of intruders coming from the same colony as the individuals of the group to that of intruders coming from an other colony.

For each test, we put 10 individuals from the same colony in a small box ($15 \times 8{,}5 \times 8$ cm) for 2 weeks; they were fed with cricket larvae twice a week. During this time, the spiders spun a web in the upper part of the box. After two weeks, an intruder was placed at the bottom of the box. We observed the spiders continuously for 45 min after the introduction and for a 5-min interval every hour for an 8-hour period. A final observation was made 24 h after the introduction of the intruder, just before we retrieved it.

### *Parameters*

Five parameters were used to characterize the relationships between the 10 individuals of the groups and the intruder.

1) The number of spiders in the group before the introduction and 24 h after; the difference would be due to mortality as the consequence of aggressive behavior between members of the group.
2) The median of the nearest neighbor distance by taking into account all the individuals of the group. This was done before the introduction of the intruder and 24 h after.
3) The distance between the intruder and its nearest neighbor in the group 5 min after its introduction and 24 h after.
4) The time necessary for the intruder to contact a member of the group.
5) The time to integrate in the group: the intruder was definitely integrated into the group when, during two successive observations, its distance to a member of the group was less than the median distance to nearest neighbor calculated for all the members of the group.

### Analysis of the cuticular products

Ten spiders from each colony were soaked in 250 ml pentane for 15 min. The samples were dried under nitrogen and then dissolved in 50 ml pentane with 375 ng hexadecane as an internal standard. Ten quantifications were completed for each colony (Ste, R 143, FRG 29, and FRG 70).

After a GLC of the total extract was made, the extracts were eluted from a Sep-pak silica cartridge (Waters-Millipore) using pentane or methanol as eluant and reanalyzed by GLC. Each extract was analyzed by GLC on a Delsi 200 apparatus equipped with a CP-Sil-5CB WCOT apolar capillary column (25 m, 0.2 mm internal diameter; Chrompack) or a CP-Sil-8CB WCOT polar capillary column (25 m, 0.2 mm internal diameter; Chrompack) and a flame ionization detector (FID). The oven temperature was programmed from 80 °C to 150 °C at 5 °C/min and from 150 °C to 320 °C at 3 °C/min. Peak areas for each GLC were obtained by integration, and the results for each peak were expressed as percentages and as nanograms of compounds per total body weight (Trabalon et al., 1996).

GC-MS of the total extract, the polar, and the apolar fraction was performed from pooled samples of 100 females. The apparatus was a Hewlett Packard GC-MS consisting of a HP 5890 GC Series II equipped with the identical column as for GLC, interfaced to a HP 5989A MS Engine and controlled by a HPUX Chemsystem. The carrier gas was Helium (2 bars), source temperature was 240 °C, quadrupole was 100 °C, and interface 300 °C. The masses were scanned between m/z 35 to 600 at 0.95 sc/sec. The oven temperature program for the GC oven was from 30 °C to 200 °C at 8 °C/min and from 200 °C to 320 °C at 3 °C/min (isotherm 5 min).

### Statistical analysis

The behavioral and temporal data for group closure tests were analyzed by nonparametric Kruskall and Wallis, Wilcoxon, and Mann-Whitney tests. The chemical data were analyzed by analysis of variance (ANOVA). Percentages were divided by 100 and then converted to $\sqrt{}$ arcsine proportion to normalize the data before ANOVA was conducted. To identify differences in the percentage of chemical compounds related to social group, the data were subjected to factor analysis (PCA, principal component analysis).

## Results

### Interindividual relationships and group closure

*Is there group closure?*

During the 24-h experiments, no intruder was killed by the members of the group. We never saw aggressive behavior in any colony during this period. There was no difference in the number of individuals in the group after the introduction of the intruder whatever its colony (Table 1, Mann-Whitney test, n.s.) nor in the parameters which characterized the integration of the intruder into the group

**Table 1.** Medians and quartiles of parameters before and after the introduction of the intruder. All the colonies were combined

| | Number of spiders | | Nearest neighbor distances (cm) | |
|---|---|---|---|---|
| | At the introduction | 24 h after | At the introduction | 24 h after |
| Intruder coming from the same colony | 10 (10–10) | 11 (11–11) | 1.7 (1.2–2.1) | 2.0 (1.6–2.9) |
| Intruder coming from a different colony | 10 (10–10) | 11 (11–11) | 1.5 (1.0–2.3) | 2.1 (1.7–2.7) |

**Table 2.** Medians and quartiles of parameters characterizing the intruder integrating in the group. All data from the different colonies were combined

| | Distance of the intruder to the group (cm) | Time necessary to | |
|---|---|---|---|
| | | contact the group (min) | integrate in the group (min) |
| Intruder coming from the same colony | 1.0 (0.7–1.7) | 105 (60–180) | 150 (109–218) |
| Intruder coming from a different colony | 0.9 (0.6–2.0) | 90 (60–131) | 112 (87–210) |

(Table 2, Mann-Whitney test, n.s.). We can conclude that the intruder, either foreign or from the same colony, was not actively rejected by the group and that there was no group closure in *Anelosimus eximius*.

*Is there a difference between colonies in the intruder treatment?*

There was no difference in colonies Ste and R 143 between the parameters characterizing the consequences of the introduction of an individual coming from the same colony or from a different one. In FRG 70, the time it took to contact a member of the group was longer for an intruder coming from a foreign colony than for an intruder coming from the same colony (Mann-Whitney test, $U = 10$, $p < 0.03$). In FRG 29, the time needed to integrate in the group was longer for the intruder coming from a foreign colony (Mann-Whitney test, $U = 9$, $p < 0.05$).

*Does the introduction of an individual affect the group structure?*

In this analysis, we combined all data from the different colonies. Before introducing an individual, all the groups were equivalent relative to the number of individuals in the group and to the structure of the group (nearest neighbor distances) (Table 1, Mann-Whitney test, n.s.). Twenty-four hours after the introduction, there was an increase in the nearest neighbor distances in both sets (Table 1, Wilcoxon

test, $p < 0.05$ for the intruder coming from the same colony and $p < 0.05$ for the intruder coming from a foreign colony). In these two sets, the distance between the intruder and a member of the colony was less than the median distance between all the members of the group (Tables 1 and 2). Thus, the increase in the distance between members of the group was a general phenomenon which concerned all the individuals of the group. By putting an intruder in a stabilized group, the structure of this group was modified.

*Is there a difference between colonies relative to the "intruder effect"?*

Since there was no global difference between the two types of intruder relative to the different parameters, we combined data on the two types of intruder for a determined colony. Twenty-four hours after the introduction, there were differences between colonies only for two parameters: the number of individuals and the nearest neighbor distances (Table 3, Kruskall and Wallis test, $p < 0.001$ for number of individuals and $p < 0.05$ for the nearest neighbor distances). After 24 h, FRG 70 differed from the other colonies for the number of individuals present in the group (Table 3, Mann-Whitney test, significant at $p < 0.001$ with the other three colonies) and for the nearest neighbor distances (Table 3, Mann-Whitney test, FRG 70 – FRG 29 $p < 0.05$, FRG 70 – R 143 $p < 0.05$, and FRG 70 – Ste, n.s.).

The fact that the number of individuals decreased after the introduction of an individual means that individuals died during this period. Dead individuals were never the intruder, but always member of the group; this was true for all colonies except FRG 70. For this colony, the introduction of a new member seemed to cause less perturbation than in the other colonies. We have no information on the cause of the spider death.

## Chemical analysis

The total extract (Table 4) of *Anelosimus eximius* is composed of a mixture of 31 esters (235 ng/spider, 80% of the total extract), 47 saturated hydrocarbons (17 ng/spider, 11% of the total extract), 2 acids (11 ng/spider, 7% of the total extract), cholesterol (2 ng/spider, 1.4% of the total extract), and 5 unknown compounds (1.20 ng/spider, 0.6% of the total extract).

The total weight of chemical compounds was not significantly different between the colonies (266 ng/spider). Quantitatively, R 143 and FRG 70 colonies showed more volatile products (acids and methyl-esters) and less non-volatile products (hydrocarbons and propyl-esters) than the other colonies (Table 4). The total extracts of Ste and FRG 29 colony were not significantly different. It seems that there is no link between the qualitative differences in chemical compounds of the colonies and the distance between colonies; close colonies showed differences, while distant colonies showed no difference.

When each compound is considered individually across colonies, several differences appear with regard to 17 esters and 24 hydrocarbons. 7-Methylheptacosane was not detected in the females of colony Ste and FRG 29. PCA of relative percentages of the chemical compounds shows that the two first axes represent 52% of the total variance (33% and 19%, respectively).

**Table 3.** Medians and quartiles of the parameters characterizing the group and the intruder (data from the different colony and from the same colony were combined)

| Colonies | Number of spiders 24 h after | Group | | Distance to the group (cm) | Intruder | |
|---|---|---|---|---|---|---|
| | | Nearest neighbor distances (cm) | | | Time (min) necessary to | |
| | | At the introduction | 24 h after | | contact the group | integrate in the group |
| R 143 | 8<br>(7–9) | 1.6<br>(1.0–2.1) | 2.5<br>(2.1–3.2) | 0.8<br>(0.6–2.5) | 90<br>(60–135) | 90<br>(82–183) |
| Ste | 7.5<br>(7–8) | 1.7<br>(1.0–2.0) | 2.0<br>(1.8–2.0) | 1.2<br>(0.8–2.2) | 105<br>(60–165) | 142<br>(105–225) |
| FRG 29 | 8<br>(7–9) | 1.7<br>(1.0–2.3) | 2.3<br>(1.4–2.8) | 1.4<br>(0.8–1.7) | 75<br>(60–120) | 120<br>(90–210) |
| FRG 70 | 10<br>(9–11) | 1.7<br>(1.3–2.3) | 1.7<br>(1.4–1.9) | 0.8<br>(0.5–1.2) | 150<br>(85–230) | 150<br>(105–235) |

**Table 4.** Percentage composition with standard deviation in parentheses of total extract from different colonies

| Chemical compounds | R 143 | | Ste | | FRG 29 | | FRG 70 | | Anova |
|---|---|---|---|---|---|---|---|---|---|
| Esters | 79.40 | (15.31) | 75.94 | (21.91) | 74.79 | (23.09) | 78.12 | (16.02) | |
| methyl esters | 7.30 | (3.01) | 6.59 | (3.51) | 5.81 | (1.83) | 8.89 | (3.16) | |
| propyl esters | 72.10 | (12.31) | 69.35 | (18.39) | 68.98 | (21.26) | 69.23 | (12.86) | |
| Acids | 3.07 | (1.16) | 1.40 | (0.67) | 1.25 | (0.65) | 2.40 | (1.03) | * |
| Hydrocarbons | 15.34 | (4.12) | 18.79 | (6.70) | 19.40 | (6.54) | 17.88 | (4.36) | |
| n-alkanes | 6.99 | (2.44) | 14.67 | (4.87) | 13.97 | (4.66) | 13.83 | (3.01) | * |
| monomethylalkanes | 7.62 | (1.45) | 3.99 | (1.18) | 5.20 | (1.81) | 3.57 | (1.05) | * |
| dimethylalkanes | 0.73 | (0.23) | 0.13 | (0.03) | 0.23 | (0.07) | 0.48 | (0.30) | |
| UK | 1.48 | (0.60) | 3.87 | (1.35) | 4.57 | (1.51) | 1.60 | (0.51) | |

Analysis of variance: * F = 4.93 to 5.55 significantly different from colony at p = 0.05.

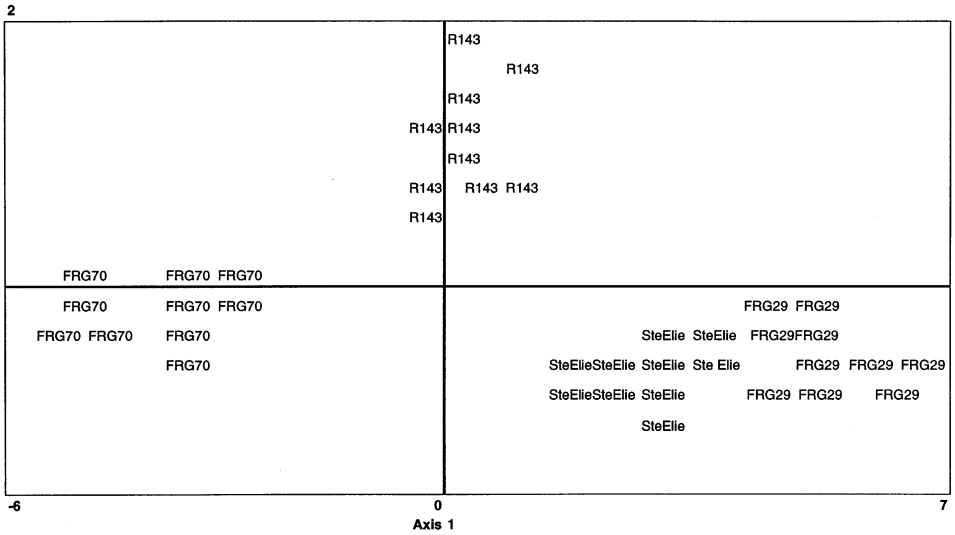


**Figure 1.** PCA carried out on percentages of chemical compounds from *Anelosimus eximius* (95% confidence ellipses). Plot of 40 individuals: R 143 colony; St Elie (Ste) colony; FRG 29 colony; and FRG 70 colony

Females of the colony FRG 29 and Ste form a very homogeneous group and are positively correlated to first axis, whereas the FRG 70 colony is negatively correlated to this axis (Fig. 1). R 143 is not correlated to first axis, but is positively correlated to the second axis. The other colonies are not correlated to this second axis. ANOVA of individual coordinates on first axis enables a significant distinction between colony FRG 70 and colonies FRG 29 and Ste ($F = 25.84$, $p < 0.0001$), whereas on axis 2, there is a significant separation between R 143 and all other colonies ($F = 4.60$, $p < 0.01$). Furthermore, PCA shows that the first axis is positively correlated to 4 chemical compounds (5-methylhentriacontane, *n*-docotriacontane, 4/2 methyldocotriacontane, and propyl 4,X,X-+6,X,X-trimethyltritricontane) and negatively to 10 compounds (*n*-octadecane, *n*-nonadecane, methylhexadecanoate, *n*-docosane, 4/2-methylpentacosane, 4/2-methylhexacosane, *n*-heptacosane, 7-methylheptacosane, propyl-24-methylpentacosanoate, and propyl-16-+26-methylheptacosanoate). These compounds separate the spider colonies into two groups: FRG 29 and Ste in one group and FRG 70 in the other. These two groups can then be separated from a third group (R 143) correlated only to the second axis, which is positively correlated to 5 compounds: *n*-hexacosane, propyl-22-methyltricosanoate, 15-+13-+11-methylnonacosane, 3-methylnonacosane, and *n*-tetratriacontane.

## Discussion

The first question was whether group closure exists in the social spider *Anelosimus eximius*. Our results showed that an intruder coming from another colony is accepted and integrated in a homogeneous group of spiders. This integration was

demonstrated during the period of observation; the intruder was left in the group for 24 hours. This 24-h period was chosen because it is known that aggression towards the intruder is immediate in social insects showing group closure; the when an intruder enters a colony different from its origin colony, it is immediately attacked, rejected, or killed. This is also the case when two solitary spiders of the same species are put in a small enclosure. This behavior was not observed with *Anelosimus eximius*, although it does not mean that the intruder was integrated in the life of the colony and that it participates in the different colony tasks which may require co-operation: prey capture, prey consumption, parental care (Krafft, 1971).

The problem of group closure is linked to the genetic isolation of the colony. In this spider species, as in some other social spiders (Roeloffs and Riechert, 1988; Lubin et al., 1985), we know that there is a high degree of inbreeding between individuals inside a colony (Smith, 1986). We also know that the colonies are patchily distributed along roads and that they are rarely found in the forest (Pasquet and Krafft, 1989). Thus, *Anelosimus eximius* colony clumping could be the result of the dispersal of one mother colony. If we refer to the mechanisms involved in the patchy distribution of colonies in social insects, group closure is one mechanism which could produce such a population structure. Here, however, the genetic isolation of the *Anelosimus eximius* colonies seems more likely due to the dynamics of the population than to the type of dispersion. No swarming is known and only the emigration of gravid females allows the dispersion of the colonies and the development of new units (Vollrath, 1986). Nevertheless, the success of such emigration is very low (Vollrath, 1986; Leborgne et al., 1994) and under these conditions, it seems unlikely that individuals coming from different colonies would found a new colony and produce inbreeding. These types of colony dispersion and inbreeding seem widespread in social spiders. In contrast to social insects (Vander Meer et al., 1990; Vienne et al., 1992; Provost and Cerdan 1990; Provost, 1994), inbreeding in social spiders is not linked to group closure so that another mechanism must be found to explain genetic isolation.

Another reason for the evolution of group closure in insects is the competition between colonies for the exploitation of resources. Ants, for example, exploit a large territory and may compete with other colonies; group closure allows them to exclude other colonies from their territory. For *Anelosimus eximius*, however, competition is not the problem. Since colonies are static and individuals of a colony only forage in the web, there is no direct competition between colonies for food. This could possibly be a problem only if two colonies develop very close together and compete for space. Therefore, in *Anelosimus eximius*, dispersion only by adult gravid females and absence of competition for food are factors that may explain why group closure has not been selected.

Group closure in social insects has been linked to the presence of group chemical products on the cuticle of the individuals; individuals of a colony may present a specific "odor" which is different from the "odor" of the individuals of another colony. In *Anelosimus eximius*, we observed no qualitative differences between colonies in the chemical cuticular products present on the individuals. There were, however, quantitative differences. In other words, the proportion of each compound was not the same in each colony. Results of the PCA analysis showed that, on one hand, FRG 70 and FRG 29 – Ste seem different from R 143 and, on the other,

FRG 70 seems to have a different mixture than FRG 29 – Ste. No difference could be noted between FRG 29 and Ste. Thus, there are differences in the cuticular cocktails of individuals coming from very close colonies (FRG 70 and FRG 29) and also from colonies very far apart, such as R 143 and all the other tested colonies.

These results suggest that the chemical cuticular products in *Anelosimus eximius* are not directly linked to the dispersion of the colonies. They may evolve independently in each colony and show a picture of the genetic background of the colony; but they may also be a product of the local diet of the spiders and depend on local potential prey.

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