

Research article

How non-nestmates affect the cohesion of swarming groups in social spiders

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Abstract. In social biology, it is often considered that an organized society cannot exist without exclusion behaviour towards newcomers from another nest. Unlike most vertebrate and invertebrate social species, social spiders such as *Anelosimus eximius* accept unrelated migrants without agonistic behaviour. Does it imply that spiders cannot recognize non-nestmates from nestmates or is there any evidence of recognition without aggression? In order to answer this question, we studied behavioural differences between groups coming from single and mixed-nests in the overall context of swarming.

Our study shows that the presence of non-nestmate conspecifics reduces the cohesion of the swarm groups during the settlement process and increases the spatial dispersion of spiders, the asymmetry in the spatial distribution being less pronounced. Individuals belonging to different nests are not as mutually attractive. This paper shows that, during the induced migration, two processes counteract each other: the amplification process resulting from the addition of silk drives individuals to form groups with non-nestmates and the recognition process reduces the cohesion of groups composed of non-nestmates. The collective decision-making during migration results from the balance between these two trends.

Keywords: Social spiders, *Anelosimus eximius*, collective swarming, nestmate recognition.

Introduction

In social biology, it is often considered that an organized society cannot exist without antagonistic behaviour towards newcomers from another nest (Hepper, 1986;

Fletcher and Michener, 1987). Unlike most vertebrate and invertebrate societies (Hepper, 1986; Fletcher and Michener, 1987), social spiders accept artificially introduced immigrants without apparent discrimination or agonistic behaviour (Evans, 1999). This absence of group closure prompts some authors to suggest that spiders cannot identify newcomers (Buskirk, 1981; Howard, 1982; Darchen and Delage-Darchen, 1986; Pasquet et al., 1997). The absence of a discrimination mechanism and the subsequent acceptance of unrelated migrants might improve the probability of colony survival. Indeed, larger spider groups have a higher probability to survive, which has been related to the web size (Avilés and Tufino, 1998; Evans, 1998). Yet the fact remains that the absence of group closure and the fact that social spiders do not kill or expel intruders does not necessarily mean that they cannot identify them as such (Evans, 1999; Bilde and Lubin, 2001; Beavis et al., 2007).

Anelosimus eximius is a social spider found in the tropical zone of South America. The individuals cooperate in a variety of collective activities such as the construction of the web and the capture of prey (Nentwig, 1985; Pasquet and Krafft, 1992; Pasquet et al., 1997). In this study, we wish to determine whether *Anelosimus eximius* is able to recognize nestmates from non-nestmates and how it responds to the latter. Indeed, a previous study clearly indicates that at least one social spider species, *Diaea ergandros*, is able to distinguish nestmates from non-nestmates (Evans, 1999). In *Delena cancerides* (Beavis et al., 2007) and *Stegodyphus lineatus* (Bilde and Lubin, 2001), non-kin were preferentially cannibalized, indicating that these species are also capable of kin recognition. During our study, we investigate these questions by studying behavioural differences between pure and mixed populations of *A. eximius* during migration, a

transient crucial phase in a colony life (Vollrath, 1982) and a highly cooperative process.

We then used a model of collective migration based on Saffre et al. (1999b) to explain our experimental results and to show how the silk following behaviour affects the collective migration.

Materials and methods

The experiment

In this study, we considered that a nest is a group of niches which, at the time specimens were collected, were part of the same web (i.e. connected by silk threads), indicating that nestmates (belonging to the same nest) at least occasionally moved between them. A niche is an area of the web (usually immediately under a leaf or cluster of leaves) in which spiders were found densely aggregated. The silk prevents individuals from dispersion and ensures group cohesion during collective displacement (Bernard and Krafft, 2002). This characteristic led us to make the basic assumption that distant nests (at least 50 m) without silk connections between them were the result of independent foundations. Therefore, spiders taken from such distant nests were assumed to be “dissimilar” and present different genetic and/or epigenetic characteristics, whereas spiders taken within the same nest were presumed more similar (Bilde and Lubin, 2001; Beavis et al., 2006).

Spiders were collected from various nests along a transect that ran for approximately 250 km, roughly following the French Guiana coast in a north-westerly direction. Spiders were collected from 17 different nests. For one night, we kept spiders outdoors in plastic bottles with mesh lids under natural temperature conditions. Collective migration was initiated in manipulated groups in French Guiana, on the forest edge, the natural habitat of *Anelosimus eximius* (Pasquet and Krafft, 1989; Furey, 1998). Nineteen implantations were made at experimental sites in edge habitat along roads. The experimental set-up comprised small fork-shaped trees chosen to provide two similar web foundation sites. A plastic cup 10 cm deep and 5 cm in diameter was placed in each tree fork (Fig. 1). The cup was perforated with a single hole in the bottom centre through which a polyester guy line ($\varnothing=0.5$ mm) was run. The cup was suspended on this guy line which rose approximately half a metre before splitting into a “y” maze (Fig. 1).

Spider groups of 200 individuals were formed so as to be the most homogeneous possible with respect to age and sex structure (similar web sizes). Two categories of experimental groups were used: mixed groups (called MG) composed of spiders coming from two distinct nests

(ratio=0.5, N=10) and single groups (called SG, N=9) composed of spiders coming from the same nest.

Spiders were placed in cups and were allowed to leave the cup freely, which they did by climbing the central guy line, and to settle on either of the two branches. The “y” maze is one of the most common and effective experimental set-ups, confronting the animal with a binary choice (Saffre et al., 1999b; Jeanson et al., 2004). During migration, each spider contributed to the growth of the webbing structure through the addition of its own dragline. An amplification process appeared that resulted from the opportunity for an individual to use a predecessor’s dragline as a shortcut. As each spider was contributing to the growth of the branching points, one of the two available foundation sites gained the advantage. An important network appeared on this side (Fig. 1) that recruited more spiders and hence spiders were asymmetrically distributed between branches. In the case of collective choice, the asymmetry between the population having chosen the left or right branch is an index of the intensity of amplification mechanisms.

Over 5 consecutive experiment-days, we measured two parameters: 1) The fraction of spiders settled anywhere in the set-up (N settled/ N settled + N leaving the site), and 2) the ratio of spiders settled on the most populated branch, a measure of aggregation.

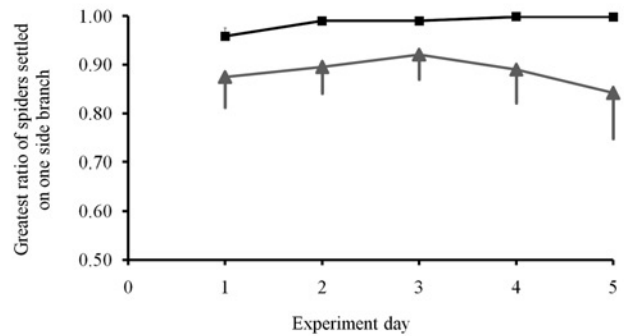


Figure 2. Fraction of settled spiders (N settled/ N settled + N leaving the website) over five experiment days. Average and standard deviation are given for single-group (SG=black square) and mixed-group (MG=grey triangle) experiments.

The model

Simulations were conducted to propose a mechanism explaining the experimental results. The chosen model was developed and analyzed in previous papers (Saffre et al., 1999b; Jeanson et al., 2004) and the general quantitative agreement between theoretical and empirical data validates the behavioural algorithms used in the model. This model followed a scenario devoted to the exploration of the amplifying properties of the spider’s dragline-following behaviour. It assumed that collective migration of *A. eximius* was coordinated by behaviours involving silk laying, since social spiders produce silk threads that recruit congeners. The first spider’s only escape route corresponds to the terminal bifurcation point so it has 50% chances of choosing either side. The second spider added a new escape route from this first bifurcation point. Each spider contributed to the growth of the silk structure through the addition of its own dragline. The amplification process resulted from the opportunity for an individual to use a predecessor’s dragline as a shortcut. As each spider was contributing to the growth of the branching points, one of the two available foundation sites gained the advantage. An important network appeared on this side that recruited more spiders and hence spiders were asymmetrically distributed between branches (Saffre et al., 1999b; Jeanson et al., 2004). We performed 1000 simulations for groups of 100 spiders. In case of mixed groups, the simulations were performed for two groups of 50 spiders. These theoretical results showed how behaviours towards non-

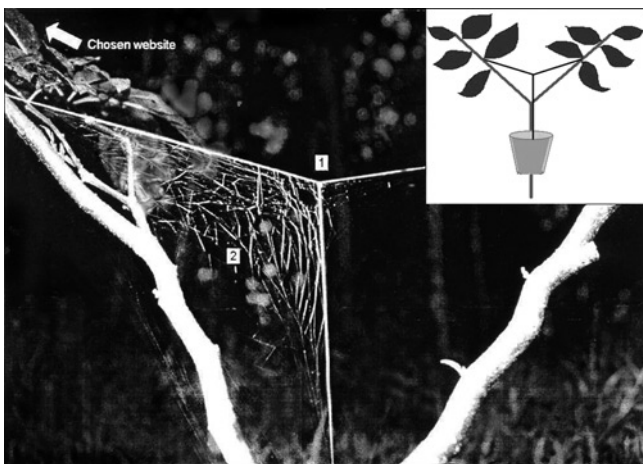


Figure 1. Experimental set-up.

nestmates affected the collective migration in mixed populations. These values (100 and 50) were chosen to take account of the spider fraction that does not settle in the tree (see Experimental results).

We quantified the inter-nest variability with the parameter β of inter-attraction between individuals belonging to different nests (Amé et al., 2004; Jeanson et al., 2004; Saffre, 2000). The value of this recognition parameter β reflects the tendency to respond to the signal (dragline) of an individual belonging to another nest and modulates the spiders' aggregation behaviour. $\beta = P'/P$ where P is the probability of choosing a nestmate dragline and P' is the probability to follow a non-nestmate dragline. The higher the value of β the lower the discrimination between nestmates and non-nestmates. For instance, for $\beta=0.5$, individuals are twice more likely to follow the silk of their own nestmates. A value of $P=P'=0$ would result in an even distribution of spiders between branches as it would imply that they do not respond to each other's dragline, which in turn would prevent the build-up of any recruitment-style positive feedback.

Results

Experimental results

Spider settlement in the experimental set-up

About fifty percent of the spiders were found in the tree branches and established a new colony: over the 5 experiment-days, the fraction of settled spiders (N settled/ N settled + N leaving the website) was on average 0.57 ± 0.05 in SG and 0.45 ± 0.06 in MG (Fig. 2). Within groups of SG, the fraction of settled spiders in the website was statistically similar in all nests (Kruskal-Wallis test, $p=0.99$, $KW=1.50$). Similarly, within groups of MG, the fraction of settled spiders in the website was statistically similar in all nests (Kruskal-Wallis test, $p=0.27$, $KW=1.11$). This fraction differed as a function of the day in the two groups (Kruskal-Wallis test, SG: $p=0.04$, $KW=10.22$; MG: $p=0.02$, $KW=10.96$). Over the entire experimental period, this variable was statistically higher in groups comprised exclusively of nestmates than it was in mixed groups (Mann-Whitney test comparing the fraction in function of experiment days: day 1: $U=13$, $P<0.01$, d2: $U=6.5$, $P<0.005$, d3: $U=6.5$, $P<0.005$, d4: $U=0.00$, $P<0.0005$, d5: $U=0.00$, $P<0.0005$). This result shows that, in contrast to groups involving non-nestmates (MG), SG groups have a higher tendency to settle in our experimental set-up.

The standard deviations of the fraction of settled spiders were not significantly different (t-test comparing the sd: day 1: $F=1.4$, NS, day 2: $F=2.7$, NS, day 3: $F=2.5$, NS, day 4: $F=2.5$, NS, day 5: $F=1.3$, NS). Over the entire experimental period, the variability among the values of the fraction of settled spiders was very low.

Spider aggregation on the branches

The population distribution remained highly aggregative over the five experiment-days: the ratio of spiders settled on the most populated branch was on average 0.99 ± 0.02 in SG and 0.89 ± 0.07 in MG (Fig. 3). This ratio of spiders

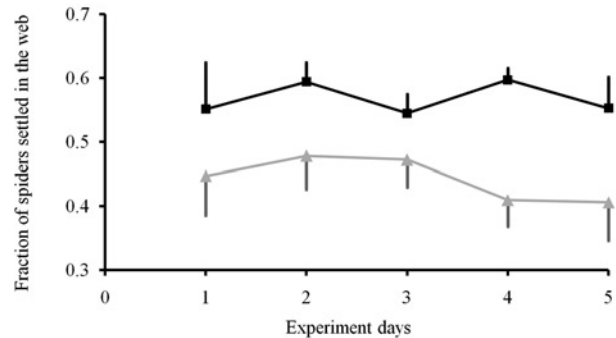


Figure 3. Fraction of spiders settled on the most populated branch over five experiment days. Average and standard deviation are given for single-group (SG=black square) and mixed-group (MG=grey triangle) experiments.

settled on the most populated branch was statistically similar in all groups for the SG (Kruskal-Wallis test, $p=0.97$, $KW=2.28$) and for the MG; (Kruskal-Wallis test, $p=0.35$, $KW=9.99$). It varied from day to day only in SG (Kruskal-Wallis test, SG: $p<0.05$, $KW=13.00$; MG: $p=0.35$, $KW=9.99$). Over the entire experimental period, this variable was statistically higher in single groups than in mixed groups (Mann-Whitney test comparing the fraction in function of experiment days: day 1: $U=11.5$, $P=0.007$, day 2: $U=0.50$, $P<0.0001$, day 3: $U=1.00$, $P<0.0001$, day 4: $U=0.00$, $P<0.0001$, day 5: $U=0.50$, $P<0.01$). This result shows that the presence of non-nestmates also reduces the spiders' tendency to aggregate, leading to a lower asymmetry in the spatial distribution of mixed groups (reduced cohesion).

It should be noted that the standard deviations were significantly different between MG and SG (t-test comparing the sd: day 1: $F=16$, $p<0.0005$, day 2: $F=129$, $p<0.0001$, day 3: $F=114.5$, $p<0.0001$, day 4: $F=450$, $p<0.0001$, day 5: $F=664$, $p<0.0001$). The cohesion of MG groups was more variable than that of SG groups. This result suggested that the factors that induced the cohesion had a variable efficiency.

Theoretical results

SG: The fraction of spiders settled on the most populated branch as a function of the probability to follow a dragline follows a sigmoid curve (Fig. 4a). As long as the value of the probability $P < 0.2$, a small increase in the latter results in a substantial increase of the fraction until a plateau value is reached. Afterwards, the relation between the ratio of spiders settled on the most populated branch and the probability to follow a dragline is linear. Comparison with field data showed that in case of single-lineage groups, the best fit between theoretical and experimental distributions was obtained for $P=0.3$.

MG: We ran simulation sets with the value of P fixed to 0.3 and observed how the fraction of spiders settled on

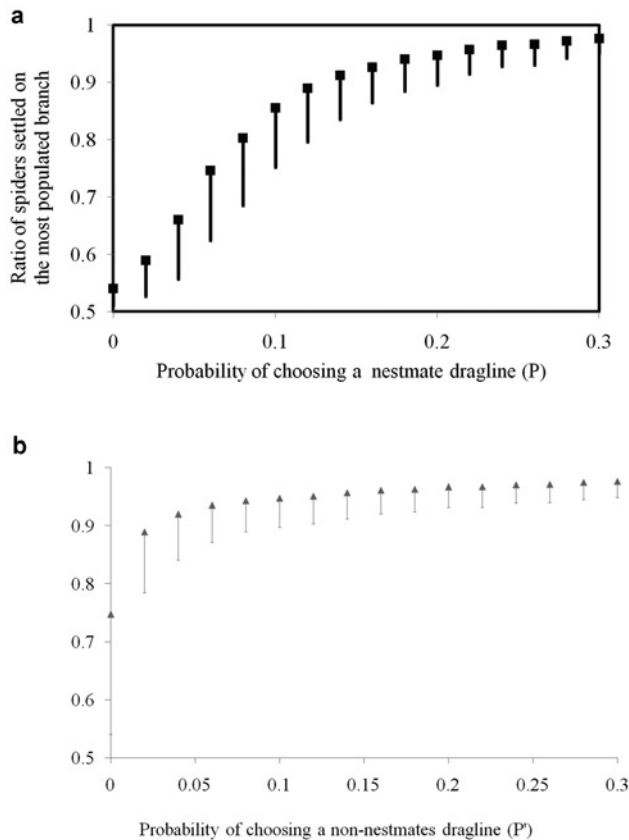


Figure 4. (a) Fraction of spiders settled on the most populated branch as a function of the probability of choosing a nestmate dragline (P) with single group. (b) Fraction of spiders settled on the most populated branch as a function of the probability of choosing a non-nestmate dragline (P') with mixed-group and $P=0.3$.

the most populated branch was influenced by P' . In case of mixed groups, the correct plateau value is reached for a very low value of the probability to follow a dragline produced by a non-nestmate. The best fit between theoretical and experimental distributions was obtained for $P'=0.02$ (Fig. 4b).

Therefore, the model predicted that, to obtain the differences observed in the field between SG and MG, the value of $\beta = P'/P = 0.07$.

Discussion

The present study is the first evidence that, in the social spiders *Anelosimus eximius*, the presence of non-nestmates has an influence on the spiders' behaviour during the migration process. This study then shows that *Anelosimus eximius* are actually capable of recognizing nestmates from non-nestmates. Indeed, the presence of non-nestmates in a group of social spiders during the migration process reduces settlement success and increases dispersion, the asymmetry in the spatial distribution being less pronounced. Foundations involving spi-

ders originating from different nests are not as stable as those involving only nest-mates which can result in a failure to successfully establish a new nest. If social spiders (unlike most social arthropods) are tolerant to each other in the sense that no antagonistic behaviour can be observed, a more subtle form of segregation may be at play.

What are the mechanisms involved in this segregation? In *Anelosimus eximius* and other social spiders, collective migration is organized through simple behaviours involving silk laying, as social spiders produce silk threads that recruit other congeners (Saffre et al., 1999a,b, 2000; Jeanson et al., 2004). Each spider contributes to the growth of the webbing structure through the addition of its own dragline. Therefore an amplification process can arise as a result of the opportunity for an individual to use the predecessor's dragline as a shortcut. Our theoretical results presented here show that the observed differences between single groups and mixed groups probably results from strong differences in silk attractiveness between individuals coming from different nests (Bernard and Krafft, 2002). The probability of following the dragline of a nestmate must be much higher than that of following one from a non-nestmate to observe such a difference in the segregation of settled spiders. Our model shows that spiders from different nests segregate only for a very low value of β . Indeed, computer simulations and experimental results are comparable when $\beta \approx 0.07$ which indicates that *A. eximius* has probably developed high capabilities to discriminate their own nestmates from non-nestmates. In other words, spiders following the silk of their own nestmates might be about ten times more numerous than spiders following the silk of non-nestmates. This paper shows that, during the induced migration, there are two processes working in opposition: the amplification process resulting from the addition of silk favours aggregation even with non-nestmates, yet the recognition process reduces the cohesion of groups composed of non-nestmates. Therefore, amplification process mediated by the silk hides the strong individual discrimination between spiders coming from different nests. This could explain why segregation was not evidenced in *Anelosimus eximius* before our study. The variable intensity of the collective decision-making between mixed (MG) and single groups (SG) results from the balance between a strong dragline-mediated recruitment process (positive feedback) and the lower attractiveness of silk threads left by non-nestmates.

In *Anelosimus eximius*, it has been shown that genetic variations between nests were high (Smith and Hagen, 1996). We speculate that the value of β might be linked to the genetic proximity between individuals from different nests: β might increase when the relatedness between individuals from different nests becomes higher. As, in social spiders, pheromone-impregnated silk is attractive for nestmates, we suggest that silk could carry some information about an individual's origin and genetic

proximity to another individual (Evans, 1999; Bernard and Krafft, 2002; Beavis et al., 2007). The value of β might be linked to genetic differences in the composition of the silk. The value of β might also be linked to epigenetic factors such as similar food consumption or environment (Arnold et al., 2000; Julian and Fewell, 2004; Wyatt, 2003: 34–36). Indeed, the identification of non-nestmates can be based on environmental and/or genetic cues (reviewed in Sherman et al., 1997). Laboratory experiments are needed to confirm that, in *A. eximius*, discrimination between non-nestmates (β) does indeed mirror genetic or epigenetic differences.

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