



## Exploratory Recruitment Plasticity in a Social Spider (*Anelosimus eximius*)

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Exploratory recruitment was investigated in an artificial experimental set-up on location in French Guyana. Groups of 200 freshly collected spiders of the neotropical social theridiid *Anelosimus eximius* were released on an open circular surface and offered a choice between two accessible shelters. Results indicated that a clear-cut collective decision was not always reached, unlike what we found using a different set-up in another set of experiments. Simulations were conducted using available information in order to explore the potential causes for this difference. Theoretical projections fit experimental data and strongly suggest that variability in the collective response results from a combination between modifications of the environment's properties and alteration of the recruitment procedure. Multiple variants of the theoretical set-up (including external bias) are investigated and emphasize plasticity in the collective response. New experimental studies are suggested and adaptative value of exploratory recruitment in social spiders is briefly discussed.

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### 1. Introduction

The emergence of collective decision and its link with individual behaviour is an important question for group living organisms. Several experimental and theoretical findings related to self-organization lead us to reconsider the level of complexity needed in information processing and coding for collective decision to emerge. In self-organized social activities, most collective decisions and patterns arise as a result of competition between different sources of information which can be amplified through a wide variety of positive feedback. In such systems, a diversity of patterns can be produced with a single set of behavioural rules, modifying nothing but

parameters' value or environmental constraints (Bonabeau *et al.*, 1997).

These collective decisions are examples of rules of thumb requiring only limited cognitive ability and reduced access to global information. This logic contrasts with some optimization points of view. Those often assume that decision is made at the individual level, and the corresponding models are consequently based on the hypothesis that each animal (arthropod) has a relatively high information processing capability (Detrain *et al.*, 1999).

Numerous social species are known to exhibit a diversity of patterns in relation with different environments, but it is often assumed that this diversity of collective responses is due to a modification of individual behaviour. It is therefore suggested that any transformation of the

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environment is perceived and induces an adaptive response at the individual level (Detrain *et al.*, 1999). Although this is usually true, it is manifest that explicit information processing is not the only way to generate this kind of adaptation.

In self-organized systems, the environment contributes to the emergence of decisions by altering amplification dynamics rather than individual response, and a diversity of patterns can still be produced only by modifying environmental constraints. This is the case of aggregation in very different organisms such as molluscs (Focardi *et al.*, 1985) or herbivorous mammals (Gérard & Loisel, 1995; Gérard *et al.*, 1997). Models of recruitment in ants show that pattern plasticity can be driven simply by an increase in the number of food sources, without requiring any change in communication system or individual behaviour. A colony can focus on exploiting a single source if there are not many or if foraging population is large. Alternatively, it can exploit all sources together if those are numerous or colony population is small (Nicolis & De-neubourg, 1999). This indirect influence of the environment can even explain some inter-specific variability: foraging patterns of army ants can be modulated changing only food density or distribution, leading one species to adopt the pattern of another (Franks *et al.*, 1991).

In spiders, numerous factors, physiological, environmental and social, influences the size and/or structure of the silk network (see e.g. Witt & Baum, 1960; Uetz & Burgess, 1979; Buskirk, 1986; Tietjen, 1986; Leborgne & Pasquet, 1987). Some authors (see e.g. Janetos, 1986) suggest that in many cases even critical decisions like web site selection are not based on complex information processing, but on giving-up rules. Consequently, social spiders provide an original material to analyse the influence of the environment on the organization of collective responses involving simple individual behaviours.

Although we do not reject the hypothesis of a modulation of individual behaviour, our main concern here is the influence of environmental properties on the dynamics of collective decision. The migration and website selection process can lead to a diversity of solutions: most spiders can select only one site and cluster there, or the population can be evenly distributed between

available locations. In a first set of experiments involving binary choice (hereafter referred to as “Y-choice”, we did show that collective decision is very easily reached, a strong majority of spiders (over 80%) selecting the same nest site (Saffre *et al.*, 1999a; Furey *et al.*, unpublished data). Fitzgerald (1995) showed that the silk trails of social caterpillars also induced extremely well-marked choice in a similar set-up. In this paper, we investigate how the collective response of social spiders is affected in a binary choice situation offering the same opportunity for silk-based recruitment, but featuring a different geometry.

## 2. Material and Methods

### 2.1. EXPERIMENTAL PROTOCOL

Preliminary experiments ( $N=10$ ) were conducted in French Guyana in March 1997. Those spiders used were collected in natural colonies and kept in plastic containers. The experimental set-up, surrounded by fresh water, was comprised of a plastic dish (30 cm in diameter) covered with paper. Two vertical polyester threads, 15 cm apart, provided access to two separate plastic containers offering shelter and located about 1 m above the horizontal circular area (Fig. 1). Groups of 200 spiders were cooled (1 min) in order to allow easy handling and deposited on the surface. After recovery, spiders were observed to attempt escaping the set-up in two different ways: exploring the environment by walk or lifting their abdomen to emit airborne threads. This behaviour, common to many spider species (see e.g. Peters, 1990), allows these animals to reach nearby places because the tip of the thread spontaneously adheres to any suitable support it enters in contact with. Spiders were allowed to do so for 1 h, after which the experiment was stopped and the spiders counted and divided into three categories: “left container”, “right container” and “on dish/drowned”.

### 2.2. THEORETICAL PROTOCOL

Numerical experiments were conducted on a square lattice, each cell being 1 cm wide. Spiders are released sequentially on a randomly selected cell. Starting on the corresponding

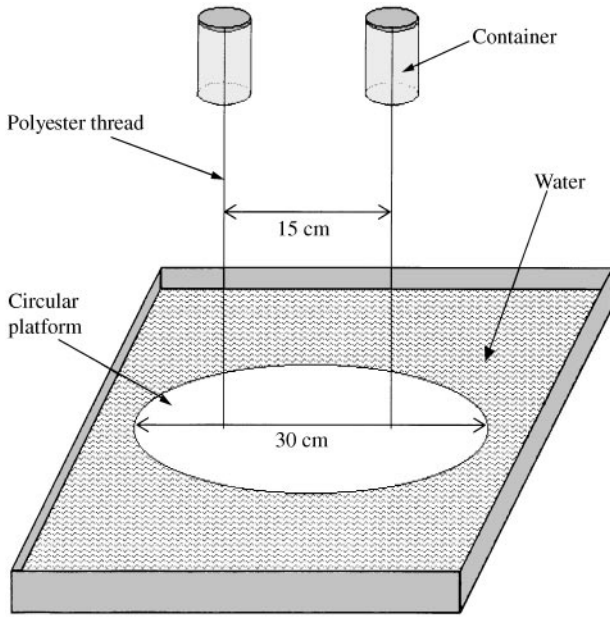


FIG. 1. Experimental set-up.

location, a random walk is initiated that consists in moving in one of four potential directions at each time step until a potential escape route is encountered. The two polyester threads are implemented as such routes, and are the only available ones in the initial conditions.

Recruitment proceeds through the multiplication of escape opportunities resulting from dragline attachment leading to a competition between both sites (a typical evolution of the recruiting structure is shown in Fig. 2). Each individual leaving the surface is assumed to have fixed its dragline somewhere on the dish before it exits, and this attachment point becomes a new potential route leading to the same container its owner has reached. Each cell of the lattice is allowed only one route (either to the left or right container). The location of the new escape thread is determined using one of two different procedures, corresponding to two behavioural scripts:

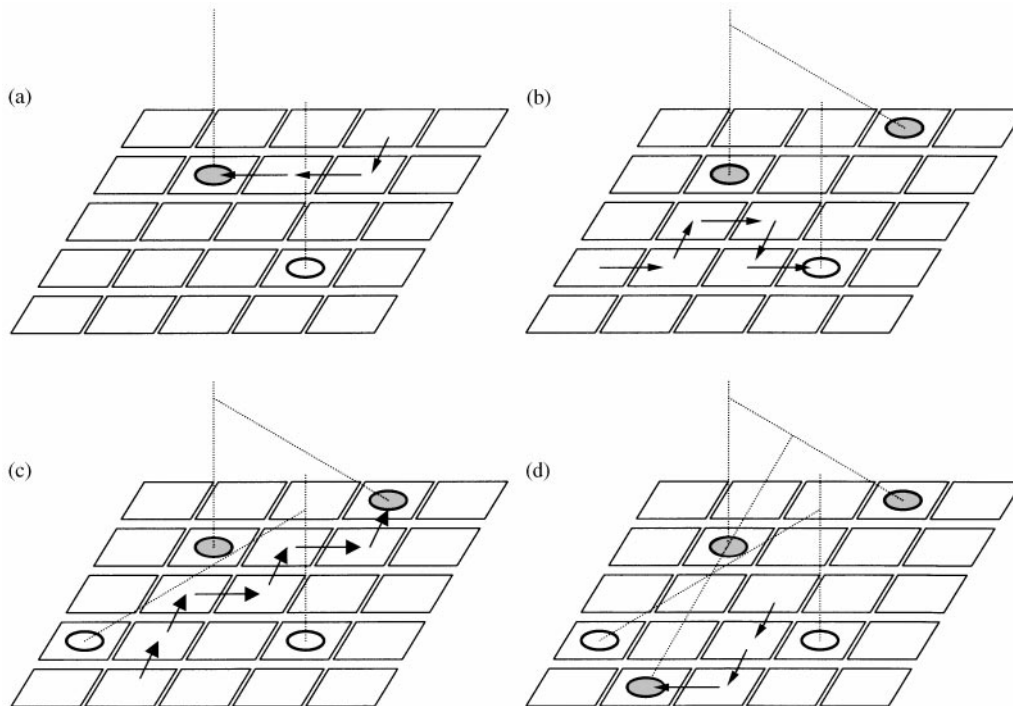


FIG. 2. Typical evolution of the recruiting structure. Grey circles identify cells where a route to container #1 is present, white circles those which lead to container #2. Arrows represent random walks ending up at the first encounter with a potential escape route. This sequence corresponds to the airborne procedure (each new route is added at the starting point of the associated random walk). The threads configuration is arbitrary and is given only as an illustration of the real web structure growth. It is not explicitly taken into account in simulations.

A. It can result from the spider movement, in which case a random test is performed in each newly entered cell to determine if the dragline was fixed there. This test is based on a constant probability  $p$  (Saffre *et al.*, 1999b) and the last attachment point is considered the origin of the new escape thread.

B. It is assumed that the thread was airborne, and the cell where the corresponding individual was released is used instead. In this second hypothesis, the random walk is assumed to reflect the trajectory of the airborne thread's tip rather than that of the spider itself.

The influence of an external bias on the recruitment process was implemented as an asymmetry in the probability associated with each direction during the random walk: this can be assimilated either to a tropism affecting the individual behaviour, or to a mechanical constraint imposed to airborne threads (directional airflow).

### 3. Results

#### 3.1. EXPERIMENTAL DATA

As summarized in Table 1 and Fig. 3(a), the outcome of the population transfer between the dish and the containers ranged from very pronounced asymmetry to practically even repartition. Yet, comparison with expected binomial distribution in the case of random choice for a similar population size demonstrates that recruitment, and so collective decision, is indeed

TABLE 1  
*Experimental results summary*

Exp. no.	Left	Right	On dish drowned	Lost
1	97	42	53	8
2	60	99	14	27
3	4	154	42	0
4	38	130	9	23
5	68	94	10	28
6	82	49	35	34
7	23	117	17	43
8	121	24	38	17
9	78	82	14	26
10	78	68	?	?
Average $\pm$ S.D.	65 $\pm$ 35	86 $\pm$ 41	26 $\pm$ 16	23 $\pm$ 13

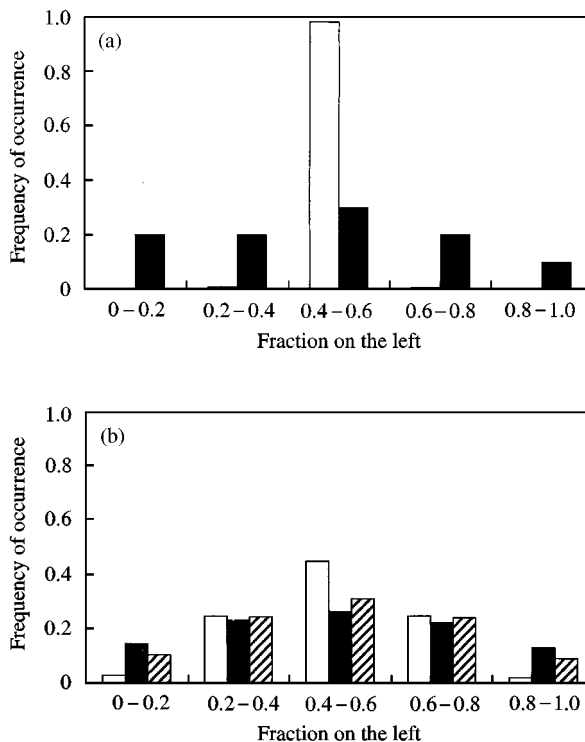


FIG. 3. (a) Comparison between expected (white), and experimental (filled,  $N = 10$ ) distributions (see text). (b) Comparison between theoretical distributions obtained for active exploration (script A, white,  $N = 10^4$ ), airborne based (script B, filled,  $N = 10^4$ ) and mixed (dashed,  $N = 10^4$ ) recruitment procedures (see text).

present, but not as intense as expected. Indeed, the experiment on exploratory recruitment conducted in the Y-choice set-up did result systematically in strongly asymmetrical distribution between both shelters (Saffre *et al.*, 1999a; Furey *et al.*, unpublished data).

Contrasting with the variability in the final distribution, the proportion of spiders that were able to reach shelter is remarkably stable, and represents about 3/4 of the initial population. This result clearly shows that in those stressful experimental conditions, emigration rate is high and a majority of spiders are able to escape the open dish. Other observations (Saffre, pers. obs.) as well as a study on another social species (Lubin & Robinson, 1982) suggest that the use of conspecifics' draglines can play an important part in boosting the swarming process.

### 3.2. NUMERICAL SET-UP EQUIVALENT TO EXPERIMENTAL SET-UP

#### 3.2.1. Active Exploration (Script A)

We made a first attempt at reproducing the experimental data using exclusively active exploration and dragline attachment as the recruitment procedure. The default value of  $p$  was chosen to be equal to 0.1, in accordance with experimental measurements obtained in another set-up (Saffre *et al.*, 1999b). The predicted distribution is different from the one expected in a random choice situation, but the amplification process is obviously too weak to account for the most asymmetrical experimental results [Fig. 3(b)]. This poor performance of the model, as well as personal observations during the experimental study, led us to develop script B.

#### 3.2.2. Influence of Airborne Threads (Script B)

As implemented in the simulation, the only effect of the particular behaviour consisting in emitting such a thread is to reduce the influence of the discovered escape route's location on that of the new one. Obviously, in the case of random walk, the probability that a spider exits using any given escape route is inversely correlated with the distance between the starting point and that route. Yet, if the dragline is attached on the substrate during the random walk (which is the case for active exploration), the probability that it is fixed in the vicinity of the escape route remains high even when the spider's trajectory is very long and/or complicated. This is not the case of the airborne thread, that will be attached on the same cell where it has been emitted, whatever the distance travelled.

This model is able to reproduce experimental data with accuracy [Fig. 3(b)], suggesting that airborne threads are the basis of the swarming dynamics in this specific experimental set-up. Numerical experiments involving a combination of both procedures show that amplification remains strong even when only part of the population is emitting airborne threads and the other obeys script A [Fig. 3(b) and 4(a)]. In fact, a better adequation with the experiment is obtained for this mixed strategy (50% chance of exhibiting each behaviour). However, the small size of the data sample does not allow us to draw any

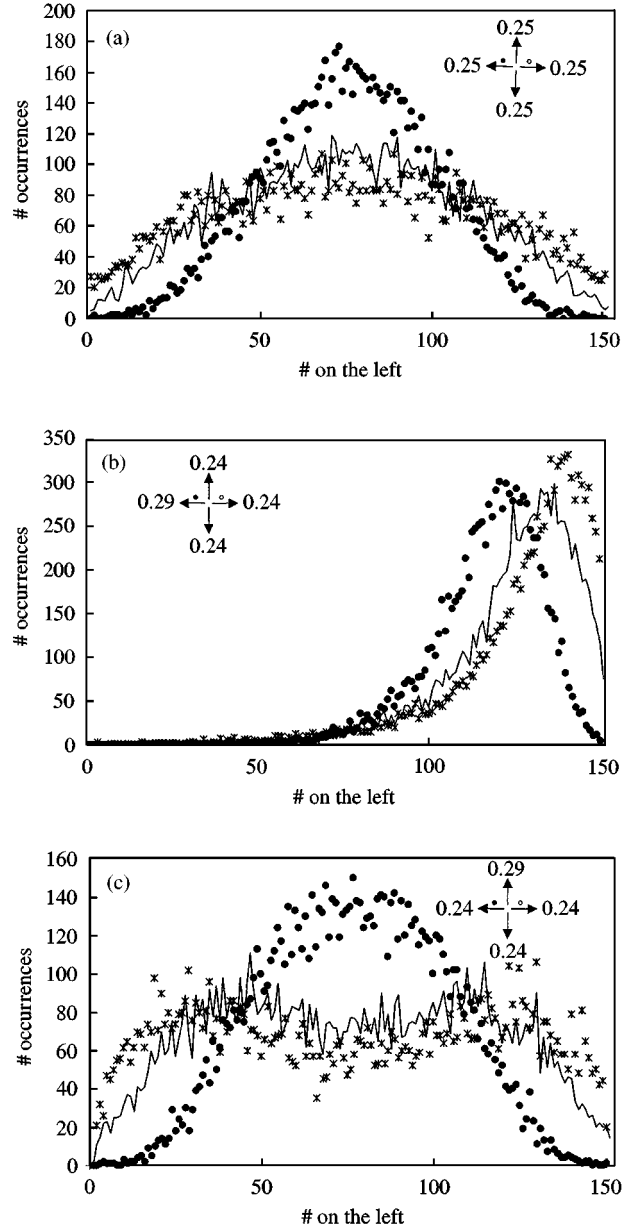


FIG. 4. Comparison between the three procedures investigated in simulations: active exploration,  $\bullet$ ; airborne,  $*$ ; mixed,  $—$ . Final distribution ( $N = 10^4$ ) without external bias (a), with a 5% parallel bias (b) and with a 5% perpendicular bias (c).

conclusion about the real frequency of each behaviour.

#### 3.2.3. Influence of Parallel Bias

Obviously, in a natural environment, the collective decision process will often be

influenced by external asymmetries affecting individual choice. This is particularly true for airborne threads since it is clear that airflow will introduce a directional bias, yet the orientation of the spiders too can take into account environmental cues (light gradient, etc.). So this possibility was investigated in the numerical set-up, for the three recruitment procedures (active exploration, airborne and mixed).

These dynamics are extremely sensitive to even a low bias. As shown in Fig. 4(b), a 5% asymmetry in favour of one of the four possible directions is enough to concentrate most of the population on an initial escape thread located “downstream”. The effect is present whatever the recruitment procedure, although it is more intense for airborne-based dynamics (over 90% of spiders on the favoured site).

### 3.2.4. Influence of Perpendicular Bias

The effect of an asymmetry perpendicular to the axis on which both initial escape routes are located was also investigated, with the same 5% bias. Understandably, the statistical similarity between both escape threads is restored, yet the recruitment dynamics and the resulting distribution are obviously affected [Fig. 4(c)].

In the case of active exploration (script A), the perpendicular asymmetry appears to have little effect on the swarming process: the population is still quasi-evenly distributed between both escape routes, and except for a weak flattening (attesting slightly stronger recruitment), it is not sensibly different from what was found in the no bias situation.

The amplification of the competition between the two initial routes by the perpendicular bias is much stronger if airborne threads are involved: the final distribution shifts from unimodal to clearly “U”-shaped configuration, the maximum corresponding to the situation where over 80% of the population is concentrated on one of two potential sites. This rather unexpected result points out that even a weak directional airflow can have a considerable facilitating effect on the collective decision process, even when its orientation with respect to potential routes is “neutral”.

## 3.3. INFLUENCE OF SET-UP SCALE

### 3.3.1. Fixed Configuration with Variable Scale

Changing the size of the theoretical set-up without modifying its relative proportions (ratio diameter/distance between initial escape routes = constant) seems to have little effect on population distribution. However, for the three tested set-up dimensions (diameter = 15, 31 and 63 cm, 31 being the default value) a gradual narrowing of the central peak is noticeable in the situation where only active exploration is present. This simply confirms the strong influence of the random component in these dynamics, the main effect of increasing the distance between initial threads while maintaining the attachment probability constant being to reduce competition even further.

It should be emphasized though that our simulation results do not explicitly take time into account. It is most likely that increasing set-up diameter would slow down the swarming process in a real situation, although the simulation suggests that the final distribution should not be affected.

### 3.3.2. Fixed Scale with Variable Configuration

Changing the configuration give more intriguing results. We tested two alternative locations for the initial escape routes, both in the default set-up (31 cm in diameter). In the first one, threads are located on the periphery of the platform, on opposite radii (30 cm apart), while in the second, they are both near the centre of the dish (2 cm apart, still on the same diameter).

In the case where escape routes are on the edge of the set-up, we obtain virtually antithetic final distributions for both recruitment procedures. If only active exploration (script A) is present, the distribution is unimodal although considerably flattened compared with the default configuration. On the contrary, if only airborne threads (script B) are involved, the resulting pattern is strongly bimodal, indicating intense competition and recruitment. Again, the mixed strategy is clearly dominated by the airborne dynamics [Fig. 5(a)].

If initial escape threads are located close to one another near the centre of the set-up (second

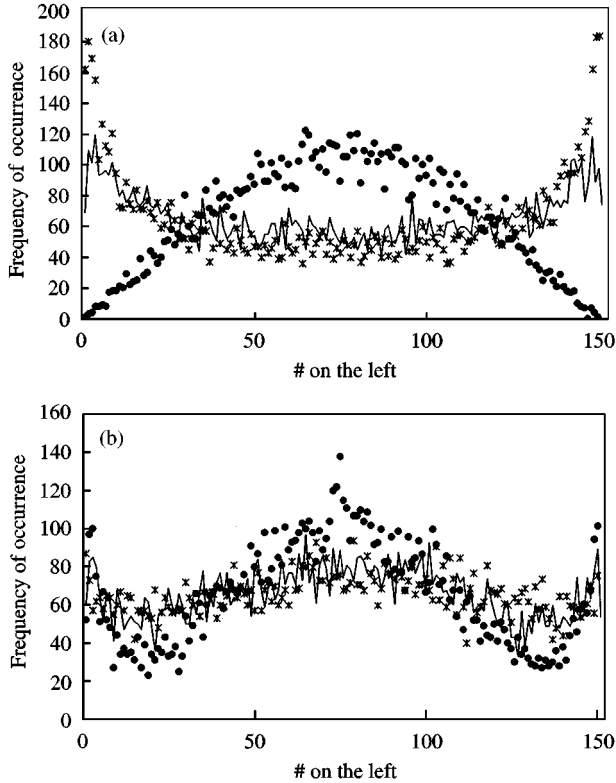


FIG. 5. Comparison between the three procedures investigated in simulations: active exploration, ●; airborne \*, mixed, . —. Final distribution ( $N = 10^4$ ) with initial routes 30 cm apart (a) and 2 cm apart (b).

hypothetical configuration), the final distribution becomes strongly trimodal for active exploration (script A). Although much weaker, the effect is still present for the airborne (script B) and mixed strategies [Fig. 5(b)].

The interpretation of this trimodal pattern involves random fluctuations in the early stages of the swarming process. These can either “kill” one of the initial options by surrounding the corresponding route with secondary escape threads leading to the opposite container, or on the contrary generate “territories” around each route, subsequently limiting competition between them. In the first case, most spiders will concentrate on one of two available options, while in the second, they will be evenly distributed between both shelters.

### 3.4. CONTINUITY BETWEEN SCRIPTS

Maybe it is worth making a few remarks about the link between active exploration (script

A) and production of airborne threads (script B) as they are implemented in the model. Indeed, script B can be regarded as a limit case for script A, where  $p$  is given the extreme value of zero: if the dragline is never attached to the substrate during the walk then, provided it was fixed in the cell where the spider entered the set-up, both scenarios are rigorously equivalent.

As shown in Fig. 6, numerical experiments conducted following script A but using a lower value of  $p$  (e.g. 0.01) generate a distribution pattern that is very close to that obtained when considering airborne threads (script B) in the same environmental conditions. This result makes it clear that it is variation in the range of the interaction between escape routes that is in fact responsible for the difference in recruitment dynamics between scripts. Indeed, this range is longer for both scripts B and A with a lower  $p$  than it is for active exploration using the default attachment probability.

These considerations, although of a theoretical nature, point out the continuity between both recruitment procedures in the real phenomenon. In fact, decreasing the value of  $p$  is equivalent to increasing the fraction of spiders obeying script B in mixed populations. We opted for the latter because airborne threads were indeed observed during the experimental study.

## 4. Discussion

From these experimental data and theoretical projections, we can derive a few insights into the mechanisms involved in silk-based coordinated swarming and resulting distribution patterns in social spiders:

(A) The basic geometrical properties of the environment has a strong influence on the effectiveness of the decision process through a modulation of the recruitment. This is illustrated both experimentally and theoretically by the comparison between the Y-choice and the two-dimensional set-up presented here. It should be recalled that in the Y-choice situation, a behavioural algorithm very similar to script A produced a strongly asymmetrical population distribution. Numerical experiments using a discrete Y-shaped set-up also resulted in a bimodal configuration,

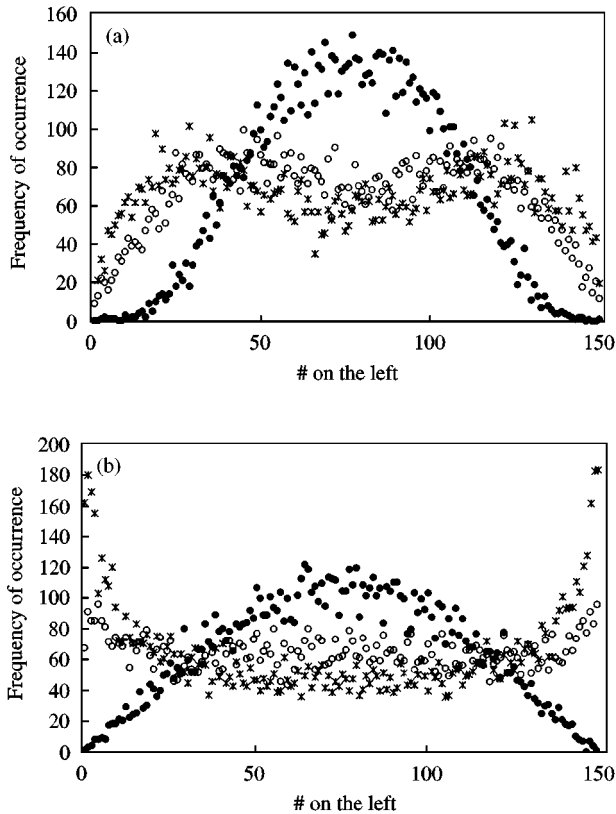


FIG. 6. Comparison between airborne, \* and active exploration with  $p = 0.1$ , ● and  $p = 0.01$ , ○ in the 31 cm set-up. Final distribution ( $N = 10^4$ ) with a 5% perpendicular bias (a), and with initial routes located on the periphery (b).

which confirms that the cellular nature of the two-dimensional environment is not involved (Saffre *et al.*, 1999a). This clearly demonstrates that the transition from 1D (Y-choice) to 2D is at least partly responsible for the observed dramatic change in recruitment dynamics, which does not result from a methodological bias.

(B) The other potential cause for the difference found between both set-ups is that in a 2D environment, *A. eximius*' swarming strategy is obviously partly based on the use of airborne threads. Although sharing a very similar logic, scripts A and B produce quantitatively but also qualitatively different recruitment patterns in the same environment. If one is preferred in specific conditions, like our results strongly suggest, this could explain some intraspecific variability between populations/colonies, simply due to a shift in the frequency of each strategy.

(C) Not only the basic geometry of the environment but also asymmetries can play an important part in the collective decision process, even when they are not explicitly in favour of a specific choice. Since in a real natural environment, the presence of an external bias is probably the most common situation, it is clearly that the influence of such local and variable environmental factors as wind direction and light gradient must have had an impact on the selection of swarming strategies. Indeed, although the behavioural scripts described here are common to many solitary spiders, it seems likely that in the social *A. eximius*, appropriate behavioural responses might have been tuned by evolution in order to maximize collective efficiency (see e.g. Saffre *et al.*, 1997), resulting in the present case in increased foundation success rate.

All together, these conclusions point out the complexity of the problem faced by social spiders when it comes to emigrating collectively to a new website, as well as the plasticity resulting from the combination between simple recruitment dynamics and external factors.

One of the main constraints encountered by group living organisms colonizing new environments is the necessity to balance benefit from cooperative effects against resource limitation. While the first is guaranteed by maintaining group cohesion, the second is best prevented by dispersal. The complex equilibrium conditions resulting from these opposite ecological pressures are the focal point of many studies dealing with the so-called "Allee effect" (Stephens & Sutherland, 1999; Courchamp *et al.*, 1999).

A diversity of hypotheses about causes and consequences of cooperation in spiders have been emitted, but it is clear from the existence of colonies regrouping hundreds or thousands of individuals that there must be some reward (Riechert, 1985; Uetz, 1989; Pasquet & Krafft, 1992; Avilés, 1997; Avilés & Tufino, 1998). Although web-building spiders are not very mobile animals (thereby reducing the risk for unwanted scattering), and long-range collective emigration might be a rare event (Vollrath, 1982), it should be noted that rebuilding of a ruined nest (probably a common situation in a tropical environment) or

passive translocation (Pasquet & Krafft, 1989) can initiate a swarming process.

Now our theoretical results here indicate that, unlike what might have been expected, an airborne-based recruitment process in a 2D environment has a facilitating effect on collective decision in favour of one available site. Also, this effect is even stronger if an external bias is present, whatever its direction, and it is known that atmospheric variables can stimulate the emission of airborne thread (Greenstone, 1981). So we are facing a situation where all factors influencing the swarming process (internal and external) concur in promoting group cohesion. In the Y-choice experiment, where no airborne-based recruitment was observed (presumably because of set-up configuration), the concentration of most spiders on one branch was assured by another procedure (Saffre *et al.*, 1999a). Basically, in both cases, an appropriate recruitment behaviour is exhibited by the spiders that, combined with a specific environment, results in maximizing group cohesion. Indeed, the fact that collective decision is globally less efficient in the 2D set-up should not occult the fact that the final population distribution is still far from binomial.

Compared with the airborne-based recruitment, active exploration tends to limit the asymmetry between both sites in the 2D set-up, whatever its scale or configuration. This means that selecting this strategy will statistically lead more often to a splitting of the colony. Although we do not know of any experimental evidence supporting this hypothesis, it seems at least possible that increased exploratory activity could be induced by overcrowding. If this is the case, then overpopulation would in fact trigger an adaptive response preventing saturation by promoting emigration of individuals in several directions. Interestingly, such a behavioural switch would very closely reflect the conflicting ecological constraints characterizing the Allee effect, therefore assuring that local population size remains close to optimal, possibly avoiding catastrophic extinctions.

To summarize, the plasticity of the silk-based exploratory recruitment is remarkable for it is sensitive to a broad variety of environmental parameters and modulations of behavioural algorithm. The next step should be to investigate

experimentally this collective response using set-ups equivalent to their theoretical counterparts analysed in this paper.

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