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Discrete dragline attachment induces aggregation in spiderlings of a solitary species

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In the early stages of their life, solitary spiders undergo a transient gregarious phase. We designed a series of experiments in which collective displacements were induced in groups of spiderlings of the solitary species *Larinioides cornutus* (Araneae: Araneidae). Spiderlings were given access to a bifurcated escape route (Y-choice set-up) from a container. Consecutive passages in the set-up led to an asymmetrical distribution of individuals between branches. Individual behaviours of spiderlings were quantified and then implemented into a model with which we simulated collective displacements. Comparison between the outcome of the model and the experimental data shows that the discrete pattern of silk dragline attachment is the key mechanism involved in this collective phenomenon. Our results show that the collective responses in spiderlings of a solitary species and in social spiders are similar, and that a simple mechanism independent of the presence of silk attraction can lead to aggregation.

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Coordinated displacements are among the most common collective behaviours in group-living animals (Dingle 1996; Parrish & Hamner 1997; Boinski & Garber 2000). In social insects, collective migration and displacement is a crucial phase in the colony life cycle. For instance, migration occurs to reach new food areas (e.g. army ants during their nomadic phase, Schneirla 1971; Gotwald 1995), or to reach a new suitable cavity after the incidental destruction of the nest, such as after flooding or fighting in ant colonies (Hölldobler & Wilson 1990; Mallon et al. 2001) or during swarming in bee colonies (Seeley & Buhrman 1999; Visscher & Camazine 1999). One crucial question is how individuals in the group move as an integrated social unit (Dyer 2000). However, the mechanisms underlying these collective displacements in group-living animals have been poorly studied. Such coordination requires the transfer of information between colony members, in the form of signals or cues (Seeley 1995). Studies have shown that coordination can be achieved through amplification processes as a result of interactions between individuals; a group can then behave as a coherent whole without global knowledge or central

coordination (Deneubourg & Goss 1989; Bonabeau et al. 1997; Camazine et al. 2001).

Synchronized and coordinated migrations might also occur in gregarious arthropods such as social spiders (Avilès 1997). For example, collective migration in *Anelosimus eximius* is observed when the web has been damaged (Vollrath 1982) and in *Achaearanea wau* when females leave their original nest to establish a new colony (Lubin & Robinson 1982). In both cases, coordination is achieved by simple behaviours involving silk laying and silk following. During their displacements, social spiders produce silk threads that are followed by nestmates (Krafft 1970; Furey 1998). This silk-laying behaviour leads to the formation of silk 'highways' that ensure group cohesion as well as collective decision-making processes during swarming (Lubin & Robinson 1982; Avilès 2000). In the same way as pheromones are used by social insects, silk might lead to amplification processes and collective decisions. In *A. eximius*, experiments using a Y-shaped set-up have illustrated this ability (Saffre et al. 1999).

Cooperation and group coordination between individuals are not restricted to social spiders but also occur in solitary spiders. Although agonistic interactions and cannibalism occur among adults, solitary spiders undergo a gregarious phase during their early stages of development (Krafft 1979; Horel et al. 1996). In this study, we analysed and quantified the behaviours of spiderlings of a solitary species leading to cohesion and coordination in experimentally induced collective displacements. Groups

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of juvenile *Larinioides cornutus* were given a Y choice, similar to the one that was used with the social spider *A. eximius* (Saffre et al. 1999). We hypothesized that dragline attachment is the key mechanism involved in the collective displacements. This hypothesis involves the following steps. Reaching the terminal bifurcation point of the Y, the first individual chooses randomly the left or right branch. Then, because of a discrete attachment pattern of the silk, the spider incidentally makes a shortcut, which increases the probability of a second spider taking this branch. Each spider contributes to the growth of the webbing structure, so one side progressively gains the advantage over the other, and spiders are asymmetrically distributed between branches. Therefore, the coordinated migration is achieved by simple discrete attachment pattern of the silk and the resulting formation of shortcuts without any active silk-following behaviour. We tested this hypothesis in the following way: we first quantified (1) individual behaviours and (2) the dynamics of collective displacements; then, to understand how the individual behaviours give rise to the collective patterns of displacement, (3) we built a model implementing the behavioural rules derived from experiments. The predictions of the model were compared to the experimental results.

METHODS

Study Species

Larinioides cornutus (Clerck) is a common orbitel ecribellate araneomorphae spider (male: 5–8 mm without legs; female: 6–12 mm) living in humid lands (Ysnel 1992). In the field, the spiderlings undergo a transient gregarious phase lasting about 10 days (F. Ysnel, personal communication) and during which individuals cluster in a silk network close to the cocoon before dispersing. Inseminated females were collected during the winters of 1999–2000 and 2000–2001 near Nailloux and Soumensac, France (44°N 1°E). In the laboratory, each spider was reared in an individual plastic box (120×60 mm and 55 mm high). Temperature was kept at 25°C, with a 16:8 h light:dark period. Flies (genus *Calliphora*) and water were provided ad libitum. Under these conditions, females lay up to 12 cocoons with 10-day intervals between each laying. After each laying, the female (who does not provide maternal care) was moved into another box. About 30 days after laying, 50–250 spiderlings hatched from a cocoon. Spiderlings were tested 24–48 h after emergence (length: 1 mm excluding the legs) and each was tested only once.

Individual Level

We analysed and quantified individual behaviours to understand how collective displacement of spiderlings emerged.

Dragline attachment

Young spiders have an innate negative geotropism. During their displacement, they lay down silk threads
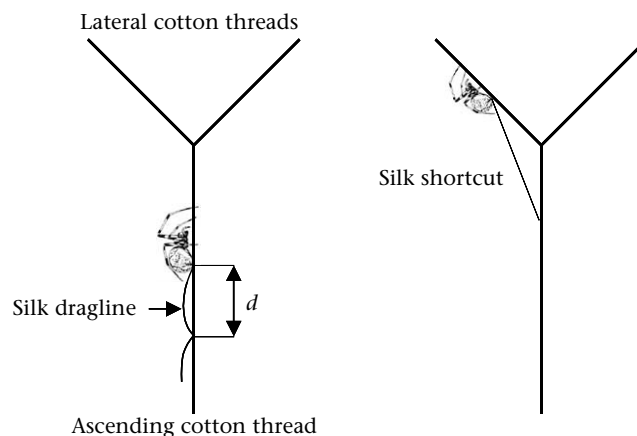

Figure 1. Experimental set-up. The distance (*d*) between two consecutive points of silk attachment was recorded. Because of the discrete pattern of dragline attachment, a silk shortcut appears between the vertical and lateral threads.

fixed to the substrate in a discrete (i.e. discontinuous) pattern, acting as a safety line (Vollrath 1999). We focused on the distribution of distance between two successive attachment points of the silk thread (Fig. 1). Attachment points were assessed by recording contacts of the tip of the abdomen with the substrate. Individual spiders were successively dropped with a paintbrush at the basis of a vertical cotton thread (diameter 0.15 mm, length 67 cm). A polyester thread fixed parallel to the cotton thread was used to mark the positions of attachment points to prevent disturbances from altering the pattern of silk attachment. The distances between two successive attachment points were recorded. The cotton thread was replaced by a new one after each individual had climbed it. We tested 30 spiders hatched from six cocoons (five individuals per cocoon), and we recorded at least 10 intervals per spider.

Probability of following a shortcut

This experiment was designed to assess the probability of a spiderling following the silk dragline laid by a nestmate. When a spider faces a Y-shaped bifurcation, it randomly chooses one of the lateral branches. Because of the discrete pattern of silk attachment, a silk shortcut is built between the vertical and the lateral branch that was followed (Fig. 1). We defined as potential escape routes the silk shortcuts laid by spiders that were likely to be followed by the next spiders instead of going along the vertical cotton thread. Thus, a shortcut provides a potential escape route for the following spiders. To assess the probability of following the silk thread (i.e. a shortcut), we allowed a spider to climb along a parallel polyester thread 1.3 cm from a cotton thread (Fig. 2a). After the spider attached its silk, it was gently moved, with a paintbrush, down the cotton thread (Fig. 2b). The silk was tightened and fixed to the cotton thread (using the natural adhesive properties of the silk) with an angle of 45° (Fig. 2c). Then another spider from the same cocoon was allowed to climb on the vertical cotton thread. We recorded whether the shortcut was followed by the spider (Fig. 2d). The cotton thread was
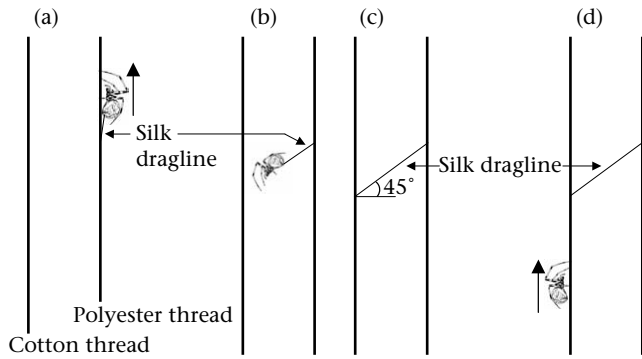
Figure 2. Procedure used to assess the probability of a spider following a silk shortcut laid by siblings. (a) A spider climbs the vertical thread, (b) is passively moved down the cotton thread, (c) the resulting dragline is tightened between the two vertical threads, and (d) a second spider is allowed to climb.

replaced after each spider had reached the top of the set-up. The probability P_f of following a silk shortcut was computed as the proportion of spiders that chose the shortcut over the total number of spiders that were tested. We performed four replications, each with 20 spiderlings hatched from the same cocoon.

Collective Level

The experimental set-up consisted of cotton threads with a vertical branch 36 cm long and two lateral symmetrical branches with an angular deviation of 45° (Fig. 3). Spiderlings were gently deposited at the base of the set-up in a small tube and were allowed to climb along the vertical thread, which gave them a choice between two identical ways of escape at the bifurcation point, i.e. to the 'right' or 'left'. We ensured that only one spider had access to the vertical thread at a time and that no direct interactions (i.e. physical) between spiders biased their choices when they encountered shortcuts. The local surroundings of each set-up were homogeneous to prevent visual or other cues from affecting the choice. We allowed 25 spiders from the same cocoon to climb over the thread successively. We recorded the side (right or left)
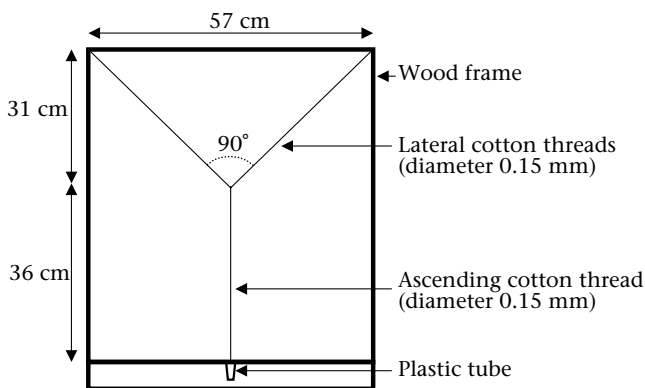
chosen by each spider ($N = 30$ replications). After each replication, the cotton thread was replaced. For each trial and after each spider had climbed the thread, we recorded the number of spiders on both branches of the set-up. To characterize the dynamics of the collective displacement process, we recorded after each spider had climbed the thread the fraction of spiders on the winning branch (i.e. the branch with 50% or more spiders). The fraction F_n of spiders on the winning branch after n spiders had climbed was computed as follows:

$$F_n = \frac{\sum_{i=1}^{i=30} n_i}{\sum_{i=1}^{i=30} n}$$

where n = number of spiders tested, and n_i = number of spiders on the winning branch in trial i.

We then computed the mean fraction of spiders on the winning side (F_n) for the 30 trials. Statistical tests were two tailed and were conducted with SPSS for Windows (v. 10, SPSS Inc., Chicago, U.S.A.), except for the Kolmogorov–Smirnov two-sample test, which was conducted following Zar (1999). For fractions, we computed the lower and upper 95% confidence limits (Zar 1999).

RESULTS

Individual Level

Dragline attachment

There was no correlation between the order of the interval and its length (Spearman rank correlation: for 27 spiders: $-0.51 < r_S < 0.47$, $10 < N < 22$, NS; for one spider: $r_S = -0.48$, $N = 23$, $P = 0.02$; for one spider: $r_S = 0.58$, $N = 23$, $P = 0.003$; for one spider: $r_S = 0.47$, $N = 18$, $P = 0.048$). There was no significant difference in the distribution of lengths between the six cocoons (median test: $\chi_5^2 = 9.7$, $P = 0.09$). Therefore, we pooled the data recorded for the 30 spiders ($N = 468$ length intervals); the resulting log-survival was linear (Fig. 4) and can be fitted by the following expression:

$$Y = 0.27 - 0.44X \ (r^2 = 0.99).$$

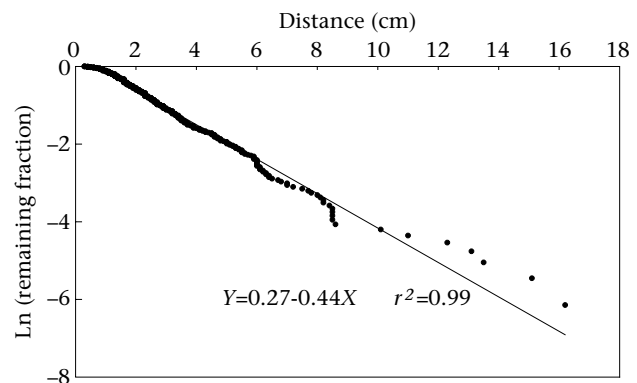**Figure 3.** Experimental set-up used to study collective behaviours.

Figure 4. Natural logarithm of the remaining fraction of all recorded intervals ($N=468$) as a function of the distance between two successive attachment points of silk thread.

This result indicated that the survival curve resulting from the distribution of interval lengths was a typical exponential decay. The memory-less property of the exponential distribution indicates that attachment events were independent and that the dragline attachment was not performed periodically on a fixed-based interval (Haccou & Meelis 1992). The probability of a spider attaching a dragline, P_a, was 0.44 per cm and the mean distance between two successive attachment points was $1/P_a = 2.27$ cm.

Probability of following a shortcut (P_f)

The proportions of spiders that followed a silk shortcut (0.45, 0.50, 0.60, 0.60) were not significantly different between the four replications (chi-square test: $\chi^2_3 = 1.35$, $P = 0.72$). Therefore the results of the four replications were pooled and the resulting probability P_f of following a shortcut was 0.54.

Collective Level

The first spider chose either side randomly (14 to the right versus 16 to the left), and of the 750 observations (30 replications × 25 spiders), 382 spiders chose the left and 368 the right side. These results confirmed the symmetry of the set-up and indicate that no biases (e.g. phototaxis or spatial or visual cues) influenced the choice of spiders.

Figure 5 shows the number of trials as a function of the number of spiders on the right side (arbitrarily chosen) after 25 spiders had climbed. The U-shaped distribution shows that the spiders tended to choose the same branch on a given trial. In about 57% of the trials, 100% of the spiders were on the same side. Other data confirm this tendency to choose the same branch (Table 1). For

instance, in 77% of the trials, the choice of the first spider and the winning branch after 25 spiders had climbed are the same. Figure 6 shows the mean fraction of spiders on the winning side (i.e. either the left or right branch that gathered more than 50% of spiders) as a function of spiders that had already climbed. The fraction of spiders on the winning side increased with the number of individuals that had already climbed.

MODELLING THE PROCESS OF COLLECTIVE DISPLACEMENT

Model Description

We used a spatially explicit agent-based numerical model, in the form of Monte Carlo simulations, to test the hypothesis that the discrete pattern of silk attachment and the resulting creation of additional escape routes were the key mechanisms leading to an asymmetrical distribution of spiderlings between the branches. In the model, as in the experiments, individuals following each other in a sequential order were set in motion at the basis of the vertical thread, and only one spider had access to the set-up at a time. The spatial scale of the experimental set-up was preserved, with one ascending and two lateral branches.

Observations and quantification of the individual behaviours suggested the following sequence of events. (1) When it climbs along the vertical thread, each spider attaches its silk on the substrate with a probability derived from experiments ($P_a = 0.44$ per cm). (2) Reaching the terminal bifurcation point of the set-up, the first spider randomly chooses the left or right branch. Because of the discrete attachment pattern of silk, the spider builds
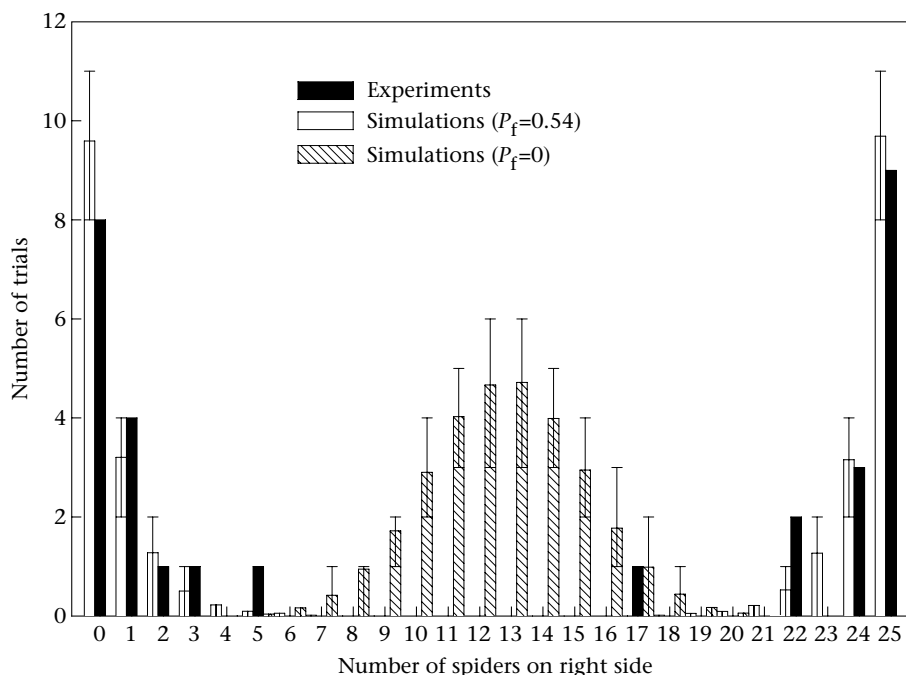

Figure 5. Number of experimental trials ($N = 30$) and mean ± quartile number of simulation runs (probability of following $P_f = 0$, $N = 1000$ and $P_f = 0.54$, $N = 1000$) as a function of the number of spiders that chose the right side after 25 spiders had climbed the thread.

Table 1. Collective results obtained in experiments and simulations

Percentage of trials with	Experiments	Simulations	χ^2_1
Identical choices for first and second climbing spider	80 (0.61–0.92)	78	NS
Same branch chosen by first spider and winning branch after 25 spiders have climbed	77 (0.58–0.9)	86	NS
80% of spiders on same side after five spiders have climbed	87 (0.7–0.96)	88	NS
80% of spiders on same side after 10 spiders have climbed	90 (0.62–0.98)	94	NS
80% of spiders on same side after 15 spiders have climbed	97 (0.73–0.99)	97	NS
80% of spiders on same side after 25 spiders have climbed	97 (0.73–0.99)	99	NS
100% of spiders on same side after 25 spiders have climbed	57 (0.37–0.74)	64	NS

Experimental percentages are given with lower and upper 95% confidence limits in parentheses. $N = 30$ experiments, 30 000 simulations. Probability of silk following = 0.54.

a shortcut that begins from the last attachment point of the dragline, just before it chooses one side. In the model, the position of the shortcut on the vertical axis of the set-up was recorded. (3) Then a second spider climbs along the vertical thread. When it encounters the silk shortcut laid by the first spider, it has a probability $P_f = 0.54$ of following this thread. If it decides to follow the shortcut, the spider creates a new shortcut on the same side. Otherwise, it randomly selects one branch at the bifurcation point and adds a new shortcut towards this branch. In both cases, the physical position of new shortcuts on the vertical thread is given by the last dragline attachment point that the spider made before it selected one branch. This process was repeated for each spider in the group. When a spider encounters at a given location two shortcuts going in opposite directions, it has an equal probability of choosing either side.

We also used the model to study the influence of various P_f values (between 0 and 1) on the pattern of aggregation and its dynamics. When $P_f = 0$, there is no silk shortcut following behaviour, and the choice made by an individual is independent of that made by previous spiders. When $P_f = 1$, a spider will in any case follow the first shortcut encountered.

Simulation Results and Comparison to Experiments

The model simulated the climbing behaviour and dragline attachment pattern of a group of spiders in a set-up of similar size and shape to the one that we used in the experiments. We performed 1000 sets of 30 simulation runs for groups of 25 spiders. There were no significant differences in the repartition of spiders between experiments and simulations performed with $P_f = 0.54$ (Kolmogorov–Smirnov two-sample test: $D = 0.05$, $N_1 = N_2 = 26$, $P = 1$; Fig. 5). Spiders were heterogeneously distributed on the branches, i.e. one side gathered almost all individuals (Fig. 5, Table 1). Figure 6 compares the simulated fraction
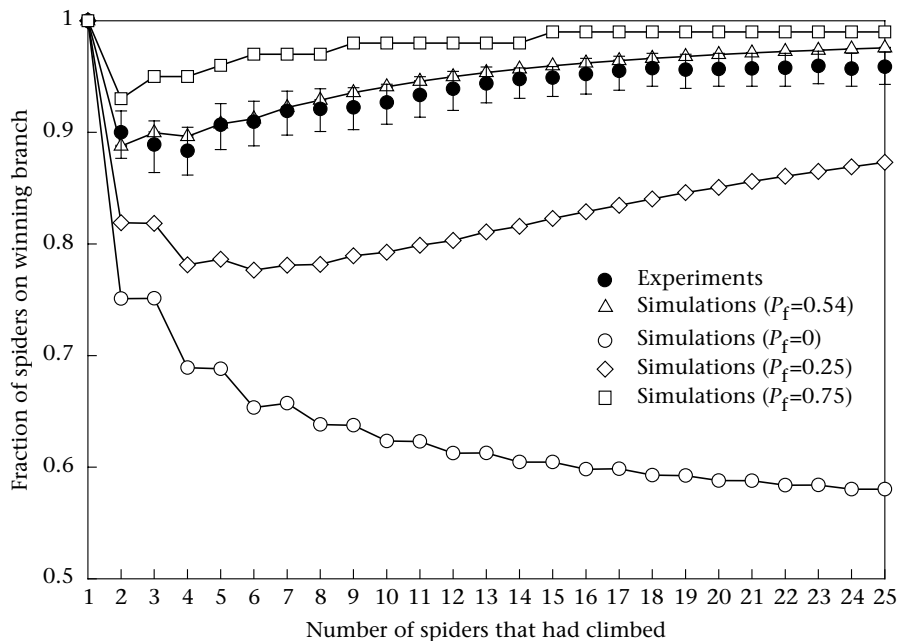

Figure 6. Fraction ± 95% confidence interval of spiders on the winning branch as a function of the number of spiders that had already climbed in experimental trials and simulation runs performed with the probability of following $P_f = 0$, $P_f = 0.25$, $P_f = 0.54$ and $P_f = 0.75$ (the confidence intervals for simulations, on the order of 10^{-4}, 10^{-5} are not shown).

of spiders on the winning side to the experimental results. The superimposition of the experimental and theoretical curves, corresponding to the simulations performed with a value of silk-following probability of 0.54 (the value derived from the experiments), indicates good agreement between the model outcome and experimental data. The more spiders that climbed, the greater the proportion of individuals that reached the winning side.

We also investigated the influence of the values of the probability of following a silk shortcut on the resulting distribution of spiders on the branches. When $P_f = 0$, the fraction of spiders decreased (Fig. 6) and the spiders divided between the left and right sides according to a binomial rule (Fig. 5). For a given number of spiders that climbed, the asymmetry in the distribution of individuals between branches (i.e. reduction in their dispersion) increased with P_f (Fig. 6). From a dynamic point of view, a larger number of spiders that climbed is required to obtain a large asymmetry with a small value of P_f.

DISCUSSION

Spiderlings of *L. cornutus* were able to maintain group cohesion when they migrated to a new site of aggregation. Our experiments, confirmed by a theoretical study, show that the collective choice of groups of juveniles of this solitary spider resulted mainly from their pattern of dragline attachment and the resulting creation of additional escape routes without active silk-following behaviour. When a spiderling encountered a silk shortcut, it chose with a nearly equal probability either the cotton thread or the shortcut to pursue its route. At the end of their collective displacements almost all spiderlings reached the same side of the set-up. These results show that the spiderlings, like other social arthropods and true social spiders, can use trailing cues to ensure cohesion during collective displacement. However, once spiderlings adopt a solitary lifestyle, the dispersion of individuals may involve several other processes, such as ballooning. Aggregation can then be achieved through the multiplication of potential escape routes. This conclusion indicates that a group of spiderlings has its own system of amplification to maintain cohesion during a collective displacement. With this kind of process, even a weak value of the probability of choosing a shortcut and therefore of following a conspecific's dragline leads to an amplification (Fig. 6). Further work should assess the influence of the orientations of the thread and the environmental conditions on the probability of following the silk thread.

According to D'Andrea's (1987) classification, *A. eximius* can be considered as a nonterritorial permanent-social species, but *L. cornutus* is a territorial periodic-social species. These two species are on the opposite ends of the scale of sociality in spiders. Our results indicate that, in the same experimental Y set-up, collective movements in spiderlings of *L. cornutus* have striking similarities with the collective behaviours observed in the social spider *A. eximius* (Saffre et al. 1999): individuals were asymmetrically distributed between the two branches of the Y set-up. Saffre et al. (1999) suggested that the aggregation of *A. eximius* in this set-up relies on mechanisms similar to the discrete pattern of silk attachment and the resulting formation of shortcuts of *L. cornutus*.

In solitary species, such a collective displacement might occur after an incidental dissociation of a group of spiderlings or to allow the spiderlings to cluster in a more favourable environment. In natural conditions, 300 juveniles of another solitary species, *Cyclosa conica* (Araneidae) have been observed to perform such coordinated group migration: leaving their resting site, they aggregated in a dense cluster a few centimetres above this site by following silk threads (personal observation). In *A. eximius*, similar aggregation was reported in adult females that found conspecifics by dragline following (Vollrath 1982). It has been suggested that the affinity for silk laid by conspecifics could lead to web aggregation in solitary spiders (Leborgne & Pasquet 1987; Kremer et al. 1990; Hodge & Storfer-Isser 1997; Schuck-Paim & Alonso 2001). However, in our experimental conditions, aggregation resulted mainly from the discrete pattern of dragline attachment of individuals behaving in a random way and did not appear to be based on an active silk-following behaviour.

Understanding the underlying mechanisms that govern aggregation, which is a prerequisite for the emergence of higher forms of cooperation, opens new perspectives such as inducing more complex forms of cooperation and social organization in a solitary species (Ruttan 1990; Gundermann et al. 1993).

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