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Effect of Retentive Markers on the Dynamics of Settlement: The Case of Arthropod Silk

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Abstract

During a settlement decision, the presence of conspecifics is crucial to species subject to Allee effects, for which the number of founders affects the subsequent growth of the colony. Marking the area (physically or chemically) conveys information about the number of conspecifics present in a new patch. Here, we study how the individual affinity for the marker affects the dynamics of a foundation process. A generic population model is presented, in which marking and affinity for the marker are at stake. Our results show that population size thresholds can appear, below which settlement is not possible. This model is then used to study the dynamics of migration and aggregation in a set of interconnected populations. We show that affinity for the marker can induce asymmetries in the population distribution. *Anelosimus eximius* is a social spider subject to Allee effects, for which silk

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potentially acts as a marker. We test our predictions with field experiments involving two populations of *A.eximius* in a Y-shaped setup. The agreement between our experimental and theoretical results strongly supports the validity of the model. This allows us to use the model to estimate a realistic set of parameters of biological significance to this social spider.

Keywords:

Population dynamics, Colonisation, Agregation, *Anelosimus eximius*, social spiders

1 Introduction

2 A key stage of population dynamics is the settlement of individuals in
 3 new environments. Settlement results from complex decision-making pro-
 4 cesses regarding habitat selection. Consequently, its dynamics can greatly
 5 vary depending on the different habitat selection strategies (Mihoub et al.,
 6 2009). Among the biotic factors which play a role in habitat selection are the
 7 conspecifics. In many species, specially in group-living species, the presence
 8 of conspecifics increases the probability of reaching a new patch (conspecific
 9 attraction) or the probability of staying in a new patch (conspecific reten-
 10 tion). Either way, the probability to settle in a patch increases with the
 11 number of conspecifics. By definition, this type of selection strategy entails
 12 positive feedback loops (DeAngelis, 1986; Ray and Gilpin, 1991), which in-
 13 duces non-linearities in the dynamics of settlement (Fletcher, 2006; Smith
 14 and Peacock, 1990). The complex and often non-intuitive behaviour of this
 15 kind of system is worthy of interest.

16 Conspecific attraction (or retention) is found in various taxonomic groups

17 throughout the animal kingdom (Mueller et al., 1997; Stamps, 1988). The
 18 most frequently mentioned benefits of settling near conspecifics include re-
 19 duced search and settlement costs (Fletcher, 2006), the use of conspecifics
 20 as indicators of habitat quality (Doligez et al., 2003), and the fitness in-
 21 crease associated with Allee effects (Courchamp et al., 2008). While these
 22 ultimate causes have received great attention, relatively little research has
 23 focused on the mechanisms used to evaluate the presence and/or the number
 24 of conspecifics.

25 The mechanisms used to assess the number of conspecifics in a given
 26 patch depend to a great extent on the type of information available to the
 27 animal. When the sensory system does not allow access to global information
 28 (e.g. Long distance view of big mammals, auditory information for birds
 29 (see references in Forbes and Kaiser, 1994)), the evaluation of the number of
 30 conspecifics has to be based on local information. This is usually the case for
 31 arthropods. Some use indirect cues that are representative of the number of
 32 conspecifics. These cues are the result of environment modification or marker
 33 production (chemical or physical) by the conspecifics in a density-dependent
 34 manner (Depickère et al., 2004; Rivault et al., 1998).

35 To our knowledge, population models of conspecific attraction (Mihoub et
 36 al., 2009; Ray and Gilpin, 1991, Smith and Peacock, 1990) or retention (Jean-
 37 son and Deneubourg, 2007) have always assumed direct attraction between
 38 conspecifics. Therefore, the consequences of conspecific attraction when it is
 39 mediated by a marker remain unexplored. Yet, one can expect the resulting
 40 population dynamics to be different, since the marker accumulates in the
 41 patch, which potentially causes delays and reinforces feedback loops. Here,

we study the effects of this habitat selection strategy on the dynamics of settlement.

We focus on the case of *Anelosimus eximius*, a social spider found in South America. The spiders of this species live in large colonies ranging from a few hundred to a few thousand individuals (Avilés and Trufiño, 1998). The benefits they obtain from living in groups are the result of cooperation in activities such as prey catching (Pasquet and Krafft, 1992), brood care (Avilés, 1986) and web construction (Christenson, 1984). Not surprisingly, they are submitted to multiple Allee effects: their survival and fecundity rates increase with colony size (Avilés and Trufiño, 1998) up to a certain extent. Although colonies are rather stable and may persist for several years in one site (Vollrath 1986), there are conditions that trigger dispersal of some individuals that then create new colonies. New foundations only take place at relatively large sizes of the mother colony (Avilés and Trufiño 1998), possibly when drought provokes a food shortage (Venticinque et al. 1993). Other causes of dispersal may be linked to sudden changes in the environment (a fallen tree, for instance) that might degrade the local conditions or the web. Departure may also be totally accidental (passive transport by animals or humans). In any case, when new colonies need to be founded, it is crucial for individuals to settle in a group, and there is experimental evidence of a group size threshold below which they are not likely to settle (Leborgne et al., 1994).

One way to ensure that there are enough settlers to guarantee the fitness of the colony is to disperse in a group. *Anelosimus eximius* exhibits various patterns of dispersal: swarming or budding (Vollrath, 1982) are the

most common (Leborgne et al., 1994). Spiders may also leave the colony individually, however it has been shown that dragline attachment acts as a recruitment process (Jeanson et al., 2004a; Saffre et al., 1999), which makes it likely that isolated individuals end up aggregated with other spiders. Indeed, a group of spiders scattered in a bush tends to aggregate (Leborgne et al., 1994). Although these strategies increase the potential number of founders on arrival, they offer no information about the actual number of founders. Therefore, one could expect that spiders use additional mechanisms to assess group size in order to make an informed decision regarding settlement.

Our hypothesis is that silk, or some chemical component in it, acts as information about the number of settlers in a patch (Giraldeau, 1997; Wagner and Danchin, 2003). The probability of settling in a given site would therefore increase with the amount of silk on that site. Bernard and Krafft (2002) used a T-maze to show that in *Anelosimus eximius*, spiders are attracted to conspecific silk. Furthermore, they showed that silk has a strong retention effect: spiders spent significantly more time on the branch containing silk. Affinity for silk has also been put forward in many other spider species (Krafft, 1970; Leborgne and Pasquet, 1987; Schuck-Paim and Jimenez Alonso, 2001).

We present a general model for the growth of a set of interconnected populations, where every individual produces and is retained by a marker (in this case, silk). First, we explore the results of the model for a single population. We show that affinity for silk can give rise to thresholds in the number of founders, below which the population does not settle. Then, we study the general case of n populations, and demonstrate that a heterogeneous distri-

92 bution of the population on equal sites can be stable due to the retentive
 93 effect of silk. Our model is validated by comparing theoretical predictions on
 94 the particular case of two interconnected populations with field experiments
 95 carried out in French Guiana on *Anelosimus eximius*. Finally, the importance
 96 of retentive markers is put forward with a comparison between our results
 97 and those of models in which retention is caused by the individuals directly.

98 **General population model**

99 The general theoretical setup consists of a system of n interconnected
 100 populations. We define two variables: N_i is the number of individuals on the
 101 i^{th} patch and S_i the quantity of silk accumulated on that patch. The model
 102 is based on the following assumptions: (1) The individual tendency to settle
 103 in a patch i increases with the amount of silk S_i accumulated in that patch.
 104 To model this, we define the probability to leave the patch as a decreasing
 105 function of the quantity of silk. The function $f(S_i) = \beta / (1 + (S_i/\alpha)^\epsilon)$ can
 106 take several shapes, among which a threshold-type S-shape. Other typically
 107 used functions (Sumpter and Pratt, 2009) such as the sigmoid function give
 108 the same results. The maximal tendency to leave β is halved for the quantity
 109 of silk α , than can be seen as a “silk threshold”. The shape of the function
 110 is determined by ϵ . Biologically, ϵ can be understood as the sensitivity of the
 111 response (tendency to leave) to changes in the amount of silk, for quantities
 112 of silk approaching α (see Fig.1 for a graphical representation of $f(S_i)$).
 113 For very high values of ϵ , the sensitivity of the response is so high that the
 114 departure rate switches sharply from the maximum to zero when the quantity
 115 of silk equals α ; (2) When individuals leave a patch, they have a probability

116 P_e of exiting the system, or a probability $1 - P_e$ of spreading into the
 117 other patches. The probabilities of moving into any of the other patches are
 118 equal $1/(n - 1)$; (3) The time-scale we focus on (a couple of days) is short
 119 enough to discount births and deaths, as it takes approximately a month after
 120 oviposition for spiderlings to emerge (Avilés, 1986); (4) Silk is produced by
 121 every individual at a constant rate γ ; (5) Silk degrades over time at a rate of
 122 θS . The system of Eq. 1 describes the population dynamics of the i th patch:

$$\begin{aligned} dN_i/dt &= -N_i f(S_i) + (1 - P_e)/(n - 1) \sum_{j \neq i} N_j f(S_j) \\ dS_i/dt &= \gamma N_i - \theta S_i \end{aligned} \quad (1)$$

123

124

125 Dynamics of one population

126 Before exploring the dynamics of the system, let us first consider the case
 127 of one population ($n = 1$). We assume that individuals have arrived using
 128 collective migration, thus there is a group of potential founders N_0 in a new
 129 patch. Individuals can settle or leave. When individuals leave, they exit the
 130 system and do not return. This particular case allows us to understand the
 131 dynamics of foundation when a group of founders arrives in a new patch, or
 132 more precisely, the effect of departure on this foundation process.

133 At this stage, it is convenient to scale the system of equations, that is to
 134 express it in non-dimensional terms (Eq. 2). Although this change of variables
 135 and parameters does not have a direct biological meaning, it reveals the
 136 links between parameters, and synthesises the information concerning their

137 respective effects. Mathematically, it simplifies the analytical resolutions by
138 reducing the number of parameters substantially.

139 We redefine the variables as follows. The number of individuals N is
140 replaced by the ratio between the number of individuals and the initial pop-
141 ulation size $X = N/N_0$. The quantity of silk S is substituted by a new
142 variable $Z = \beta S/\gamma N_0$ that is directly proportional to the quantity of silk.
143 We also define two new parameters a and b , that are directly proportional to
144 α (threshold quantity of silk) and θ (degradation coefficient of silk) respec-
145 tively. Finally, we define a new time ($\tau = \beta t$). The results obtained with
146 these scaled variables and parameters can easily be converted back into the
147 biologically meaningful variables (See Table 1 for a summary of all variables
148 and parameters).

$$\begin{aligned} dX/d\tau &= -X/(1 + (Z/a)^\epsilon) \\ dZ/d\tau &= X - bZ \end{aligned} \quad (2)$$

149

150

151 This system has only one stable steady state ($X = 0, Z = 0$). However,
152 the behaviour of the system is qualitatively different for $\epsilon \leq 1$ and $\epsilon > 1$.
153 For analytical clarity, we will develop only the case of $\epsilon = 1$ and $\epsilon = 2$ as
154 examples of the two subsets. Numerical resolutions show consistency in the
155 results for other values of ϵ in both subsets.

156 For $\epsilon = 1$, the behaviour of the system is intuitive: regardless of the
157 parameter set, population decreases until it becomes extinct. What varies
158 with the parameters is the amount of time it takes. The slowest case possible
159 is when $b = 0$ (silk degradation rate θ is negligible). For non-zero values of

160 b , the decrease of the population occurs more quickly (Fig. 2A,B).

161 For $\epsilon = 2$ (or in fact for values of $\epsilon > 1$), the non-linearity of the sys-
 162 tem makes its behaviour less intuitive. The system presents a particular
 163 behaviour if $b = 0$. For some values of a , there is an asymptotic steady state
 164 $X_A > 0$ (Fig. 2C). By “asymptotic steady state of a variable”, we mean the
 165 value towards which the variable tends asymptotically, as time tends to in-
 166 finity. It is not a steady state *sensu stricto*, because the other variable (Z)
 167 continues to increase. Nevertheless it is the value of X towards which the
 168 system converges. In biological terms, it means that eventually, the quantity
 169 of silk is such that the departure rate tends to zero and the population size
 170 tends asymptotically to a given fraction X_A of the initial population (Eq. 3).
 171 For details on the calculations, see Appendix A.

$$X_A = X_0 - a\pi/2 \quad (3)$$

$$X_A > 0 \text{ if } 0 < a < 2/\pi \text{ or } N_0 > \alpha\beta\pi/2\gamma$$

172 Our model can be used to determine the necessary conditions for a suc-
 173 cessful establishment. The parameter space in which the population stabilises
 174 at a fraction X_A of the initial population can be interpreted biologically. First
 175 of all, $\epsilon > 1$ means that the response of the spiders to the presence of silk has
 176 to be S-shaped. Secondly, $N_0 > \alpha\beta\pi/2\gamma$ means that the initial population
 177 has to exceed a critical size, for the colony to be viable. Note that the larger
 178 the silk threshold (α) and the maximal departure rate β , the larger the pop-
 179 ulation has to be in order to settle successfully. Logically, if silk production
 180 (γ) is very intense, the population threshold is lowered.

181 This asymptotic steady state is a particularity of the case where degra-

182 dation is negligible, however for $b \neq 0$, X is also attracted to asymptotical
 183 steady state X_A , although not indefinitely (Fig. 2C). Nevertheless, if the
 184 population is maintained near the asymptotic steady state for long enough,
 185 reproduction can compensate for the departure rate of individuals until there
 186 is enough silk for the establishment to be successful.

187 **Flow between n interconnected populations**

188 In this section, we focus on the flow between populations. Hence we will
 189 temporarily consider the probability of exiting the system (P_e) to be nil. The
 190 combined effects of flow and departure (P_e) are discussed in the next section.
 191 The general form of the model for n interconnected populations is given by
 192 Eq. 4 (in its scaled form).

$$\begin{aligned} dX_i/d\tau &= -X_i/(1 + (Z_i/a)^\epsilon) + 1/(n-1) \sum_{j \neq i} X_j/(1 + (Z_j/a)^\epsilon) \\ dZ_i/d\tau &= X_i - bZ_i \end{aligned} \quad (4)$$

193
 194 As for the isolated population, the dynamics vary depending on ϵ . If $\epsilon \leq 1$
 195 there is only one stable steady state $X_1 = X_2 \dots = X_n$, which means that
 196 regardless of the initial conditions, the flow tends to equalise the size of the
 197 populations and they eventually reach the same size. If $\epsilon > 1$, however, the
 198 system may exhibit an asymmetric stable steady state with one population
 199 greater than all the others $X_1 > X_2 = X_3 \dots = X_n$. Equation 5 gives the
 200 sizes of the populations at the asymmetric steady state when $\epsilon = 2$.

$$\begin{aligned} X_1 &= (1 + \sqrt{1 - 4(n-1)(ab)^2})/2 \\ X_j &= (1 - X_1)/(n-1) \quad \text{for } j \neq 1 \end{aligned} \quad (5)$$

201 This asymmetric steady state is real and positive (and therefore biologi-
 202 cally meaningful) if $n < 1 + 1/(2ab)^2$. In these conditions, it is always stable.
 203 On the other hand, the symmetrical steady state is unstable when the asym-
 204 metrical steady state exists, except when $n > 1/ab$, in which case they are
 205 both stable (see Appendix B for the stability analysis). The initial condi-
 206 tions determine which of the two steady states is reached. See Fig. 3 for a
 207 stability diagram. A bifurcation diagram (Fig. 4) shows the solutions for the
 208 particular case of two populations ($n = 2$).

209 To summarise, the lower the product ab , the greater the asymmetry be-
 210 tween the two populations. In biological terms, ($ab = \alpha\theta/\gamma N_0$), this means
 211 that a high silk threshold (α) and a high degradation rate (θ) result in a high
 212 asymmetry, even for a very fragmented ($n \gg 1$) landscape (Fig 3.). On the
 213 contrary, high silk production rates (γ) and high initial population sizes (N_0)
 214 have an inhibiting effect on the asymmetry.

215
 216 The evolutionary advantage of this heterogeneous distribution is easy to
 217 understand for species subject to Allee effects. By definition, the individual
 218 fitness F of such species is an increasing function of the number of individuals
 219 N , at least up to some extent. Clearly, at very high population sizes the
 220 cost of competition outweighs the benefits of group living. Nevertheless, the
 221 population sizes we consider here (founding populations) are far below that
 222 point. Let N_1 and N_2 be two connected populations in a closed system. The
 223 inclusive fitness IF of an individual can be calculated as the sum of his direct
 224 fitness (his own offspring) and his indirect fitness (his conspecifics' offspring
 225 multiplied by their relatedness coefficient r). Eq. 6 gives the inclusive fitness

of an individual i of the first population IF_{i1} and the inclusive fitness for that same individual if he were to move to the second population IF_{i2} .

$$\begin{aligned} IF_{i1} &= F(N_1)(1 + r(N_1 - 1)) + rF(N_2)N_2 \\ IF_{i2} &= rF(N_1)(N_1 - 1) + F(N_2)(1 + rN_2) \end{aligned} \quad (6)$$

The fitness difference ΔIF for the movement from the first population to the second is expressed as $\Delta IF = IF_{i2} - IF_{i1} = F(N_2) - F(N_1)$. This fitness difference is a gain when $N_2 > N_1$ and a loss when $N_2 < N_1$. This means that it is always beneficial in terms of fitness to move to the largest population. Therefore, any asymmetry between the two populations should be amplified to maximize the inclusive fitness of all individuals.

Experimental validation of the model

In order to test the validity of our model on the social spider *Anelosimus eximius*, we conducted a field experiment on *Anelosimus eximius*. Previous experiments on a T-maze (Bernard and Krafft, 2002) show that the silk of conspecifics has a retention effect on these spiders. Here, we test whether this retention effect results in the dynamics we predict. We artificially reproduce the particular case of two interconnected founding populations in the field and compare it with our theoretical predictions. This setup offers the possibility to analyse the coupled effects of flow between populations and of departure from the system.

Experimental methods

Anelosimus eximius is a highly cooperative theridiid spider found throughout Central and South American forests, occupying edge habitat along open

byways such as roads or riverbanks. The experiments were carried out in this natural habitat. Spiders were collected from various nests along a transect of about 250 km on the coast of French Guiana following a previously used procedure (Mailleux et al., 2008; Saffre et al., 1999). Thirteen fork shaped trees were used as the setups for thirteen experiments. Each tree was shaped so as to be as similar as possible on each side, by removing branches, then adjusting branch lengths and trimming the number of leaves on either side (Fig. 5A). The local surroundings (a radius of 2m) of each tree were cleared of vegetation to minimize immediate emigration of the spiders after release. At $t=0$, we placed plastic cups (10 cm deep, 5 cm wide) containing 50 spiders on each of the two branches. After $t_1 = 24\text{hrs}$ and $t_2 = 48\text{hrs}$, the number of spiders on each branch was counted.

Individual Based Model

It is not convenient to compare experimental results with the solutions of ordinary differential equations (ODE), because the latter only give the mean field results or more precisely the most likely results. Therefore, we formulated an individual based model (IBM), which can be thought of as a stochastic version of our deterministic ODE model. The algorithm for the IBM simulations is described in Fig. 5B. In the IBM, we included the probability P_a of spinning an amount γ/P_a of silk. This allowed us to incorporate the fact that spiders do not spin all the time. It is not really a difference with the ODE model, in the sense that on average, each spider spins γ silk per time unit. Therefore, the mean of the results of the IBM simulations match the ODE numerical resolutions (see an example in Fig. 6).

271 *Results*

272 After 24 hours, the distribution of the spiders between the two cups was
 273 already noticeably asymmetric (Fig. 7). We performed binomial tests to
 274 show that the distribution of the spiders between the two sides was different
 275 from the expected distribution if they had chosen at random, independently
 276 from each other, with an equal probability of going to either side (binomial
 277 distribution). All experiments except one clearly differed from a binomial
 278 distribution (p-values always lower than 0.0005). The selection of one of the
 279 branches did not result from a bias in the setup, because the number of times
 280 the left and the right branch were selected was not statistically different from
 281 a binomial choice of probability 0.5 (P-value=0.1334). From then onwards,
 282 the populations on each side remained stable: a linear regression ($R^2 =$
 283 $0,9249$) between the populations at 24 hours and 48 hours ($P_{48} = s \cdot P_{24} + y_0$)
 284 shows that the slope is not different from 1 ($s = 1.046$ (0.9201, 1.171)) and
 285 that the y -intercept is not different from zero ($y_0 = -0.3966$ ($-5.918, 5.125$)).

286 We ran the IBM simulations, conducting a systematic parameter search
 287 (see Appendix C) and found that the parameter set in table 1 provides the
 288 best correspondence between the experiments and the simulations (Fig. 7).
 289 Although the model does not reproduce the great variability of the experi-
 290 mental results, we found that, on average, the experimental and theoretical
 291 results were very close (Table 2).

292 **Markers versus conspecifics**

293 It is interesting at this point to assess the extent to which the patterns
 294 we observe in our model are caused by the intervention of a marker. In

other words, could direct evaluation of the number of individuals produce the same results? In an alternative model where markers do not intervene, the probability to leave decreases with the number of individuals instead of the quantity of silk, according to the same function $f(X) = 1/(1 + (X_i/a')^\epsilon)$, where $a' = \alpha/N_0$. This function is used in other models of conspecific retention (Amé et al., 2004; Jeanson and Deneubourg, 2007).

Let us first look at the case of n interconnected populations in a closed system (there is no departure from the system). The population on the i^{th} patch is described by Eq. 7.

$$dX_i/d\tau = -X_i f(X_i) + 1/(n-1) \sum_{j \neq i} X_j f(X_j) \quad (7)$$

All that is said about the silk model in n interconnected sites is true of this model too, at least qualitatively. For $\epsilon > 1$, there are asymmetric steady states with one population greater than all the others. The values and the stability of the steady states have the same form as the ones of our marker model (see Fig.3 and Fig.4), except for a parameter (a' instead of ab).

However, this similarity between the two models ceases to be true in an open system that allows exits. Indeed, the transfer of information through markers can provoke qualitative changes in the behaviour of the system. If we look at the effect of departures only (the case of one population), the system is described by Eq. 8.

$$dX/d\tau = -X/(1 + (X/a')^\epsilon) \quad (8)$$

Like the marker model, the alternative model has only one stable steady state ($X_s = 0$). However, in this case there is no asymptotic steady state,

regardless of the exponent ϵ . We can see this by looking at the evolution of the population X as a function of time. Integration of Eq. 8 gives:

$$\ln X/X_0 + (X^{\epsilon-1} - X_0^{\epsilon-1})/\epsilon a' = -\tau$$

It appears clearly that when time τ tends to infinity, X tends to zero. Therefore we can conclude that in the alternative model there are no asymptotic steady states. This is an important difference, because it means that the population goes extinct unless the retention effect is secured by a marker that accumulates.

Furthermore, we ran individual-based simulations with the alternative model, searching a wide range of parameters (following the method described in Appendix C), and we could not reproduce our experimental results (see Fig.8). The main feature that we were unable to obtain with the simulations is the stability of the results between 24 and 48 hours. It is impossible for the simulated populations to remain at a constant size for that long, because the retention effect of conspecifics is not sufficiently stable. As conspecifics leave, the probability of leaving increases, and this positive feedback leads the population to extinction. A marker that does not degrade on the other hand creates a much more stable retention effect.

Discussion

In this study, we examine how retention caused by an indirect indicator of the number of conspecifics – such as the quantity of a marker secreted by conspecifics – affects the dynamics of settlement. The theoretical part of this study provides a few insights into the growth and distribution patterns

331 of populations that exhibit this type of positive response to conspecifics.
 332 The experimental part allows us to validate and parameterise the model on
 333 *Anelosimus eximius*.

334 One key feature of the theoretical results is the importance of the shape of
 335 the response function. Indeed, thresholds and asymmetries appear only when
 336 the function describing the response to the marker is S-shaped. As Sumpter
 337 and Pratt (2009) point out, the non-linearity of individual responses, in par-
 338 ticular of sigmoidal responses is key to the speed and accuracy of collective
 339 decisions. They call this type of sigmoidal response “quorum response”. The
 340 difference between our response function and quorum responses, is that in
 341 this case the response is not a function of the number of conspecifics, but of a
 342 marker that is, in turn, a cumulative function of the number of conspecifics.
 343 This difference is crucial because it is precisely this property that is respon-
 344 sible for the appearance of asymptotic steady states, thresholds, and the
 345 stability of the populations in an open system. In a closed system, however,
 346 the spatial patterns observed (aggregation versus homogeneous distribution)
 347 are similar to those obtained with other quorum models (Amé et al., 2004;
 348 Jeanson and Deneubourg, 2007), as we show in the previous section.

349 The agreement between the experiments and the simulations suggests
 350 that social spiders respond to silk in a sigmoidal way. This agreement alone
 351 is not in itself sufficient to validate the model with certainty. To complete
 352 this validation, further experiments would be useful (eg. film the whole
 353 experiment to observe the fine kinetics of the collective choice, test different
 354 sizes for the total population, or measure individual time of residence in
 355 a patch as a function of silk...). Nonetheless, the fact that *A. eximius* are

356 attracted and retained by silk (Bernard and Krafft, 2002), the agreement
 357 between our model and the experiments, and the disagreement between the
 358 latter and the alternative model (direct evaluation of conspecifics), altogether
 359 make a strong case for our hypothesis.

360 According to our theoretical predictions on a single population, this sig-
 361 moidal response to silk implies that the number of founders has to exceed a
 362 critical value for settlement to be successful. This would explain the results
 363 of Leborgne et al. (1994), namely that big groups (> 100 spiders) settle
 364 successfully where they are released whereas isolated females mostly leave
 365 the area after a very short time. It has been shown that isolated females can
 366 and do settle alone (Avilés and Trufiño, 1998), although it is quite rare and
 367 their survival chances are relatively small (Vollrath, 1982).

368 There is a substantial amount of evidence that suggests that *A. ex-*
 369 *imus*, like most cooperative species, is submitted to Allee effects (Avilés and
 370 Trufiño, 1998 and the references therein). Strong Allee effects can give rise to
 371 thresholds (called Allee thresholds) of colony size under which the population
 372 is not viable: if there are not enough individuals in the population, it dies
 373 out (Courchamp et al., 2008; Stephens and Sutherland, 1999). The threshold
 374 in population size that results from our model is somewhat different from an
 375 Allee threshold. In populations below the threshold of our model, the indi-
 376 viduals do not die, they just leave. We suspect that both types of threshold
 377 exist. The thresholds provoked by silk retention would guarantee that the
 378 settling populations are large enough to overcome Allee effects. Silk attrac-
 379 tion/retention could therefore have been selected, amongst other reasons,
 380 because it ensures that colonies do not settle under a non-viable size.

381 We used a binary choice setup to show that spiders tend to adopt an
 382 asymmetrical distribution. An almost identical Y-choice setup had been used
 383 to show that silk draglines can act as a recruitment factor and lead to group
 384 migration (Jeanson et al., 2004a; Saffre et al., 1999). In these experiments,
 385 the initial population was placed in the middle of the setup and the spiders
 386 were given the choice between the two branches. Eventually they made a
 387 collective choice for one of these branches. In our experiments, we start
 388 with two populations and observe that the individuals tend to aggregate
 389 into one population. The mechanisms at stake are somewhat different but
 390 the two phenomena are complementary: while the former experiments show
 391 that silk maintains the cohesion of the group, in the latter silk triggers the
 392 aggregation and provokes the cohesion of a fragmented group. These two
 393 strategies (group migration and settling where the amount of settlers exceeds
 394 a threshold) serve the same functional purpose of insuring subsequent growth
 395 of the colony. This redundancy confers a high degree of robustness to the
 396 system (Hammerstein, 2006): if the group migration fails, silk attraction
 397 offers the possibility for the cohesion to be restored.

398 Although on average our simulations agree with the experiments, they are
 399 slightly less scattered than the experimental results. However, this should
 400 not discredit the model: the experimental variability could be due to other
 401 external parameters that we did not measure or control (micro-climate, par-
 402 ticularities of each experimental tree). Nevertheless, we should point out that
 403 for the sake of generality, we had to sacrifice some precision in the model. For
 404 example, we assumed throughout our study that all the sites were of equal
 405 quality. However, in a natural context where the sites may differ in lighting,

406 availability of prey, etc... it is likely that the quality of the site influences the
 407 decision to leave or to settle and thereby the quantity of silk. In modelling
 408 terms, the quality of the site would affect parameter β (probability to leave
 409 the site when there is no silk), and indirectly also affect the quantity of silk.
 410 It would be an interesting perspective to test the distribution and aggrega-
 411 tion patterns of the spiders on two sites of different quality experimentally
 412 (eg. by controlling the number of leaves on each site). Indeed, the interplay
 413 between conspecific attraction and environmental preference can produce a
 414 wide range of distribution patterns (Jeanson and Deneubourg, 2007). This
 415 question has been studied in other species (Franks et al., 2003; Pratt et al.,
 416 2002; Halloy et al., 2007; Jeanson et al., 2004b). Also, we did not take any
 417 saturation effect into account, however it would be reasonable to expect set-
 418 tlers to avoid overcrowded areas (Avilés and Trufiño, 1998). Bernard and
 419 Krafft (2002) show that hunger decreases attraction for silk. In overcrowded
 420 areas, food shortage could provoke a decrease in the retention effect of silk,
 421 and hungry individuals would have a higher probability of leaving.

422 Our model applies to *A. eximius* but also possibly to other social spi-
 423 ders, and even to gregarious territorial spiders, that show different degrees
 424 of affinity for silk (Krafft, 1970; Leborgne and Pasquet, 1987; Schuck-Paim
 425 and Jimenez Alonso, 2001). Furthermore, silk is spun by many arthropods
 426 (see Craig, 1997 for a review). Well-documented examples are caterpillars
 427 (Fitzgerald and Costa, 1999), weaver ants (*Oecophylla*) (Hölldobler and Wil-
 428 son, 1983), spider mites (*Tetranychidae*) (Saito, 1986) and of course, spiders
 429 (see Vollrath and Selden, 2007 for a review). In many of these species, silk
 430 plays a key role in communication, and in favouring cooperative interactions

431 (Bernard and Kraft, 2002). There is evidence of affinity for conspecific silk in
 432 other spinning arthropods, such as spider mites (Yano, 2008) and caterpillars
 433 (Colasurdo and Despland, 2005, Fitzgerald, 1995), therefore it is likely that
 434 the predictions we make apply to other species.

435 In this context, silk can be thought of as an extended phenotype used as
 436 a signal. Employing the extended phenotype – such as a retentive secretion –
 437 as a signal is common practice in a great number of gregarious species such as
 438 cockroaches (Amé et al., 2004) or ants (Depickère et al., 2004; Sempo et al.,
 439 2006). Silk carries information about the number of conspecifics in a patch,
 440 and it is likely that spiders use that information as a signal. This type of
 441 communication offers several advantages. For instance, extended phenotypes
 442 are by definition separated in space and in time from the signaller (Schaedelin
 443 and Taborsky, 2009). This enables the signaller to allocate energy and time
 444 to other purposes whilst the information is conveyed. Furthermore, once
 445 produced, the information can be used by any number of receivers for an
 446 extended period with no further expenditure of energy.

447 Colonisation is one of the crucial processes underlying metapopulation
 448 dynamics, and is of great importance in the study of invasions and range
 449 expansions. In this study we show that affinity for a marker can greatly
 450 affect the decision to leave or to settle in a patch. This may have strong
 451 implications on colonisation dynamics and in the spatial distribution of pop-
 452 ulations, specially for species exhibiting fission-fusion patterns (Couzin and
 453 Laidre, 2009). Our future work aims at quantifying the influence of retentive
 454 markers in an explicitly defined space, where the connexions between differ-
 455 ent sites are more complex than the ones defined in the present study. So far,

our results contribute further evidence to a concept that has only recently begun to receive sufficient attention, namely the importance of considering social interactions other than competition in population dynamics.

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Appendix A.Integration in the phase plane

In our model, there are two variables, and there is no simple analytical way of integrating both equations at once. What we propose instead is to look at the behaviour of the system in the phase plane. The phase plane is the plane defined by the variables X and Z . We can describe the trajectory of the system from an initial point (X_0, Z_0) , by integrating the following expression:

$$dX/dZ = -X/((X - bZ)(1 + (Z/a)^\epsilon))$$

This equation can be simplified because we focus on the case where $b = 0$:

$$dX/dZ = -1/(1 + (Z/a)^\epsilon)$$

The integral of this equation differs according to ϵ :

If $\epsilon = 1$,

$$X = X_0 - a \ln(1 + Z/a)$$

This curve describes how the population X will vary according to Z , starting in the initial point ($X = X_0, Z = 0$). As time advances, the system will move along that curve: the population will logarithmically decrease and the quantity of silk will increase. At the point when the curve crosses the Z -axis, the population goes extinct $X = 0$. This takes place when $Z = a(e^{1/a} - 1)$. From then onwards, the system will remain at that point because no individuals will arrive and no silk will be spun.

if $\epsilon = 2$, the integral is different:

$$X = X_0 - a \tan^{-1}(aZ)$$

This curve approaches a horizontal asymptote: as Z tends to infinity, X tends to $X_A = X_0 - a\pi/2$. This is an asymptotic steady state because it will never be reached, no matter how far we travel along that curve. Therefore as long as X_A is positive, the population never goes extinct.

Appendix B. Stability of the symmetric steady state in n interconnected populations

At the symmetric steady state $X_1 = X_2 \cdots = X_n = 1/n$ and $Z_1 = Z_2 \cdots = Z_n = 1/nb$. The jacobian matrix can be written as follows:

$$\begin{array}{c}
 \partial \dot{X}_1 \\
 \partial \dot{X}_2 \\
 \vdots \\
 \partial \dot{X}_n \\
 \partial \dot{Z}_1 \\
 \partial \dot{Z}_2 \\
 \vdots \\
 \partial \dot{Z}_n
 \end{array}
 \begin{pmatrix}
 \partial X_1 & \partial X_2 & \cdots & \partial X_n & \partial Z_1 & \partial Z_2 & \cdots & \partial Z_n \\
 -F & \frac{F}{n-1} & \cdots & \frac{F}{n-1} & -GF2 & \frac{GF^2}{n-1} & \cdots & \frac{GF^2}{n-1} \\
 \frac{F}{n-1} & -F & \ddots & \frac{F}{n-1} & \frac{GF^2}{n-1} & -GF2 & \ddots & \frac{GF^2}{n-1} \\
 \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \ddots & \vdots \\
 \frac{F}{n-1} & \frac{F}{n-1} & \cdots & -F & \frac{GF^2}{n-1} & \frac{GF^2}{n-1} & \cdots & -GF2 \\
 1 & 0 & \cdots & 0 & -b & 0 & \cdots & 0 \\
 0 & 1 & \ddots & 0 & 0 & -b & \ddots & 0 \\
 \vdots & \vdots & \ddots & \vdots & \vdots & \ddots & \ddots & \vdots \\
 0 & 0 & \cdots & 1 & 0 & 0 & \cdots & -b
 \end{pmatrix}$$

With

$$F = \frac{1}{1 + (1/abn)^2} \quad \text{and} \quad G = \frac{2}{a^2bn^2}$$

We calculate the eigen values associated with the jacobian matrix. The steady state is stable when all of its eigenvalues are negative or zero. There are only four different eigen values of which two (ω_3 and ω_4) are repeated $n/2 - 1$ times:

$$\begin{aligned}
 \omega_1 &= 0 \\
 \omega_2 &= -b \\
 \omega_3 &= \frac{b - nb - nF - \sqrt{(b - nb + nF)^2 + 4n(n-1)GF^2}}{2(n-1)} \\
 \omega_4 &= \frac{b - nb - nF + \sqrt{(b - nb + nF)^2 + 4n(n-1)GF^2}}{2(n-1)}
 \end{aligned}$$

All eigen values are always negative or equal to zero, except ω_4 . For the symmetric steady state to be stable ω_4 cannot be positive. Solving $\omega_4 \geq 0$

leads to

$$GF \leq b$$

If we replace G and F by their respective expressions, we have

$$\frac{2}{a^2bn^2(1 + (1/abn)^2)} \leq b$$

which can be reduced to

$$n \geq \frac{1}{ab}$$

Appendix C. Systematic parameter search

Out of the seven parameters of the IBM model, four could be estimated thanks to the following assumptions. We set a time step of one minute as it took approximately one minute for spiders to move from one branch to the other. The asymmetry of the experimental results suggested that $\epsilon > 1$, so we took $\epsilon = 2$. We assumed that silk did not degrade over the two days of the experiment ($\theta = 0$). We defined one unit of silk as the amount of silk spun by an active spider in one minute, so $\gamma = 1$. On average 30 spiders left the setup during the first 48 hours. This allowed us to estimate the probability to exit the setup $P_e = 0.01$.

The remaining 3 parameters (α, β, P_a) had to be fine tuned. Our knowledge of the system and a preliminary random search helped us define the range that we would test for each of the 3 parameters:

$$0 \leq \beta \leq 1$$

$$0 \leq P_a \leq 1$$

$$1000 \leq \alpha \leq 2000$$

It is now useful to visualise this parameter space as a three-dimensional grid, each dimension being a parameter and each intersection of the grid being a parameter set. We searched this three-dimensional parameter space by brute force, that is we tested every parameter set (every intersection) and searched for the best correspondence between the experiments and the simulations. Of course near the best correspondence zone, we narrowed the grid in order to get more precision. We chose two criteria to define a good correspondence: (1) a minimal difference between the experimental and simulated averages (total number of spiders and number of spiders in the selected side) for both 24 hours and 48 hours, (2) a maximum number of experiments falling in the 95% confidence interval of the simulations (see Fig. 6). Expectedly, the optimum for the two criteria coincided in the parameter set we propose.

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Table .1: Variables and parameters.

Var/Par.	Biological significance	dimension	range of values	fitted values
N	number of individuals	N	$0 - \infty$	-
S	quantity of silk	S	$0 - \infty$	-
N_0	initial population size	N	$0 - \infty$	100
α	silk threshold	S	$0 - \infty$	1846
β	maximal departure rate	t^{-1}	$0 - 1$	0.535
γ	silk production coefficient	$SN^{-1}t^{-1}$	$0 - \infty$	1
ϵ	sensitivity to threshold	-	$0 - \infty$	2
θ	silk degradation coefficient	t^{-1}	$0 - 1$	0
P_e	Probability to exit the system	-	$0 - 1$	0.01
P_a	Probability to be active	-	$0 - 1$	0.05
Scaled:				
X	N/N_0	-	$[0; 1]$	
Z	$\beta S/\gamma N_0$	-	$[0; \infty[$	
a	$\alpha\beta/\gamma N_0$	-	$[0; \infty[$	
b	θ/β	-	$[0; \infty[$	
τ	βt	-	$[0; \infty[$	

Table .2: Average results : number of spiders in the largest population (X_g) and total number of spiders left in the tree (X_{TOT}) after 24 hours and 48 hours. The parameter sets used to compute the simulations in A., B. and C. are the same as in figure 8.

	$t_1 = 24h$		$t_2 = 48h$	
	X_g	X_{TOT}	X_g	X_{TOT}
Experiments (13 replicates)	57.85	68.00	61.92	70.31
IBM with silk (2000 simulations)	56.64	71.42	59.62	71.19
IBM without silk (2000 simulations) A.	57.48	63.74	5.51	8.67
B.	81.57	84.35	62.23	66.02
C.	77.64	71.42	49.07	52.15

Figure .1: Shape of the function describing individual departure rates. When $\epsilon \leq 1$ (A), the shape is hyperbolic. When $\epsilon > 1$ (B), the shape is sigmoidal. The maximal departure rate β is halved when the quantity of silk reaches α .

Figure .2: Timeplots of the fraction of individuals left in the population (X) for different values of a , ϵ and b . For large values of a (B and D), the other parameters (ϵ, b) do not greatly affect the dynamics. On the contrary, for low values of a (A and C), the other parameters have an important influence. When $b = 0$ (dashed line), the decrease in population size is the slowest. The population can even stabilise at a given value, provided that $\epsilon > 1$ (C). Positive values of b (solid lines) accelerate the extinction process.

Figure .3: Stability diagram in the parameter space defined by n and the product ab , for the case of $\epsilon = 2$. In the white area, the only stable steady state is the asymmetrical one. In the light grey area, it is the symmetric steady state that is stable. In the dark grey area, both steady states are stable.

Figure .4: Three-dimensional bifurcation diagram: Values of the steady states X_s as a function of the two parameters a and b . The black surface represents the unstable steady states, whereas the grayscale surface represents the stable steady states.

Figure .5: Experimental setup (A) and IBM algorithm (B). The dimensions of the trees in cm (mean $\pm$ STD): $d = 54.5 \pm 6.0$, $D = 72.6 \pm 13.3$, $h = 41.1 \pm 7.2$, $H = 47.5 \pm 9.1$. Number of leaves in the right: 15.4 ± 6.0 and on the left $d = 14.8 \pm 6.0$.

Figure .6: Comparison between the stochastic (solid line) and the deterministic (dashed line) model with equal sets of parameters (IBM: $\alpha = 250$, $\beta = 0.5$, $\gamma = 1$, $\epsilon = 2$, $\theta = 0.14$, $P_e = 0$, $P_a = 1$; ODE: $a = 2.5$, $b = 0.28$, $\epsilon = 2$). The grey surface represents the standard deviation of the simulations. The steady states are identical, but they are reached faster in the IBM. This is easily explained by the discrete nature of the IBM. While increases in population size in the ODE model are infinitesimal, they are at least of one unit in the IBM, therefore the feedbacks are launched faster.

Figure .7: Experimental and simulation results. The experimental results significantly differ from the binomial distribution with one exception. Our simulation results coincide with the experiments, with the difference that they are slightly less scattered. The contour graph contains two areas: the light grey area contains the 95% most likely results from 2000 simulations. The dark grey area contains the remaining 5%. The parameter set used in the simulations is $\alpha = 1846$, $\beta = 0.535$, $\gamma = 1$, $\epsilon = 2$, $\theta = 0$, $P_e = 0.01$, $P_a = 0.05$.

Figure .8: Experimental and simulation (2000 simulations) results for the alternative model. The best fits for 24 hours are rather bad fits for 48 hours and vice versa. If we maximise the goodness of fit for both 24 hours and 48 hours simultaneously, the goodness of fit is poor for both. The parameter sets used are A. $\alpha = 18.2$, $\beta = 0.525$, $\epsilon = 2$, $P_e = 0.0058$; B. $\alpha = 14.8$, $\beta = 0.375$, $\epsilon = 2$, $P_e = 0.0058$; C. $\alpha = 11.4$, $\beta = 0.45$, $\epsilon = 2$, $P_e = 0.0105$.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

A. Best fit for 24 h

B. Best fit for 48 h

C. Best fit for both 24h and 48 h