



## Swarming Strategies for Cooperative Species

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In this paper, we propose a model to investigate the relative efficiency of simple swarming strategies based on the interplay between spontaneous and recruitment-based emigration. We conduct a dynamical study of the model which combines inverse density dependence, saturation effects and induced vs. diffusion-like population transfer. The influence of the most relevant parameters is explored on a systematic basis, and transition values for which qualitative changes occur in the system's behaviour are given. The model is then used to study colonization of a multiple sites environment, as well as confrontation between species featuring different swarming strategies. Simulation results indicate that cooperative organisms should have an interest in evolving recruitment-based emigration. The corresponding population transfer patterns prove more efficient in invading new territories, eliminating competitors in the process. We suggest that this advantage could have promoted a simple form of coordinated swarming in species featuring a primitive type of cooperation.

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### Introduction

The dynamics of a population of organisms in a given environment is the result of multiple factors. Among these, the most basic are carrying capacity, maximum reproduction rate and death rate. Moreover, it can incorporate cooperative effects, which can affect population dynamics in various ways. Reproduction rate and/or survivorship can be density-dependent, which is usually known as the Allee, group or cooperative effect (Stephens & Sutherland, 1999; Courchamp *et al.*, 1999).

The inclusion of cooperation can be done in several ways. In this paper, we will assume the *per capita* reproduction rate to be a growing function

of population density:

$$\frac{dx}{dt} = (\alpha + \mu x^\beta)x(1 - x) - \lambda x \quad (1)$$

with  $x$  being the population size relative to the carrying capacity of the environment,  $\alpha + \mu x^\beta$  (with  $\mu$  and  $\beta > 0$ ) the maximum reproduction rate *per capita* and  $\lambda$  the death rate. In this paper, we will limit ourselves to the simple case where the positive relationship between population size and individual reproduction rate is strictly linear ( $\beta = 1$ ).

### Introducing Population Flows

Investigating spatial population dynamics requires the introduction of emigration into expression (1). In the simplest case, outgoing flow will

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only be proportional to total population:

$$\frac{dx}{dt} = (\alpha + \mu x)x(1 - x) - (\lambda + \eta)x \quad (2)$$

with  $\eta$  being the individual probability to leave the group.

In many social species, however, emigration will also include a form of recruitment, usually mediated by a physical or chemical signal (e.g. pheromone trail, silk threads). In the model, we assume this signal ( $y$ ) to have a facilitating effect on emigration, parameter  $\theta$  being the recruitment strength per signal unit:

$$\frac{dx}{dt} = (\alpha + \mu x)x(1 - x) - (\lambda + \eta + \theta y)x \quad (3a)$$

The dynamics of  $y$  will result from a combination between two independent phenomena:

- (A) Reinforcement by each outgoing individual.
- (B) Spontaneous decay, proportional to  $y$  (due to evaporation or mechanical factors):

$$\frac{dy}{dt} = \gamma(\eta + \theta y)x - \varepsilon y \quad (3b)$$

with  $\gamma$  being the amount emitted per outgoing individual, and  $1/\varepsilon$  the mean lifetime of the signal. A simple change of variables ( $y, t$ ) and of the other parameters allows us to choose  $\gamma = \varepsilon = 1$ , making the analysis of the model easier.

### Steady States and Stability

Obviously, system (3) has a trivial solution for  $x = y = 0$ , other steady states being solutions of

$$x^3 + \frac{\alpha\theta - \mu - \mu\theta}{\mu\theta}x^2 + \frac{\mu - \alpha - \alpha\theta + \lambda\theta}{\mu\theta}x + \frac{\alpha - \eta - \lambda}{\mu\theta} = 0$$

$$y = \frac{\eta x}{1 - \theta x} \quad (4)$$

Analysis of the stability of solutions of expression (4) can be done by introducing small perturbations  $\delta x = \delta x_0 e^{\omega t}$  and  $\delta y = \delta y_0 e^{\omega t}$ ,  $\omega$  obeying

$$\omega^2 + A\omega + B = 0$$

with

$$A = -x(\mu - \alpha - 2\mu x) - \theta x + 1,$$

$$B = x(\mu - \alpha - 2\mu x)(-\theta x + 1) + (\eta + \theta y)\theta x. \quad (5)$$

This model, that in our opinion reproduces only the most basic aspects of a potentially cooperative species' biology, is obviously capable of oscillations in some areas of the parameter space. This raises the following questions: how easy to find are these oscillations, what do they look like, and how do they affect population dynamics?

It is clear from expression (3a) that if there is no swarming recruitment whatsoever ( $\theta = 0$ ), there are no oscillations either. Indeed, this comes down to suppressing the system's memory by removing the relationship between past and present emigration ( $dx/dt$  only depends on  $x$  and not on  $y$ ). On the other hand, even a strictly non-cooperative species ( $\alpha > 0, \mu = 0$ ) can feature damped oscillations, provided that it exhibits recruitment ( $\theta > 0$ ).

Let us consider a theoretical species where breeding is exclusively cooperative ( $\alpha = 0, \mu > 0$ ). In our continuous approximation, posing  $\alpha = 0$  is simply an easy way to reproduce any type of density-dependence. This might appear a drastic simplification, but it is in fact not. Features of sexual reproduction can be regarded as being cooperative, although in this case, cooperation is nothing but the mating process itself. Indeed, it is obvious that a small population size, by affecting negatively the encounter probability between potential sexual partners, can lead to extinction: fitness is thus density-dependent. Similarly, exhibiting any kind of division of labour is strongly related to cooperativity: specialization of some individuals into a given function can be beneficial only if others compensate for the loss of effectiveness in other functions. Finally, even limiting ourselves to the most

classical case, a formal description similar to eqn (1) with  $\alpha = 0$  can still be used to approximate the population dynamics of species featuring cooperative hunting (Pulliam & Caraco, 1984), breeding (Crick, 1992) or protection against predators (see e.g. Lazarus, 1979; Millor *et al.*, 1999).

An interesting limit case is found for  $\eta = 0$ , meaning that there is no spontaneous emigration. Although this situation is obviously unrealistic (since swarming is made impossible in the deterministic model if initial conditions involve  $y = 0$ ), it can be regarded as an approximation for the case where  $\eta$  is negligible compared with  $\theta y$ . Indeed, numerical testing confirms that there is no discontinuity for  $\eta = 0$ . Simplifying expression (3a) and (b) accordingly, one obtains

$$\begin{aligned} \frac{dx}{dt} &= \mu x^2(1-x) - (\lambda + \theta y)x \\ \frac{dy}{dt} &= y(\theta x - 1) \end{aligned} \quad (6)$$

which has four solutions corresponding to

$$\begin{aligned} x &= \frac{1}{\theta} \\ y &= \frac{\mu}{\theta^2} \left(1 - \frac{1}{\theta}\right) - \frac{\lambda}{\theta} \end{aligned} \quad (7a)$$

$$\begin{aligned} x^\pm &= \frac{1}{2} \pm \frac{1}{2} \sqrt{1 - \frac{4\lambda}{\mu}} \\ y &= 0 \end{aligned} \quad (7b)$$

$$\begin{aligned} x &= 0 \\ y &= 0 \end{aligned} \quad (7c)$$

Solution (7a) exists only when  $x^- < 1/\theta < x^+$ , in which case solutions (7b) are always unstable. On the contrary, if this condition is not satisfied, only solutions (7b) and (c) stand, among which eqn (7c) is always stable for  $\lambda > 0$ , and eqn (7b)  $x^+$  is stable if smaller than  $1/\theta$ . Figure 1 shows the stationary state given by eqn (7a) and its stability as a function of  $\theta$  for  $\mu = 0.5$  and  $\lambda = 0$  [Fig. 1(a)], for  $\mu = 0.5$  and  $\lambda = 0.1$  [Fig. 1(b)].

Figure 1(c) shows the stability regions in the  $\mu$ - $\theta$  plane for  $\lambda = 0$ . Whatever the death rate, as soon as eqn (7a) exists and corresponds to an oscillation, there is a critical value of  $\theta$  which determines whether it is damped ( $\theta < 2$ ) or sustained ( $\theta > 2$ ).

### Local Population Dynamics

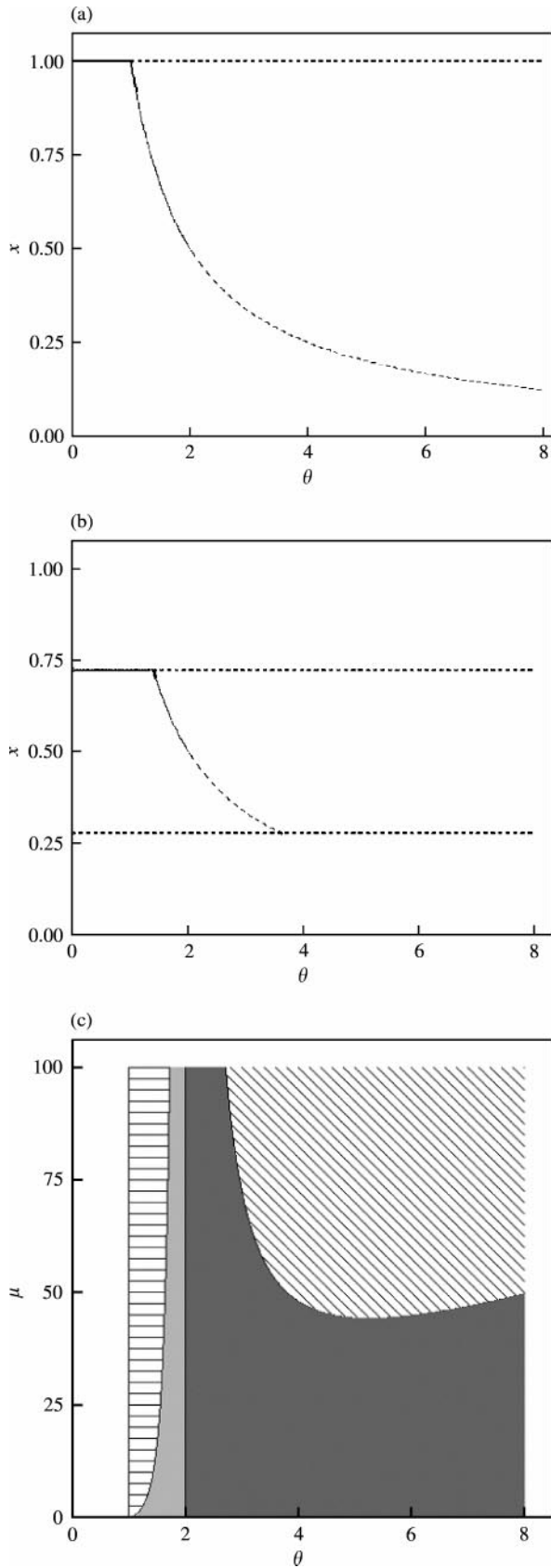
After having explored the model's properties for the limit case  $\eta = 0$ , the next logical step is to move to the more general situation where spontaneous emigration does occur and can be involved in triggering the swarming process. We choose parameter values that are reasonably close to those found in real biological systems, because the time scale of the dynamics they generate appear to be realistic. Indeed, colony growth rate and emigration rate are of the same order of magnitude.

Figure 2 shows the stationary states and their stability as a function of  $\eta$ , for  $\lambda = 0.05$  and several values of  $\theta$ . Understandably, the lower branch is always unstable and is in fact the size below which the population goes extinct. As soon as this critical value is reached, the population rapidly grows to the size corresponding to solution (7a). This can correspond to a stable point, reached either directly or after a damped oscillation, or to an unstable focus around which sustained oscillation is observed if the recruitment parameter  $\theta$  is greater than 2.

The different stability regions for the upper branches of Fig. 2 in the parameter space  $\eta$ - $\theta$  are summarized in Fig. 3(a). The population dynamics for two chosen  $(\eta, \theta)$  couples in the area corresponding to sustained oscillations are shown in Fig. 3(b). These two examples illustrate how the periodic behaviour of the system can range from relatively small variations around the value of the unstable focus to high-amplitude oscillations. The first case would correspond to a regular emission of a fraction of the total population, while the second would correspond to the massive emigration of most individuals.

### Optimal Population Distribution

In order to evaluate the efficiency of a swarming strategy, it is necessary to determine what is



the optimal distribution for a given population in a multiple site environment. Indeed, the migration rate and its variation through time should lead to the best possible approximation of this target distribution. It seems reasonable to assume that, ideally, a population of organisms should maximize its reproductive rate. In order to reach this maximum, a non-cooperative species in a homogeneous environment should always promote dispersion in order to limit saturation and competition for resources. But for cooperative animals, there is obviously a critical size below which group splitting reduces individual fitness.

If we consider a discrete environment made of  $n$  identical sites, the total population growth is given by

$$\frac{dx_{tot}}{dt} = \sum_{i=1}^n \mu x_i^2 (1 - x_i) - \lambda x_i \quad (8)$$

Hypothesizing a closed system, the migration term disappears in expression (8) because of the conservation of the total population.

As in our model, cooperative effects grow linearly with group size ( $x$ ), it is clear that individuals should always be evenly distributed between  $n'$  occupied sites,  $n'$  being a function of the population. The global size  $x_{tot}$  for which the number of occupied sites should switch from  $n'$  to  $n' + 1$  in order to maximize (8) is given by:

$$x_{tot} = \frac{n'(n' + 1)}{2n' + 1} \quad (9)$$

FIG. 1. (a) Solution of eqn (7),  $x = 1/\theta$ , exists only below the upper solution of eqn (7b)  $x^+$ , equal to 1 for  $\lambda = 0$  ( $\alpha = 0$ ,  $\mu = 0.5$ ,  $\eta = 0$ ). The solution can be a stable node or focus (continuous line), an unstable node (dotted thick line), or a sustained oscillation (dotted thin line). (b) Solution of eqn (7a),  $x = 1/\theta$ , exists only between solutions of eqn (7b)  $x^-$  and  $x^+$ , independent from  $\theta$ . The lower limit value  $x^-$  (critical size) is larger than zero for  $\lambda > 0$  ( $\alpha = 0$ ,  $\mu = 0.5$ ,  $\eta = 0$ ,  $\lambda = 0.1$ ). The solution can be a stable node or focus (continuous line), an unstable node (dotted thick line), or a sustained oscillation (dotted thin line). (c) Parameters space  $\mu-\theta$ , showing the regions corresponding to the different types of stationary states for solutions of eqn (7a) with  $\alpha = \eta = \lambda = 0$ : sustained oscillation (dark grey), damped oscillation (light grey) and stable point (horizontal stripes). The region where only the upper (unstable) solution of eqn (7b) holds ( $1/\theta < x^-$ ) is also given (diagonal stripes).

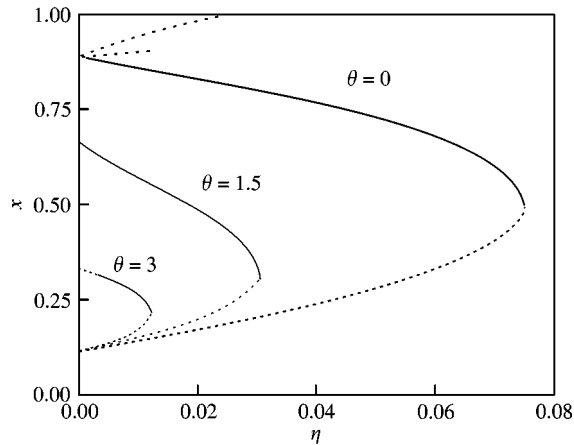


FIG. 2. Stationary states corresponding to solutions of expression (3) given as a function of  $\eta$ , with  $\alpha = 0$ ,  $\mu = 0.5$  and  $\lambda = 0.05$ , for several values of  $\theta$ . These can be a stable node or focus (continuous line), an unstable node (dotted line) or, in the upper branch showing solutions for values of  $\theta > 2$ , a sustained oscillation (dotted thin line).

### Reaching Optimal Population Dynamics Through Swarming Recruitment

Up to this point we have demonstrated that a simple form of swarming recruitment can produce oscillations and that optimal distribution for a cooperative species should involve a modulation of the number of occupied sites. In order to attain this goal, cooperative organisms should rely on a mix between spontaneous and recruitment-based emigration. A first obvious but not necessarily irrelevant advantage of featuring coordinated swarming rather than diffusion-like population transfer is that it can prevent premature dispersion of small groups. If we consider two nearly identical species  $A$  and  $B$  ( $\mu_A = \mu_B = \mu$ ,  $\lambda_A = \lambda_B = \lambda$ ) with the same upper stationary state but different values of  $\eta$  and  $\theta$ , the critical size (lower stationary state) below which a population cannot survive is lower for that species relying the most on swarming recruitment (higher  $\theta$ , refer to Fig. 2 for corresponding  $\eta$  values). Indeed, when a population is small, the recruitment signal ( $y$ ) does not build up easily. When swarming is based on the exploitation of that signal ( $\eta$  low,  $\theta$  high), this situation results in more organisms staying within the group, thereby maximizing cooperative effects and limiting losses until the colony has grown well beyond its initial size.

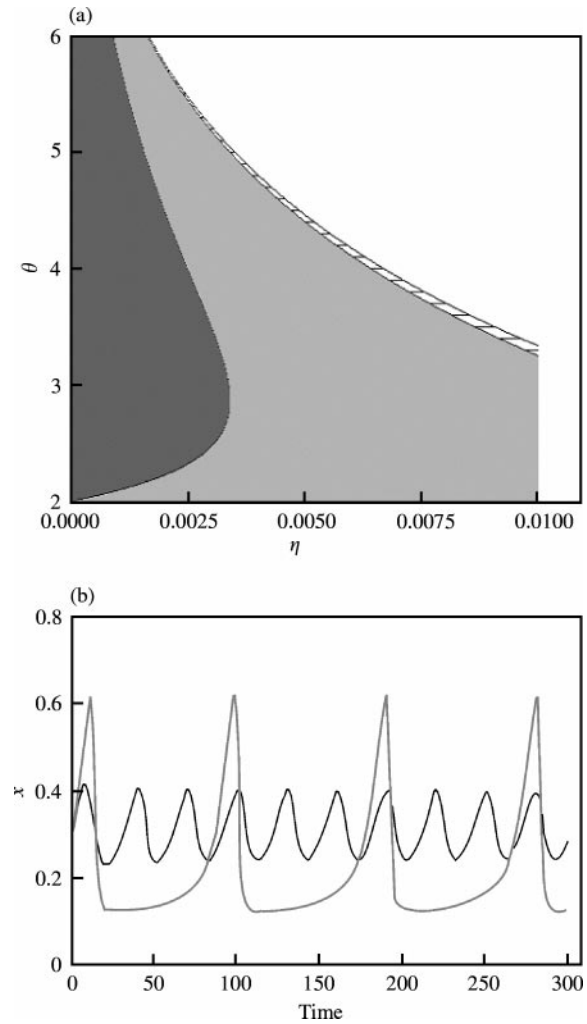


FIG. 3. (a) Parameters space  $\eta$ - $\theta$ , showing the regions corresponding to the different types of upper stationary states for  $\alpha = 0$ ,  $\mu = 0.5$  and  $\lambda = 0.05$ : sustained oscillation (dark grey), damped oscillation (light grey) and stable node (horizontal stripes). (b) Two examples of sustained oscillations:  $\alpha = 0$ ,  $\mu = 0.5$ ,  $\lambda = 0.05$ ,  $\theta = 3$ ,  $\eta = 0.0025$  (thin black line) and  $\eta = 0.0001$  (thick grey line).

Also, if we cross the value of  $\theta = 2$  above which oscillations are sustained, swarming recruitment can result in a fairly good approximation of the local pattern corresponding to a “perfect” species, able to perform instantaneous splitting when the proper size is reached. Expression (9) predicts that the optimal distribution switches from 1 occupied site to 2 when  $x = \frac{2}{3}$ . In an environment offering an infinite number of available sites, an isolated group of organisms should grow to this size, preferably with no emigration at all, then create a propagule regrouping a half of the colony. This would result in the local population

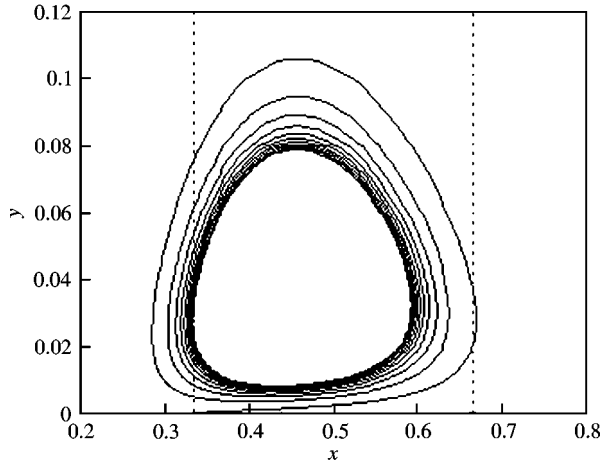


FIG. 4. Phase diagram for chosen values of  $\eta$  and  $\theta$  ( $\eta = 0.001$ ,  $\theta = 2.275$ ). Vertical dotted lines are the ideal limit values between which the local population should oscillate, as given by expression (9). As can be seen, the limit cycle is not a bad approximation, particularly considering the fact that  $\mu$  and  $\lambda$  were not adjusted ( $\alpha = 0$ ,  $\mu = 0.5$ ,  $\lambda = 0.05$ ) and recruitment is strictly linear.

slowly growing to  $\frac{2}{3}$ , then suddenly reverting to  $\frac{1}{3}$ , and so on. Of course, using our continuous model, this ideal management of population size cannot be exactly reproduced. Indeed, emigration is never equal to zero (meaning that some losses occur during the colony growth process) and once initiated, swarming recruitment cannot be both infinitely strong and infinitely brief. Yet as shown in Fig. 4, the chosen parameter values (we assume that their natural counterparts can be tuned by selection) are able to produce oscillation patterns of the appropriate amplitude.

Another potential advantage is found when considering a cooperative species' ability to quickly and efficiently colonise new territories. If  $\theta$  is negligible ( $\sim 0$ ), spontaneous emigration rate  $\eta$  is critical in that respect and should be between 2 limit values, hereafter referred to as  $\eta^-$  and  $\eta^+$ . The lower value corresponds to the spontaneous emigration rate, below which population transfer toward an adjacent site is too weak for the foundation to be successful, while the higher value is the threshold above which dispersion is too fast for the mother group to survive.

Let us consider a theoretical environment made of only two available sites, the first one being occupied by a population  $x_1$ , and the second initially empty ( $x_2 = 0$ ). If we make the further hypothesis that emigration is only possible

from sites 1 to 2, and that all individuals leaving site 2 are lost, we have a relatively simple model to explore non-local dynamics. Populations  $x_1$  and  $x_2$  will vary as

$$\begin{aligned} \frac{dx_1}{dt} &= \mu x_1^2(1 - x_1) - (\lambda + \eta + \theta y_1)x_1 \\ \frac{dx_2}{dt} &= \mu x_2^2(1 - x_2) - (\lambda + \eta + \theta y_2)x_2 \\ &\quad + (\eta + \theta y_1)x_1 \end{aligned} \quad (10)$$

If we keep  $\theta = 0$ , then if  $\eta > \eta^-$ ,  $x_2$  will grow to its upper stationary state, and when both groups have reached equilibrium, the total loss for the entire population  $x_{tot}$  will simply be  $\eta x_2$ . Obviously, if time is not an issue and we still use a deterministic and continuous description,  $\eta$  should be as close to  $\eta^-$  as possible, in order to minimise this loss. But if we introduce some noise in the model, or if the time spent by population  $x_2$  to reach its stationary state is taken into account, then this option is probably not very adaptive. So a species featuring only spontaneous emigration is facing the difficult question of its optimal rate.

If  $\theta > 0$ , things are quite different. Let us compare two species  $A$  and  $B$  ( $\mu_A = \mu_B = 0.5$ ,  $\lambda_A = \lambda_B = 0.05$ ,  $\eta_A = 0.007$ ,  $\eta_B = 0.07$ ,  $\theta_A = 1.5$  and  $\theta_B = 0$ ), both starting well above the non-recruiting species' critical size ( $x_A = x_B = 0.5$ ) and in the two sites environment. As can be seen in Fig. 5(a), the total population  $x_{tot} = x_1 + x_2$  for  $B$  tends to a higher size than for  $A$ , but in the early stages,  $A$  grows faster, temporarily "outrunning"  $B$ . So it all comes down to a question of balance between speed and target size. If time is critical, for example because delaying full occupation of the available sites is dangerous and/or because shortening the period spent near the lower critical stationary state is important, then species  $A$ , featuring lower spontaneous emigration but capable of swarming recruitment, has the advantage.

### Introducing Competition

The potential advantages of swarming recruitment can be dramatically illustrated if one

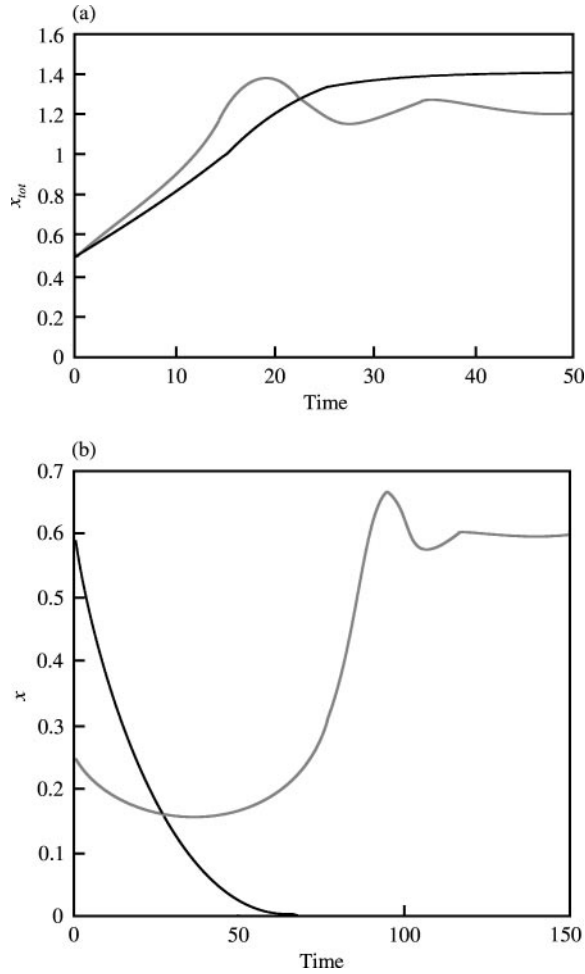


FIG. 5. (a) Evolution of the total population in a two-site environment, with site 2 receiving emigrants from site 1 (see text). The non-recruiting species ( $B$ , thin black line) reaches a higher plateau, but the recruiting species ( $A$ , thick grey line) grows faster. (b) Competition between the recruiting ( $A$ , thick grey line) and the non-recruiting species ( $B$ , thin black line) in a single-site environment. In the long term, lower critical size and better group cohesion (see text) allow  $A$  to eliminate  $B$ .

considers the competition between those two species when forced to share the same environment. In this case, assuming there are no agonistic reactions between  $A$  and  $B$  but only competition for resources, and removing some parameters that are set to zero, as well as irrelevant variables ( $y_B$ ), population dynamics for  $A$  obey

$$\frac{dx_A}{dt} = \mu x_A^2 (1 - x_A - x_B) - (\lambda + \eta_A + \theta_A y_A) x_A$$

$$\frac{dy_A}{dt} = (\eta_A + \theta_A y_A) x_A - \varepsilon y_A \quad (11a)$$

and for  $B$

$$\frac{dx_B}{dt} = \mu x_B^2 (1 - x_B - x_A) - (\lambda + \eta_B) x_B \quad (11b)$$

Figure 5(b) shows in a very demonstrative fashion how species  $A$  can eliminate  $B$  in the long term, even though  $B$  starts on its upper stationary state when isolated ( $x_B = 0.6$ ), while  $A$  invades the site with a considerably smaller initial population ( $x_A = 0.25$ ). This is only because the combination of a lower critical size and weaker spontaneous emigration allows  $A$  to better resist the competition. Of course, it is possible to find initial values of  $x_A$  and  $x_B$  for which  $B$  prevails, but the conditions leading to such an end involve an even greater advantage to  $B$ , and are in fact quite rare: in most cases, either only  $A$  survives, or both species go extinct.

These findings can be generalized to a multiple site environment, thereby providing a global picture of the spatial population dynamics resulting from the interplay between competition for local resources and different swarming strategies. As a first step, let us consider a very simple case involving only two interconnected sites occupied by two species  $A$  and  $B$ . Assuming that this environment is symmetrical and open, individuals can only be transferred between sites or leave the system. We also make the further hypothesis that when present, swarming recruitment only promotes emigration, with no directional information. So whatever the swarming strategy, only a half of the organisms leaving one site are effectively transferred, the other half being lost (with  $n = 2$ ). In this situation, equilibrium is reached for species  $A$  when:

$$\frac{dx_{1A}}{dt} = \mu x_{1A}^2 (1 - x_{1A} - x_{1B}) - (\lambda + \eta_A + \theta_A y_{1A}) x_{1A} + \frac{\eta_A + \theta_A y_{2A}}{2} x_{2A} = 0$$

$$\frac{dx_{2A}}{dt} = \mu x_{2A}^2 (1 - x_{2A} - x_{2B})$$

$$\begin{aligned}
 & -(\lambda + \eta_A + \theta_A y_{2A})x_{2A} \\
 & + \frac{\eta_A + \theta_A y_{1A}}{2} x_{1A} = 0 \quad (12)
 \end{aligned}$$

and the same conditions apply for species *B*. Using rules of symmetry, it is possible to demonstrate that if *A* and *B* are identical (as if they represent two colonies belonging to the same species for example), there are regions of the parameter space where coexistence is possible, either with  $x_{1A} = x_{2B} = x_{2A} = x_{1B}$  (with  $\theta > 0$ ), or with  $x_{1A} = x_{2B} \neq x_{2A} = x_{1B}$  (with  $\theta \geq 0$ ).

On the other hand, it seems very difficult for two different species to coexist in a two-site environment, at least in the long term. As illustrated in Fig. 6 for the same species *A* and *B* we used before, most initial conditions lead to the extinction of the non-recruiting species.

Although this cannot be formally extended to larger environments, because the existence of critical domain size is well known in this kind of dynamical systems, it is another indication that swarming recruitment is an important parameter for population growth success. Indeed, numerical testing has shown that one-dimensional environments counting up to 15 available sites ( $n = 15$ ) are still usually invaded by the recruiting species, even when initial populations are placed at opposite ends of the environment (reducing competition in the early stages, see Fig. 7).

### Discussion

The model we developed here was initially designed to explore the properties of swarming in social spiders. The mechanisms we hypothesised and dynamics we observed are not limited to these animals, although social arthropods, in general, might represent the best possible illustration (Wilson, 1971, 1975; Grassé, 1984; Hölldobler & Wilson, 1991; Gotwald, 1995).

The use of trailing cues left by conspecifics is a very common feature in many gregarious organisms: insects (see e.g. Deneubourg *et al.*, 1989; Aron *et al.*, 1990; Verhaeghe *et al.*, 1992; Fitzgerald & Costa, 1999) but also molluscs for example (Focardi *et al.*, 1985). It could even be argued that the coupling of individual memory and imitative behaviour belongs to the same

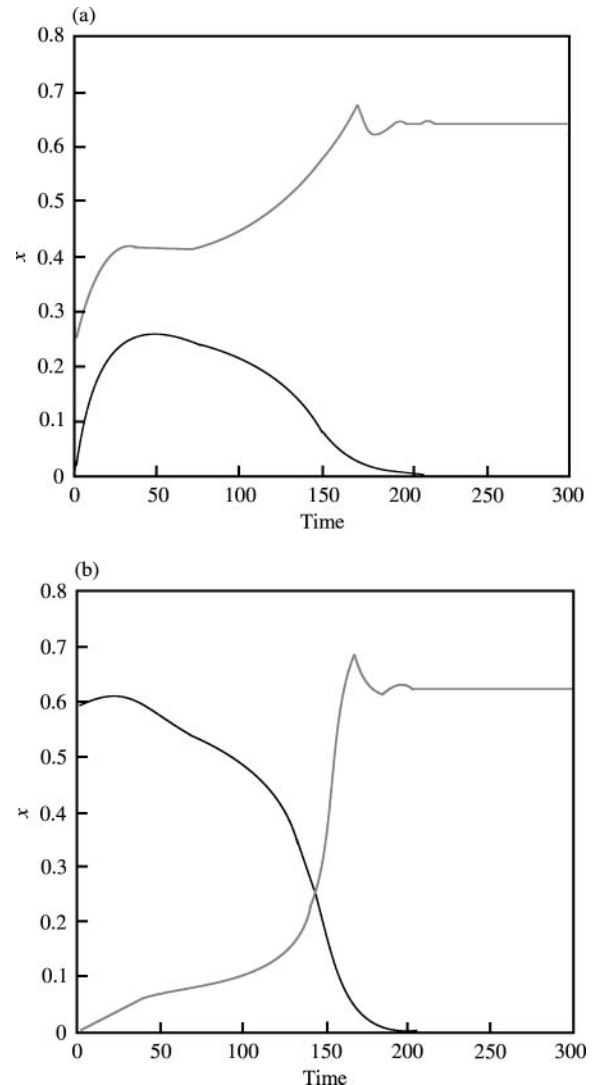


FIG. 6. Evolution of populations *A* (thick grey line) and *B* (thin black line) through time in the two-site environment. *A* starts in site 1 (a), with  $x_{1A} = 0.25$ ,  $x_{1B} = 0$ . *B* starts in site 2 (b), with  $x_{2A} = 0$ ,  $x_{2B} = 0.6$ . See text for parameter values.

category of collective response, in which case we could also mention fishes (see e.g. Shaw & Tucker, 1965), birds (De Schutter, 1997) and mammals (Gérard *et al.*, 1997). Indeed, the decay of a chemical signal or the extinction of an individual memory can be formalized in the same way, and this analogy can easily be extended to the reinforcement of a behavioural response and that of a foraging trail. Yet the structure of the model and parameter values were chosen so as to be consistent with what we know of social spiders, reflecting the potential recruitment

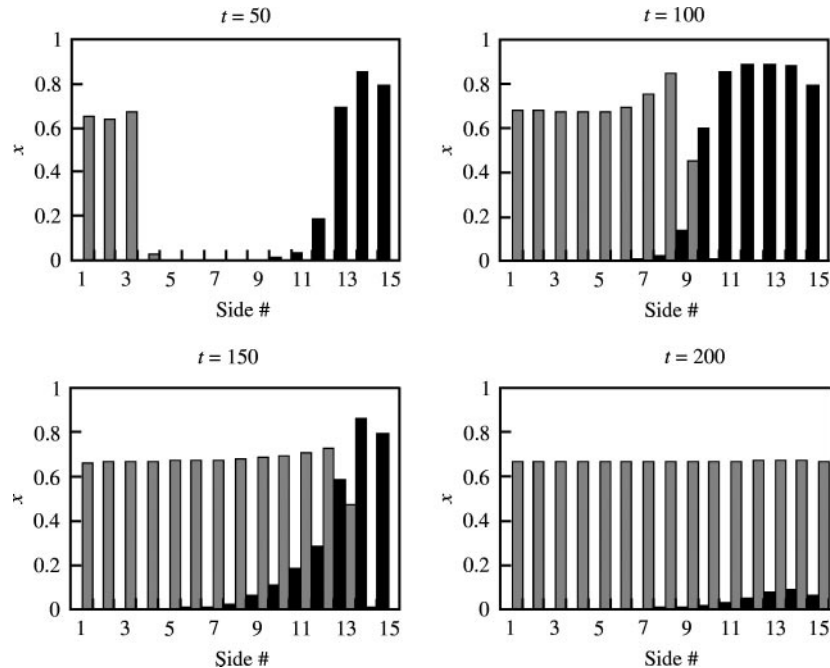


FIG. 7. Evolution of populations *A* (grey bars) and *B* (black bars) through time in the 15-site environment. In the long term, *B* (non-recruiting) is eliminated by *A* (recruiting), even though each species is able to effectively propagate from its “own” end of the set-up before the fronts collide ( $t \sim 100$ ). See text for parameter values.

procedure (Lubin & Robinson, 1982; Saffre *et al.*, 1999) and capable of generating appropriate colony distributions (Pasquet & Krafft, 1989; Furey & Krafft, unpubl.).

Similarly, we did not take into account the fact that inverse density dependence can also affect death rate in species exhibiting collective defence for example. Although this is probably the case for social spiders as well (Avilés, 1997), recent data (Avilés & Tufino, 1998) suggest that reproduction rate is also higher in larger colonies. However, we acknowledge that in social arthropods, classical counter-examples are known (“Michener’s paradox”, Michener 1974), so our model might require additional tuning if it is to be generalized. Because this makes mathematical treatment easier and the resulting dynamics are fundamentally identical, we chose to build on these findings, and assumed that cooperative effects only influenced colony growth rate, disregarding their probable role in survivorship (Vollrath, 1982; Christenson, 1984; Riechert *et al.*, 1986). Yet we agree that including this effect would be a most valuable addition to the model. Indeed, in some conditions, survivorship can be more critical to social species than growth.

We wish to emphasize the extreme simplicity of the model, contrasting with the plasticity of its behaviour. This makes it more plausible, because this kind of organization fits particularly well with the requirements of real biological systems: simplicity is synonymous to easy implementation and robustness, while plasticity means many tuning opportunities by natural selection. Of course, other procedures allowing better synchronization have evolved in many species (see e.g. Visscher and Camazine, 1999), but the kind of dynamics we describe here could have been an easily accessible form of coordinated swarming for organisms featuring a primitive type of cooperation (one that would not yet involve signalling between individuals for example). In this paper, we intentionally limited ourselves to the simplest possible case, considering only the lowest cooperativity level for growth ( $\beta = 1$ ), with a strictly linear recruitment, and neglecting the known influence of the individuals’ internal state on group cohesion (Rypstra, 1986; Krafft *et al.*, 1986). We are aware that without these restrictions it is possible to improve the efficiency of the response, for example by introducing some limited information treatment about resource

availability (Bernstein *et al.*, 1999). But finding out what kind of procedure can lead to optimal population dynamics was not our concern: our objective was to study the simplest possible way to achieve a reasonable approximation of the target solution.

Now what information can we draw from these theoretical results about the advantage for a cooperative species to develop swarming recruitment? A first and somewhat trivial answer is given by expression (9): obviously, as soon as there are cooperative effects, constant emigration rate is not the best strategy, since there is an optimal budding size below which one should never leave the group. This may look like a good reason to develop some kind of coordinated swarming, but the most convincing illustration of its usefulness is probably found in the competition between a recruiting and a non-recruiting species.

Indeed, in a single-site environment with only one species present, there seems to be very little interest in evolving any form of synchronized emigration: the same stationary state can be reached with or without recruitment just by tuning  $\eta$  and  $\theta$  (see Fig. 2), and the highest possible stationary state (corresponding to  $\eta = 0$ ) is an inverse function of  $\theta$ , meaning it drops as recruitment intensity rises (see Fig. 1). If we look at it in the long term, the same considerations apply to a multiple sites environment: even though its overall growth rate is lower, a non-recruiting species is able to reach a higher total population than its recruiting counterparts [same local stationary state, see Fig. 5(a)].

Yet as soon as competition is introduced in the model, whatever the size of the system, it appears that the species relying the most on coordinated swarming gains a substantial advantage. Once again, this is understandable considering its lower critical size and better group cohesion between emigration phases, but we did not anticipate that the recruiting species would perform so much better that it would be able to completely wipe out its competitor in most situations [see Figs. 5(b), 6 and 7]. These results should be compared to those of Bolker & Pacala (1999), who found a strong advantage to short-range dispersal in the admittedly different context of plant interactions. Indeed, in the model we propose, coordinated and periodic population transfer

typically results in fast, intense but localised and brief exchanges between sites, therefore limiting spontaneous long-range emigration.

The resulting competitive advantage is likely to have promoted recruitment-based swarming strategies in many cooperative species. Indeed, it increases their ability to claim new available sites while maintaining high population density on already occupied ones, a form of space utilization that can lead to the emergence of implicit territories (Hölldobler & Lumsden, 1980).

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