



Collective decision-making and behavioral polymorphism in group living organisms

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ABSTRACT

Collective foraging in group living animal populations displaying behavioral polymorphism is considered. Using mathematical modeling it is shown that symmetric, spatially homogeneous (food sources are used equally) and asymmetric, spatially inhomogeneous (only one food source is used) regimes can coexist, as a result of differential amplification of choice depending on behavioral type. The model accounts for recent experimental results on social caterpillars not only confirming this coexistence, but also showing the relationship between the two types of regime and the ratio of active to inactive individuals.

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1. Introduction

In group living animals collective decisions occur when a group is faced with several opportunities, for example different food sources. Numerous studies have shown that the group is able to focus its activity on one particular option (e.g. one food source), even though no single individual is aware of all the alternatives. This raises the interesting question of how groups make collective decisions. The most common mechanisms leading to reliable collective decisions in group living animals are allelomimesis (roughly speaking, imitate what the neighbor is doing; see e.g. Sudd, 1957; Deneubourg and Goss, 1989) and differential signaling. Allelomimesis, by definition, leads to amplification, or a snowball effect whereby all individuals end up doing the same thing. Amplification is an essential component of many collective decisions observed in social insects such as, for example, recruitment to a single food source (ants: Pasteels et al., 1987; honeybees: Seeley et al., 1991; social caterpillars: Fitzgerald, 1995). Here an individual that has discovered a profitable food source conveys a signal leading to the source. This signal is attractive to congeners and triggers the onset of a recruitment process. Recruited individuals follow the signal to the food source

and in turn reinforce it. After a certain amount of time the majority of the foragers exploit the same food source. A decision thus emerges because an individual behavior is amplified by the action of many other individuals.

In most of the research on collective decision-making it is assumed that all individuals within a group behave in the same way (Camazine et al., 2001). At the modeling level, this assumption is reflected by adopting a unique set of parameters descriptive of individual behavior, like for instance mobility or the uptake/deposit frequency of a certain object. However, it is known that slight differences in the tendency of individual animals to display certain behaviors may lead to very different results at the collective level (Dussutour et al., 2005; Camazine et al., 2001). An extreme case of individual differences is behavioral polymorphism (polyethism), where individuals within a population can be categorized into types or strategies according to their behavior (West-Eberhard, 1989, 2003). Polyethism achieves its most marked form in eusocial insects (Wilson, 1971), but examples of consistent individual differences in behavior are found throughout the animal kingdom (rodents: Kotler and Brown, 1988; Benus et al., 1991; marine and freshwater snails: Wilson et al., 1999; Chase et al., 2001; fruit flies: Sokolowski, 1980; Pereira and Sokolowski, 1993; Debelle et al., 1989, 1993; Osborne et al., 1997; nematodes: DeBono and Bargmann, 1998; DeBono, 2003). They often pertain to foraging, where explorative and sedentary foraging strategies coexist. Still, the role of individual differences in the collective behavior remains largely unexplored.

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Social caterpillars provide an interesting illustration of how the plasticity of collective behavioral patterns may arise as a result of the interplay between amplifying interactions, individual differences and environmental factors such as the quality of food sources. Recent experimental studies indicate the existence of two alternative foraging strategies, which become evident under dietary imbalance but are not apparent when foods are nutritionally balanced (Dussutour et al., 2008). Specifically, when available food sources lack carbohydrate, caterpillars within a group fall into two clearly distinguishable behavioral categories: active and inactive. The active caterpillars spend considerable time in exploring the environment and relatively little time in feeding, whereas the inactive caterpillars move moderately and have longer meals. Interestingly, these individual differences in behavior lead to colony decisions that are dependent upon the ratio of populations of the two categories present in the group. Active caterpillar-biased colonies seem less cohesive than colonies comprising proportionately fewer active caterpillars. They do not focus their activity on one source but split and exploit two sources at the same time. In contrast, the more cohesive, “sluggish” caterpillar-biased groups focus their activity on only one source. The outcome of the collective decision thus depends on the composition of the group.

The present work uses mathematical modeling to show that the coexistence of symmetric, spatially homogeneous (both sources used equally) and asymmetric, spatially inhomogeneous (only one source is used) solutions constitutes in fact a generic and robust type of behavior, arising through differential amplification of a choice depending on behavioral phenotype. This coexistence has not previously been observed or modeled in collectively foraging animals. We argue that in addition to providing an explanation of the experimental findings in social caterpillars, it should provide a framework for addressing a variety of collective choice related problems across many fields.

The model and the associated evolution equations are introduced in Section 2. Sections 3 and 4 are devoted, respectively, to the steady-state solutions and their stability. The comparison between the model predictions and experiments on social caterpillars is discussed in Section 5 and the main conclusions are summarized in Section 6.

2. The model

Consider a colony of caterpillars confronted with the choice between two identical food sources. Let X_i and Y_i ($i = 1, 2$) denote the “active” and “inactive” individuals engaged primarily in, respectively, exploration and feeding activities within the range of food source i . While Y_1 and Y_2 remain localized at the vicinity of sources 1 and 2, X_1 and X_2 move across space, both around sources 1 or 2 as well as from 1 towards 2 or vice versa. According to the experimental data summarized in the Introduction when the sources are nutritionally balanced, behavioral polymorphism has no direct effect in the sense that only the asymmetric solution prevails, whereas in the unbalanced case X and Y are clearly differentiated and a symmetric exploitation becomes simultaneously possible. In what follows we shall focus on this latter case and, in particular, on the mechanisms for choices as to whether spatially symmetric or asymmetric solutions occur. In doing so we shall adopt a mean-field description, in where individual variability is not entering explicitly in the formulation of the evolution laws. For a total number of individuals of the order of 100 as in the present problem such a description not only remains meaningful, but provides also valuable insights on the mechanisms underlying the different modes of exploitation. In the future,

it would certainly be worth undertaking agent type simulations incorporating the effects of fluctuations.

We stipulate that the rate of change of the population densities x_i , y_i of individuals in states X_i and Y_i is determined by the following processes:

- An inflow, ϕ , of individuals of type X from a source, here constituted by the bivouac,

$$\xrightarrow{\phi} X_i \quad (i = 1, 2) \quad (1)$$

- The loss, at a rate equal to r , of a fraction of Y , which becomes disconnected from the group owing, for instance, to their trapping in the complex network of silk trails built by the colony:

$$Y_i \xrightarrow{r} \quad (i = 1, 2) \quad (2)$$

- The traffic of individuals of type X between sources 1 and 2,

$$X_1 \rightleftharpoons X_2 \quad (3)$$

In view of the above-mentioned nature of the trails built by the species this traffic is expected to be cooperative and, in particular, to include positive feedback.

- The transitions of individuals between states X and Y , expected again to be cooperative, in connection with the imitating action of Y type individuals on X ones, or from Y type individuals imitating X ones

$$X_i \rightleftharpoons Y_i \quad (i = 1, 2) \quad (4)$$

Combining mechanisms (1)–(4) one is led to the following structure of the evolution equations:

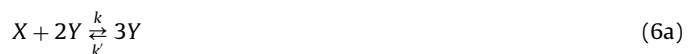
$$\begin{aligned} \frac{dx_1}{dt} &= \phi - \left(\frac{dx_1}{dt} \right)_{trans} + \left(\frac{dx_1}{dt} \right)_{traffic} \\ \frac{dy_1}{dt} &= \left(\frac{dx_1}{dt} \right)_{trans} - ry_1 \\ \frac{dx_2}{dt} &= \phi - \left(\frac{dx_2}{dt} \right)_{trans} + \left(\frac{dx_2}{dt} \right)_{traffic} \\ \frac{dy_2}{dt} &= \left(\frac{dx_2}{dt} \right)_{trans} - ry_2 \end{aligned} \quad (5)$$

where indices trans and traffic stand, respectively, for the contributions of processes (4) and (3) in the rate of change of each subpopulation.

Different cooperativity models can be adopted for the transition and traffic terms in the above equations. In what follows we choose the following generic forms.

2.1. For the transition between states

The cooperativity underlying these transitions is taken to be of order higher than two. Stated differently, we stipulate that transitions occur when at least three individuals are simultaneously present within a small distance. A rule of the “majority” type is then operating if the individuals happen to be found in different states. The simplest kinetic scheme corresponding to such a mechanism is



with parameters k , k' standing for the forward and backward rates of transitions, respectively. The value of k' relative to k will reflect the possibility that a cluster of three Y type of individuals may either remain predominantly in an inactive state, or split with some probability to yield a mixed state containing one X type of individual. The rate equation corresponding to

this scheme is

$$\left(\frac{dx_i}{dt}\right)_{trans} = kx_i y_i^2 - k' y_i^3 \quad (i = 1, 2) \quad (6b)$$

2.2. For the traffic

To account for the cooperative character of this process we augment the classical passive (linear) dependence of the rate on the density difference (driving its force), by the presence of a nonlinear term. The simplest expression possessing this structure and satisfying the necessary symmetry requirements is

$$\left(\frac{dx_1}{dt}\right)_{traffic} = -\left(\frac{dx_2}{dt}\right)_{traffic} = D_0 z + D z^3 \quad (7a)$$

where we have set

$$z = x_2 - x_1 \quad (7b)$$

The link between (6) and (7) on the one side and the experimental data on caterpillars on the other, will be addressed in more detail in Sections 5 and 6. The model predictions presented below depend, to a large extent, on the interplay between the two sources of cooperativity in transitions and traffic (Eqs. (6a) and (7a)). To highlight the role of cooperativity in the latter we shall set from now on $D_0 = 0$.

3. Steady-state solutions

Our first step is to determine the steady-state (time-independent) solutions of Eqs. (5), which are expected to describe the long time behavior of the subpopulations. On inspecting the second and fourth relations (5), complemented with (6a) and setting the time derivatives of y_1 and y_2 equal to zero one gets

$$\begin{aligned} kx_1 y_1^2 - k' y_1^3 - r y_1 &= 0 \\ kx_2 y_2^2 - k' y_2^3 - r y_2 &= 0 \end{aligned} \quad (8)$$

These equations admit four types of solutions.

3.1. The trivial solution

$$y_1 = y_2 = 0 \quad (9a)$$

corresponding to the absence of inactive individuals.

Upon substituting these values into the first and third relations (5), complemented with Eq. (7a) with $D_0 = 0$, one sees that there cannot be a steady state for x_1 and x_2 unless $\phi = 0$. More specifically, by adding and by subtracting these equations one gets

$$\begin{aligned} x_1(t) + x_2(t) &= x_1(0) + x_2(0) + 2\phi t \\ z(t) &= \frac{z(0)}{(1 + 4z^2(0)Dt)^{1/2}} \end{aligned} \quad (9b)$$

$z(0)$ being the initial value of z . This solution is unacceptable, since the total population $x_1(t) + x_2(t)$ of active individuals does not remain bounded in time as should be expected on physical grounds.

3.2. The first semi-trivial solution

$$y_1 = 0, \quad y_2 \neq 0 \quad (10a)$$

corresponding to an exclusive exploitation of source 2.

Substituting into the first equation (5) and setting the time derivative of x_1 to zero yields then

$$z = -\left(\frac{\phi}{D}\right)^{1/3} \quad (10b)$$

This allows one to compute the non-trivial value of y_2 by summing the last two equations (5) after setting the time derivative of x_2 to zero,

$$y_2 = \frac{1}{r}(\phi - Dz^3) = \frac{2\phi}{r} \quad (10c)$$

Writing the fourth equation (5) in the form

$$x_2 = \frac{r + k'y_2^2}{ky_2} \quad (10d)$$

one obtains x_2 and, finally, x_1 through

$$x_1 = x_2 - z = x_2 + \left(\frac{\phi}{D}\right)^{1/3} \quad (10e)$$

3.3. The second semi-trivial solution

$$y_1 \neq 0, \quad y_2 = 0 \quad (11a)$$

corresponding to an exclusive exploitation of source 1.

Following similar manipulations as in Section 3.2 we obtain the following values of the other variables:

$$z = \left(\frac{\phi}{D}\right)^{1/3} \quad (11b)$$

$$y_1 = \frac{1}{r}(\phi + Dz^3) = \frac{2\phi}{r} \quad (11c)$$

$$x_1 = \frac{r + k'y_1^2}{ky_1} \quad (11d)$$

$$x_2 = x_1 + z = x_1 + \left(\frac{\phi}{D}\right)^{1/3} \quad (11e)$$

3.4. The fully non-trivial solution

$$y_1, y_2 \neq 0$$

where both sources 1 and 2 are being exploited. To compute the associated values of the variables we first observe that on adding the first two and the last two equations of (5) at the steady state we obtain

$$\begin{aligned} y_1 &= \frac{1}{r}(\phi + Dz^3) \\ y_2 &= \frac{1}{r}(\phi - Dz^3) \end{aligned} \quad (12)$$

Writing the second equation (5) at the steady state in a form similar to (11d), substituting into the last equation (5) and setting $x_2 = x_1 + z$ we arrive at a closed equation for z ,

$$z \left(\frac{2k'D^3}{r^2} z^8 + \frac{kD^2}{r} z^6 - \left(\frac{2k'D\phi^2}{r^2} - 2rD \right) z^2 - \frac{k}{r} \phi^2 \right) = 0 \quad (13)$$

This equation admits the homogeneous solution

$$z_0 = 0 \quad (14a)$$

corresponding to the symmetric exploitation of the two sources.

Among the remaining solutions only two are acceptable, in view of the number of sign changes in the coefficients of the polynomial of 8th degree, and they are of opposite sign,

$$z_{\pm} = \pm a \quad (a > 0) \quad (14b)$$

For each z , the original variables can thus be evaluated using relations (12), (11d) and $x_2 = x_1 + z$.

Summarizing, the model admits five physically acceptable steady-state solutions for the key variable z ,

$$\begin{aligned} 0 & \text{ (symmetric exploitation)} \\ \pm a & \text{ (asymmetric exploitation)} \\ \pm (\phi/D)^{1/3} & \text{ (exclusive exploitation)} \end{aligned} \quad (15)$$

from which the values of the original variables can be deduced through relations (10)–(14).

4. Linear stability analysis and bifurcation diagram

In view of the multiplicity of steady states found in the analysis of the preceding section it becomes necessary to identify the conditions under which these states may coexist or, on the contrary, those under which a particular state will prevail. This is achieved by testing their response towards perturbations (Nicolis, 1995).

Linearizing Eqs. (5) around a reference state corresponding to each of the five solutions in Eq. (15) one obtains a characteristic equation of fourth degree for the rate of change, ω of the perturbations, around these states. As well known, asymptotic stability of the reference state is secured as long as the real part of ω is negative, $\text{Re } \omega < 0$. When $\text{Re } \omega$ crosses zero, a change of stability of this state is expected to occur, leading to the bifurcation of new branches of solutions. The latter will be stationary or time periodic depending on whether the imaginary part of ω , $\text{Im } \omega$ is zero or non-zero, respectively.

A detailed analysis of the characteristic equation shows that states $z_{\pm} = \pm a$ are unstable, and thus physically unaccessible, for all ranges of parameter values considered. The stability of the $z_0 = 0$ state can be fully assessed analytically, since the characteristic equation factorizes into two equations of second degree in ω . This leads to two identical pairs of ω 's, each of which is a solution of the equation

$$\omega^2 + \left((k+k') \frac{\phi^2}{r^2} - r \right) \omega + \frac{k\phi^2}{r} = 0 \quad (16)$$

As can be seen, there is a critical value

$$\phi_c = \left(\frac{r^3}{k+k'} \right)^{1/2} \quad (17)$$

separating two different regimes. For $\phi > \phi_c$ state $z_0 = 0$ is stable. When slightly perturbed around it the system performs damped oscillations whose frequency (for ϕ near to ϕ_c) is close to $\phi(k/r)^{1/2}$ (see Fig. 1). For $\phi < \phi_c$ the state becomes, on the contrary, unstable. $\phi = \phi_c$ is thus a bifurcation point but, owing to the degeneracy of the values of ω , the nature of the bifurcating branches cannot be fully assessed.

Coming finally to states $\pm(\phi/D)^{1/3}$ a similar, though more cumbersome, analysis reveals also a change of stability at some critical value ϕ'_c , where there is a pair of purely imaginary ω 's and two negative real ones. One of the latter is equal to $-r$ and keeps this value away from ϕ'_c as well, for the entire range of the parameters. For $\phi > \phi'_c$ the states are stable, the opposite being true for $\phi < \phi'_c$. Since there is here no degeneracy, the Hopf bifurcation theorem guarantees the existence of a periodic solution bifurcating at $\phi = \phi'_c$ out of each of the states $\pm(\phi/D)^{1/3}$. Numerical investigations show that this solution is

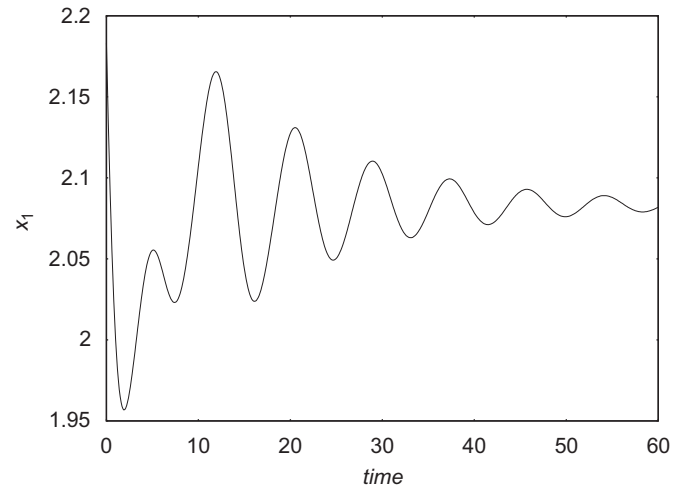


Fig. 1. Time evolution of x_1 with initial conditions around the symmetric solution $z = 0$ with a ϕ value $\phi = 0.75$ slightly above the critical value ϕ_c . Other parameter values $k = k' = r = 1$ and $D = 0.2$.

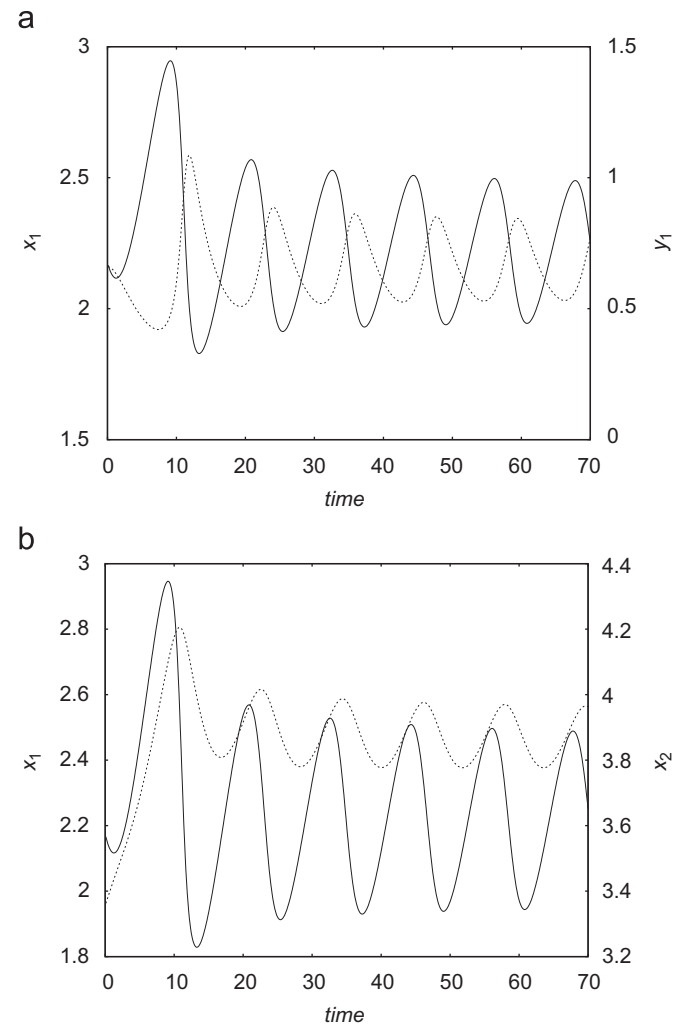


Fig. 2. As in Fig. 1 but initial conditions around the asymmetric state $z_+ = (\phi/D)^{1/3}$ corresponding to the exploitation of source 1 and $\phi = 0.33$, leading to a periodic solution associated to a regime of synchronization. Full lines refer to the variables in the left ordinates.

supercritical, in the sense of developing in the range of $\phi < \phi'_c$ where the steady state is unstable. Figs. 2a and b depict the time dependence of x_1 , y_1 and x_2 , for the state given by Eqs. (11). As can be seen x_1 and y_1 oscillate in near phase opposition. In other words, there is near synchronization between the individuals of the two types around source 1. A similar situation prevails for the solution given by Eqs. (10).

Compared to ϕ_c (Eq. (17)), the critical value ϕ'_c is smaller in a wide range of the values of parameters r , k , k' and D . Notice that all five states in (15) merge at $\phi = 0$ and remain distinct for $\phi > 0$. On the basis of the above information one can infer the bifurcation diagram in Fig. 3. The diagram is limited to the local bifurcations only and does not account for solutions that could arise from global bifurcations occurring between ϕ_c and ϕ'_c . As clearly seen, for $\phi > \phi'_c$ one has coexistence of the inhomogeneous solutions $\pm(\phi/D)^{1/3}$, describing the exclusive exploitation of a single source, with the homogeneous one $z_0 = 0$ in which both sources are equally being exploited. The particular state that will be attained in the course of time depends on the initial values. Specifically, as seen in Fig. 4, if the individuals are initially spread nearly symmetrically on both sides one tends to the symmetric solution and if there is initially a heavy bias towards one particular side one tends to the asymmetric solution. Notice that each of the three simultaneously stable states possesses its own *domain of attraction* containing states whose constitution may be significantly different from the above two limiting cases. These domains partition the system's state space (which here is four-dimensional) into subregions, separated by frontiers containing the unstable states. In this perspective the ratio of active and inactive individuals, which according to the experiments is closely associated to the mode of exploitation, appears to be the consequence, rather than the cause, of the final outcome. In contrast to the foregoing, in the range $\phi'_c < \phi < \phi_c$ one witnesses only the asymmetric exploitation of the resources.

We stress that the bifurcation diagram of Fig. 3 is both robust against the choices of parameters and non-standard in the field of collective behavior of social insects. Normalizing time through $\tau = k't$ one is left with four independent parameters in the evolution equations of the model variables: ϕ/k' , k/k' , D/k' and r/k' . But actually, this number collapses into a single combination in the

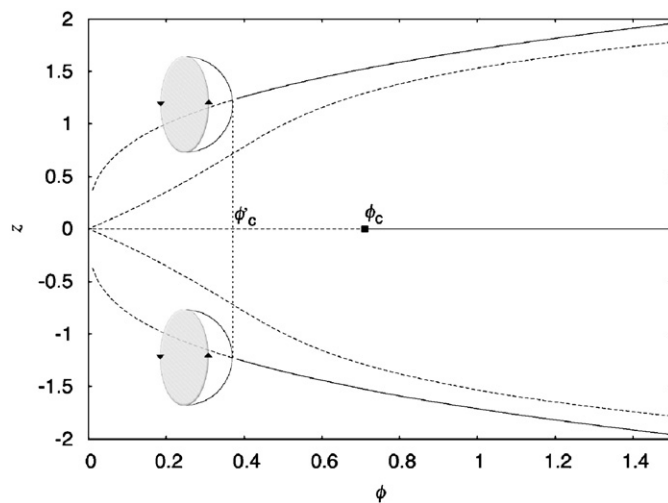


Fig. 3. Bifurcation diagram indicating the values of variable $z = x_2 - x_1$ as a function of parameter ϕ . ϕ_c : critical value at which the symmetric exploitation mode undergoes a change of stability. ϕ'_c : critical value at which the exclusive exploitation modes undergo a change of stability. Full and dashed lines stand for stable and unstable solutions, respectively. The two paraboloids in the region $\phi < \phi'_c$ stand for the periodic solutions born at ϕ'_c through a Hopf bifurcation. Other parameter values as in Fig. 1.

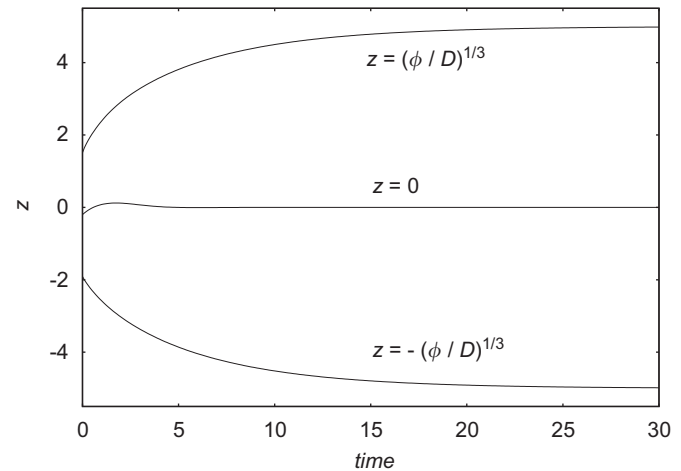


Fig. 4. Time evolutions of variable z starting from three different initial conditions in the parameter region for which three stable states coexist. Parameter values as in Fig. 1 with $\phi = 1$.

vicinity of the bifurcation points ϕ_c and ϕ'_c , which are the principal organizing elements of the bifurcation diagram and condition the stability of the solutions. As for the coexistence of the trivial, semi-trivial and fully non-trivial steady-state solutions, it is basically determined by the nature of the kinetic processes present and subsists for all specific choices of parameter values as long as ϕ and r are not strictly zero.

The diagram of Fig. 3 contains also a number of novel features as far as the modeling of the collective behavior of social insects is concerned. Most, prominent among them is the coexistence of stable symmetric and asymmetric solutions present already in a situation of binary choice, contrary to other foraging models where asymmetric exploitation simply replaces the symmetric one beyond some critical value of the flux. In addition, the diagram predicts the occurrence of sustained oscillations, not found so far in typical foraging models. This additional richness arises from the conjunction of the cooperativity in the transport and of the cooperativity in transitions between the two groups of individuals in which the population is split.

5. Comparison with experiment

The stable coexistence of both homogeneous and inhomogeneous modes of exploitation of the resources, in a wide range of parameter values and ambient conditions predicted by our model provides a qualitative interpretation of the experiments summarized in the Introduction (Dussutour et al., 2008) and highlights some of the mechanisms that are at the origin of this behavior.

To establish a more quantitative connection with experiment we now address the role of the ratio of inactive versus active individuals in the prevalence of a particular mode of exploitation. To this end we evaluate the ratio y/x around a particular food source as predicted by the model. Using Eqs. (10) one finds straightforwardly that in the exclusive exploitation mode the ratio for the source exploited is

$$\left(\frac{y}{x}\right)_{inh} = \frac{4k(\phi/r)^2}{r + 4k'(\phi/r)^2} \quad (18)$$

while for the homogeneous exploitation mode one gets

$$\left(\frac{y}{x}\right)_{hom} = \frac{k(\phi/r)^2}{r + k'(\phi/r)^2} < \left(\frac{y}{x}\right)_{inh} \quad (19)$$

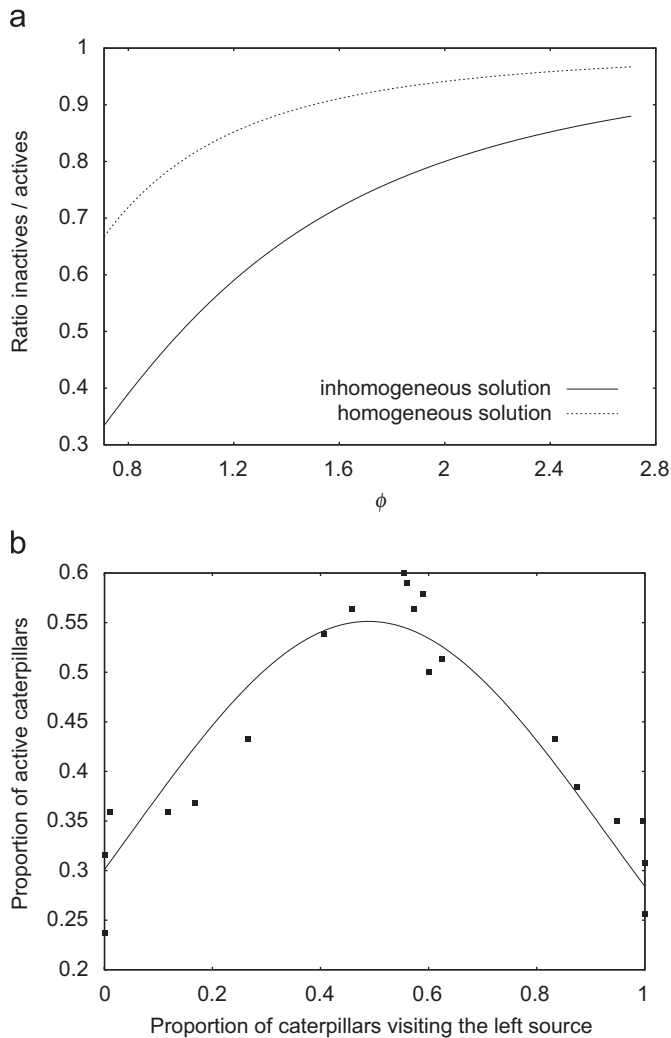


Fig. 5. (a) Ratio of inactive individuals over active individuals characterizing the inhomogeneous solution (Eq. (1)) and the homogeneous solution (Eq. (4)) versus parameter ϕ . Parameters values are $k = k' = r = 1$. (b) Experimental result of the proportion of active caterpillars versus the proportion of caterpillars visiting one particular unbalanced food source.

Fig. 5a depicts relations (18) and (19) for the reference values $k = k' = r = 1$ used in the numerical construction of the figures. While for large ϕ values both ratios tend to unity, one observes significant differences for moderate (and larger than ϕ_c) ϕ 's. Such values seem to be more appropriate for the problem at hand since, according to experiment, the fraction of recruited individuals of any form engaged in foraging hardly exceeds 50%. Taking $\phi = 1$ to fix ideas, one obtains $(y/x)_{inh} = 0.8$ and $(y/x)_{hom} = 0.5$ implying a higher proportion ($\approx 66\%$) of active individuals in the homogeneous state compared to the proportion (55%) in the inhomogeneous one. This is not far from the experimental data depicted in Fig. 5b, where the corresponding proportions are here closer to 60% and 45%, respectively. The agreement can be improved by tuning the parameters k' and r , while ensuring that the three states of exploitation remain stable. In fact, the very occurrence of a maximum in Fig. 5b around the value 0.5 of the abscissa (corresponding to the homogeneous exploitation) is a different way to express that the curve corresponding to the inhomogeneous solution in Fig. 5a lies always above the curve corresponding to the homogeneous one.

6. Conclusions

In this work we developed a kinetic model for analyzing the relative roles of cooperativity and behavioral variability in the process of collective decision making in group living organisms, in connection with the exploitation of simultaneously available food sources. The model incorporates such processes as influx towards the sources, trapping in the trails, feeding, transport (exploration) and transitions between two states associated with “active” and “inactive” individuals. It shows the existence of a generic, hitherto unexplored mode of resource exploitation associated with the coexistence of both symmetric and asymmetric solutions. It accounts for experimental results on social caterpillars concerning not only the coexistence per se but also the relationship between the two types of solutions and the ratio of active to inactive individuals. Previous studies conducted on ants have focussed on the emergence of asymmetric solutions arising from the loss of stability of the symmetric solution. It would undoubtedly be interesting to inquire on conditions, if any, under which mixed solutions might be observed in this case as well, in the light of our results.

In addition to the above the model predicts the occurrence of sustained oscillations, descriptive of a regime of synchronization, in the range of influx values less than the stability limit of the inhomogeneous mode of exploitation. For the reference parameter values used (Fig. 2) the periodicity of this regime is slightly more than 10 time units, i.e., considerably longer than the characteristic time scales associated to the kinetic parameters k , k' and r . There is preliminary experimental evidence that oscillatory resource exploitation does indeed occur, but it would undoubtedly be interesting to conduct further experimental studies and perform quantitative comparisons with the theoretical predictions. Synchronization of behavior in social groups is expected to maintain group cohesion. It arises, typically, from social facilitation whereby certain patterns of behavior are imitated, or increased in frequency, by the presence or the actions of other animals. For instance (Cole, 1991), the activity patterns of ant colonies are synchronized even in a constant environment, because workers are stimulated to become active by the activity of their neighbors. In our model the transitions of individuals between states X and Y are expected to arise from this type of mechanism, with X individuals imitating Y ones. As shown in our analysis, these transitions play a key role in the synchronization observed. In this respect it is also worth emphasizing that in the experiments by Dussutour et al. (2008) inactive-biased groups turn out to be more cohesive and more synchronized in their foraging behavior than the active-biased ones. Throughout the calculations and the numerical experiments, a minimal model of cooperative transport was used, as described by Eq. (7a). Despite apparent differences this model can easily be related to other cooperative models of choice between options encountered in the literature such as the model used by Deneubourg and coworkers (Beckers et al., 1992; Deneubourg and Goss, 1989; Nicolis and Deneubourg, 1999). Indeed let us denote by f , Deneubourg's choice function and write $\phi f = \phi/2 + \phi(f - \frac{1}{2})$. One obtains thus a term similar to the first term in the right-hand sides of the first and third equations (5), plus a term that vanishes for $x_1 = x_2$ (or $z = 0$) and is thus analogous to a transport term. The difference between this representation of transport and the one adopted here is in the presence of a linear part in z subsisting in the absence of cooperativity. Actually, this type of term should allow for the crossover between our analysis and the case of balanced food sources.

Our study provides a basis for explaining plasticity in collective behavioral patterns as a result of individual differences. This question is novel, yet critical to understanding the role of collective behavior in biological systems where no two individuals are ever the same. Another area where the work may lead to interesting insights pertains to insect outbreaks. Considerable

work has been devoted in predicting insect outbreaks using population-level factors and top-down approaches. Our bottom-up approach investigating the role of individual behavior and how it generates group-level patterns may bring a key contribution to the field of outbreak ecology.

Some time ago, Wellington suggested that behavioral differences between active and sluggish caterpillars lead to different colony dynamics based on the number of individuals of different phenotypes within a colony, and that these polyethisms contributed to outbreaking dynamics. According to him, colonies with many active members feed often and develop rapidly. In contrast, less active colonies forage over shorter distances, develop more slowly, and show poorer survival than their more active counterparts. This entails that caterpillars from egg masses with higher numbers of active individuals will grow faster and be better foragers, and this may lead to population increases and outbreak. Conversely, egg masses with a greater proportion of sluggish individuals may be associated with population decline implying that they are somehow adaptively “senescent”.

Now, sluggishness at the group level, which results in focusing on a unbalanced diet, may be the most appropriate strategy in degrading environments where better alternative foods are rare or unavailable as reported by Kause et al. (1999) for mountain birch caterpillars. Additionally colony with many active members is less cohesive and consequently has a greater chance of splitting into more vulnerable small groups, as has been observed in some of our experiments with the emergence of two bivouacs (Dussutour et al., 2008). Wellington found that colonies with a high proportion of active caterpillars were too active to stay together in their early age, so that many individuals wandered away from the protection of the group (Wellington, 1960, 1975). It is well known in caterpillars (Fitzgerald, 1993); forest tent caterpillars (Costa and Ross, 2003; Despland and Le Huu, 2007), as in other gregarious animals (Krause and Ruxton, 2002), that survivorship of individuals in group are influenced by the size of the group. Individuals gain protection from predators by surrounding themselves with others as reviewed in Fitzgerald (1993), Krause and Ruxton (2002) and Sword (2005). In addition to its direct effect on predation, in social caterpillars, being in a big group may also enhance larval growth rates due to the joint benefits of group thermoregulation (Porter, 1982; Bryant et al., 2000) and cooperative foraging (Denno and Benrey, 1997). As a consequence the coexistence of the individual differences may provide a balance between maintaining colony cohesion and optimizing food location. Moreover collective behavior needs a balance between efficiency in making group decision and flexibility which allows the discovery of new resources. In caterpillars such flexibility can be provided by the existence of individual differences.

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