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Fishing out collective memory of migratory schools

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Abstract

Animals form groups for many reasons but there are costs and benefit associated with group formation. One of the benefits is collective memory. In groups on the move, social interactions play a crucial role in the cohesion and the ability to make consensus decisions. When migrating from spawning to feeding areas fish schools need to retain a collective memory of the destination site over thousand of kilometres and changes in group formation or individual preference can produce sudden changes in migration pathways. We propose a modelling framework, based on stochastic adaptive networks, that can reproduce this collective behaviour. We assume that three factors control group formation and school migration behaviour: the intensity of social interaction, the relative number of informed individuals and the strength of preference that informed individuals have for a particular migration area. We treat these factors independently and relate the individuals' preferences to the experience and memory for certain migration sites. We demonstrate that removal of knowledgeable individuals or alteration of individual preference can produce rapid changes in group formation and collective behaviour. For example, intensive fishing targeting the migratory species and also their preferred prey can reduce both terms to a point at which migration to the destination sites is suddenly stopped. The conceptual approaches represented by our modelling framework may therefore be able to explain large-scale changes in fish migration and spatial distribution.

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1 Introduction

Grouping behaviour is a widespread phenomenon in animal ecology and is thought to be an emerging property of the self-organisation of individual organisms [1]. While living in groups, social animals benefit from several advantages among which is a more efficient capacity in problem solving [2–4]. Of particular interest is the ability of the group to make collective decisions also when it is composed of individuals with contrasting preferences and information [5,6]. How groups reach a consensus decision has recently received much attention [5,7–9] and several mechanisms to pool information in the group have been proposed [1,6].

Often no obvious reason can be adduced to explain the social behaviour of certain species except the fact that those groups are more efficient than single individuals in retrieving information from the environment [9,11,12]. For groups on the move, such as fish schooling, bird flocking or mammal herding, it has been shown that information transfer and social interactions are important factors of group cohesion and can promote the ability of making consensus decisions [5,13,14].

An example of such a collective decision making problem is the structure of migration routes in some fish species. Migration between widely separated but geographically stable locations of spawning and feeding sites raises several questions about how these animals manage to learn and *remember* the migration route between feeding and spawning sites. Where is the information on the path stored? How is it retrieved, shared and elaborated by a migrating group? Are these tasks performed significantly better by the group with respect to the individuals? Shedding light on the functioning of these mechanisms is a fundamental issue in ecology but may also be relevant to fields such as sociology and economy where it is common to deal with large systems of competitive agents that share information [4,11]. We hypothesize that *collective memory* might play an important role in the migration process of fish populations [13] and model its effects on schooling behaviour and migration efficiency. We tackle these questions by assuming that individuals have different amounts of information about migration routes and that only a fraction of them possesses some information, whereas the rest only exhibit a social behaviour. Those assumptions are consistent with numerical simulations of the evolution of leader and social traits in migratory populations [15,16] but are introduced in our model in a different way. In fact previous approaches mainly fall in a class of agent based models with spatial interaction [1,15,17–19] where "social" individuals tend to align and to follow the individuals that are nearby, in a finite spatial range. This reproduces a realistic dynamics, but it gives little insight on the mechanisms by which the collective behaviour emerges from individual interactions. Indeed due to their complexity, spatial dynamics models can only be studied with extensive numerical simulations.

Here, instead, we take a stochastic adaptive network approach. Network approaches have already been successfully applied to address collective behaviour in animal groups [8,20,21]: adaptive network models provide, in fact, a simpler mathematical structure which can be analysed more easily than real space models (i.e. without relying on simulations). In all these models, as in ours, spatial dynamics is implicitly taken into account through link creation and destruction processes: changes in the neighbourhood of the individuals due to spatial dynamics are reproduced by link dynamics between nodes (see Figure 1).

Capitalizing on previous models [22,23], we build a model introducing the key ingredient of memory for preferred route directions in a fraction of the individuals (the informed ones). This is introduced as an *a priori* bias for a particular route in the

choice behaviour of the informed individuals, that is based on their experience in that particular habitat: their *memory*. Therefore, the collective choice of the route direction, is a function of individual and social processes. We are able to find an exact solution for the model that provides a clear picture of how information is elaborated, stored and shared in the group and allows us to describe an observed switch of migratory path in fish populations as a result of a loss of group level information.
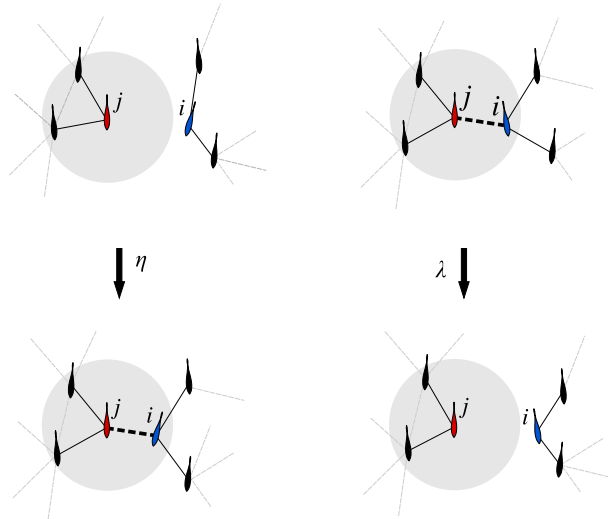

Figure 1: Connection between link creation and destruction process and real space models where η is the link creation rate and λ the link destruction rate.

2   Theoretical framework

Most studies about swarming phenomena in animal groups have relied on real space dynamical models [1]. Here, we address the issue of group formation using a network dynamical model [22, 23]. neighbouring nodes in the graph correspond to neighbouring individuals in space (Figure 1).

Let us consider a group with N individuals. In our network model each individual is represented by a node (thus N is the total number of nodes) and each node i has an internal dynamical variable a_i that can take integer values ranging from 1 to q. Although the mathematical solution does not depend on the specific interpretation of the variable a_i, in the context of migrating groups, a_i might be considered as the direction taken by a single individual to reach the destination site. Links between nodes represent interactions among individuals by which they influence each other in their choice of the destination. While space is not explicitly resolved we assume that neighbouring nodes in the graph correspond to neighbouring individuals in space (Figure 1). Yet nearby individuals need not necessarily influence each other (see below).

More precisely, a state of the system is defined by the adjacency matrix of the system g_{ij} and by the set of the internal dynamical states variables a_i. In our model, links are *mutual* and, thus, the adjacency matrix is a symmetric matrix (i.e. for all i, j we have that $g_{ij} = g_{ji}$) such that $g_{ij} = 1$ if there is a link between the nodes i and j, $g_{ij} = 0$ otherwise. The evolution of the system is governed by stochastic dynamics in

which both the neighbourhood and the values of the internal dynamical state may vary, according to stochastic Poissonian processes. These are discussed in the following (we refer the reader to the Supplementary Material for a detailed mathematical definition).

2.1 Network dynamics

The network evolves by creation and destruction of links, that mimic the spatial interaction between individuals. Link creation is quantified by the rate η at which individuals form new links with other individuals, This rate encodes both evolutionarily selected traits for pro-social behaviour and environmental factors, notably the average distance between individuals. In our model we assume that the interactions between individuals heading towards different directions decay much faster than interactions between close individuals heading towards the same direction. This is in agreement with real space dynamical model and is achieved in the network by assuming that link creation can occur only when individuals have the same internal state $a_i = a_j$. This is equivalent to saying that if $a_i \neq a_j$ the link between nodes decays immediately.

Finally, individuals linked and moving in the same direction can also move further apart from each other, which is formally encoded by assuming that links between nodes decay with a constant rate λ. These two processes provide a *mean field* description of the real space dynamics. Indeed link creation and decay depend on the geometry of the neighbourhood in spatially explicit models, which is averaged out within the mean field description. Mean field approximations such as this one work very well to capture the qualitative behaviour of complex systems. To set an analogy, in a gas, one does not need to trace the trajectory of each molecule. It is enough to provide a "collision integral", that loosely speaking gives the probability that a particle moving in a certain direction will interact with a particle moving in a different direction. Here we are taking the same approach.

2.2 Internal state dynamics

The change of the internal state is a Poissonian process that occurs with rate ν for each individual. The choice of the destination a_i is influenced by two factors: *i)* pro-social behaviour, by which an individual keeps the same destination of their neighbours and *ii)* memory, by which an isolated individual preferentially heads toward a destination α_i that is encoded in its memory.

More precisely, when an individual updates its internal state, *i)* if it is linked to other individuals(s), it will update its internal state conforming to the state of the majority in its neighbourhood; i.e., the new state a_i' is:

$$a_i' = \operatorname*{argmax}_x \left(\sum_j g_{ij} \delta_{x a_j} \right) \tag{1}$$

In this formula δ_{xy} is Kronecker delta function: i.e. if $x = y$, $\delta_{xy} = 1$, otherwise $\delta_{xy} = 0$. Again this rule is necessary within our mean field description of spatial interaction because if an individual were to chose a direction which is different from that of the (majority of the) group it is in, it would quickly move far apart and its links would decay.

On the other hand, *ii)* if an individual is isolated (not linked), its choice of the internal state is influenced by its preference for a destination that is encoded in their memory. More precisely, we assume that each individual has a preferred value of the

internal variable, let us call it α_i. In the case of an internal state update event, an unlinked individual will pick up a state according to the following probability distribution:

$$\text{Prob}(a_i = a) = \frac{e^{h_{\alpha_i} \delta_{a \alpha_i}}}{q - 1 + e^{h_{\alpha_i}}} \tag{2}$$

where h_{α_i} is a parameter that measures the intensity of the preference. This encodes, besides information processing and storage capabilities, also environmental factors related to the properties of a given feeding site, such as quantity of prey, water temperature, water quality etc.

The fraction of individuals with a preferred destination α is n^α but we also contemplate a fraction n^0 of "uninformed" individuals, that have no *a priori* preference for any memorized destination. We use the convention that uninformed individuals have $\alpha_i = 0$ and $h_{\alpha_i} = 0$. Therefore, uninformed individuals update their direction at random, which is described by Eq. (2) with $h_{\alpha=0} = 0$.

Previous network approaches used a voter model update rule instead of a majority rule [8, 20, 21]; this choice makes no qualitative difference in the stationary case, since our main results are based on a state space decomposition (see Supplementary Materials) that remains valid as long as the update rule promotes local uniformity. However, we expect detectable differences in the transient behaviour of these systems. Biologically, a majority rule captures the non-linearity of group behaviour.

As in spatially explicit models, in our description individuals compromise about directional choices. The majority rule does not prohibit that an individual i heading towards a given destination may change its route upon the encounter of another individual j. While this is not an elementary event described by the processes above, it can clearly occur as a composite event that entails the decay of all the links of i, an update of its choice and the formation of a link with j. The probability of this event is non-zero and it decreases with the number of individuals i is interacting with, as one expects.

In some cases individuals in groups need to compromise between information gathering from the environment and social cohesion of the group [9, 24] and thus some previous modelling approaches have assumed a trade-off between information capabilities and pro-social behaviour, in that informed individuals have a reduced tendency to follow their peers. The present modelling framework may be extended to encompass this situation also by making, for example η take different values for informed and uninformed individuals. This generalization of the model leads to the same conclusions as those discussed below but it comes at the cost of more complex mathematics. In addition, there is no conclusive evidence, as far as we are aware of, that such trade-off really exist in populations of fishes (see e.g. [5]). We have however checked that adding these trade-offs to the model is inconsequential as far as the main results of the model discussed here is concerned, that is why we discuss these aspects in the supplementary materials.

2.3 Invariant distribution

Given the above transition rates, we can write down the master equation (see the Supplementary Material) and derive the invariant distribution which describes the stationary state. One key observation in this is that, since only links between nodes with the same internal state can be established, the process will converge to states where all links (i, j) are between nodes with $a_i = a_j$. Any state with links (i, j) connecting nodes

with $a_i \neq a_j$ is transient, i.e. is not going to occur in the long run. This allows us to partition the states of the system into a transient class and a closed ergodic class. This ensures that the invariant distribution is *unique*. It can be shown (see Supplementary Materials for the details) that the process satisfies detailed balance and the probability to observe state with a given network $\{g_{ij}\}$ and profile of choices $\{a_i\}$ in the stationary state, is given by:

$$\pi(\{g_{ij}\}, \{a_i\}) = \frac{1}{\mathscr{Z}} \prod_{j<i} e^{\sum_i h_{\alpha_i} \delta_{a_i \alpha_i}} \left(\frac{2\eta \delta_{a_i a_j}}{\lambda(N-1)} \right)^{g_{ij}}. \tag{3}$$

where $\mathscr{Z}$ is the normalization constant. In particular, when, for some i and j we have that $a_i \neq a_j$ and $g_{ij} = 1$, the invariant distribution is zero. We are also assuming the convention that $0^0 = 1$.

Let $N_a^\alpha = \sum_j \delta_{a_j a} \delta_{\alpha_j \alpha}$ be the number of individuals that are in state a but would like to be in state α and let $n_a^\alpha = \frac{N_a^\alpha}{N}$.

If, in eq. (3), we call

$$z = 2\frac{\eta}{\lambda} \tag{4}$$

the non-dimensional parameter that accounts for the effective creation of links in the network, thus measuring the *sociality* of the group, then with standard mathematical manipulations (see Supplementary Materials) we can easily write the stationary state distribution in terms of the densities $\mathbf{n} = \{n_a^\alpha\}$ as follow:

$$p(\mathbf{n}) = \frac{1}{\mathscr{Z}} e^{-N\left[F(\mathbf{n};z,\mathbf{h}) + O(1/N) \right]} \tag{5}$$

where

$$F(\mathbf{n};z,\mathbf{h}) = \sum_a n_a^0 \log(n_a^0) + \sum_{a\alpha} n_a^\alpha \log(n_a^\alpha) - \sum_{a\alpha} h_\alpha n_a^\alpha \delta_{\alpha a} - \frac{z}{2} \sum_a (n_a)^2 \tag{6}$$

and $\mathscr{Z}$ is the normalization constant. In the large population limit ($N \to \infty$) this distribution peaks exponentially in N around the minima of F.

The stationary points of $F(\mathbf{n};z,\mathbf{h})$ satisfies the following system of equations:

$$n_a^\alpha = e^{h_\alpha \delta_{a\alpha} + z n_a} \frac{n^\alpha}{(e^{h_\alpha} - 1)e^{z n_\alpha} + \sum_a e^{z n_a}} \tag{7}$$

where $n_a = \sum_i n_a^i$ is the total density of individuals whose internal state is a (See Supplementary Materials for detailed calculation).

Therefore with a large number of individuals and in the stationary state of the system we are able to use Eq. (7) to analytically describe the fraction of individuals with *a priori* preference α that end up heading towards destination a.

This set of non-linear equations has many solutions in principle. Those corresponding to stationary states can be fully characterized in terms of the average degree of the network $\langle k \rangle$ (i.e. the average number of neighbours of individuals) that is a proxy for the school density. It can be shown that one measure of the network degree is $\langle k \rangle = z \left(1 - \frac{1}{q} \right) \sigma + \frac{z}{q}$ where the quantity:

$$\sigma = \frac{q \sum_i (n_i)^2 - 1}{q - 1}. \tag{8}$$

is a direct measure of the school efficiency and it takes values between $\sigma = 1$, when all individuals belong to a group that migrates towards the same destination; and $\sigma = 0$ when individuals distribute equally between different destinations. Hence the solution with high coordination ($\sigma \simeq 1$) also corresponds to high network densities $\langle k \rangle \simeq z$.

Among all the solutions of Eq. (7), we shall focus on those corresponding to the global minimum of $F(\mathbf{n}; z, \mathbf{h})$ that determine the behaviour of the system, since they correspond to the values around which the stationary distribution shall peak.

3   Results

We shall analyse two cases 1) the case of a population without informed individuals, $n^0 = 1$, and 2) the case where a fraction $n^1 = 1 - n^0$ of the individuals have a preferred migratory destination, whereas the rest is not informed.
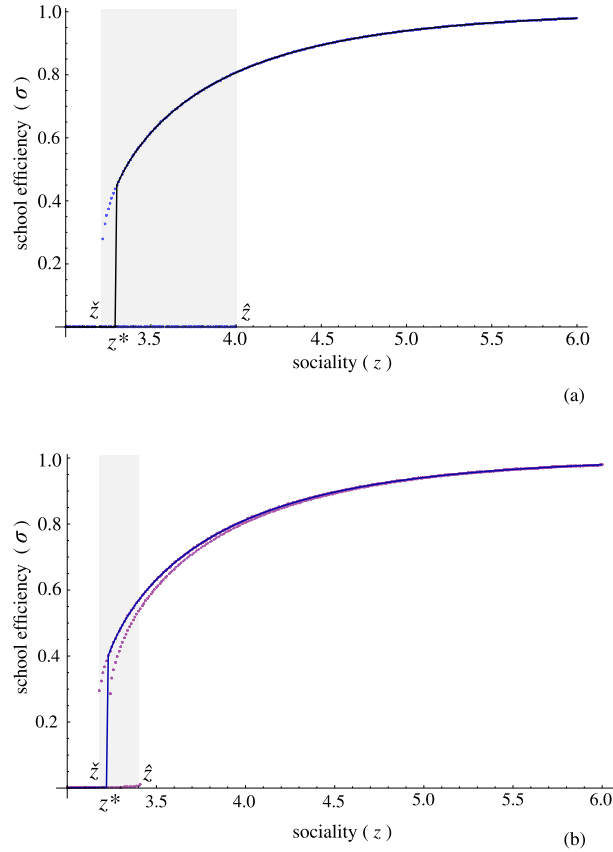

Figure 2: Critical group dynamic: school efficiency, σ as function of the social parameter z in (a) non informed group $n^1 = 0$ and (b) informed group $n^1 = 0.05$, $h = 0.5$. The dotted lines correspond to all the stable solutions of (7), the shadowed areas identify the coexistence region whereas the solid lines correspond to the equilibrium solution.

3.1 Migration without information

When no information is available in the group, the system reduces to an adaptive network model in which group coordination only depends on the rates at which links are created or destroyed [22, 23].

Below a certain threshold $\check{z}$ only one local minimum exists which corresponds to a symmetric solution $\sigma = 0$ (Figure 2 a); there the network is sparse, $\langle k \rangle < 1$, and the group does not migrate. At $\check{z}$, a new bundle of q local minima appears at which $\sigma > 0$. There the network is dense, $\langle k \rangle > 1$, and a fraction of the individuals comparable with N (called in graph theory *giant component*) is connected with one another and coordinated on the same destination choice.

The analysis also produces the full probability distribution of different states that allows ranking the solutions in terms of their probability (see Supplementary Materials). Between $\check{z}$ and $\hat{z}$ both solutions coexist and individuals can migrate in a coordinated manner or not. Above $\hat{z}$ the only local minima are for $\sigma > 0$ while the sparse solution $\sigma = 0$ becomes unstable. There is an intermediate point z^* below which the sparse solution is the most likely outcome whereas, above it, the high density solution will prevail.
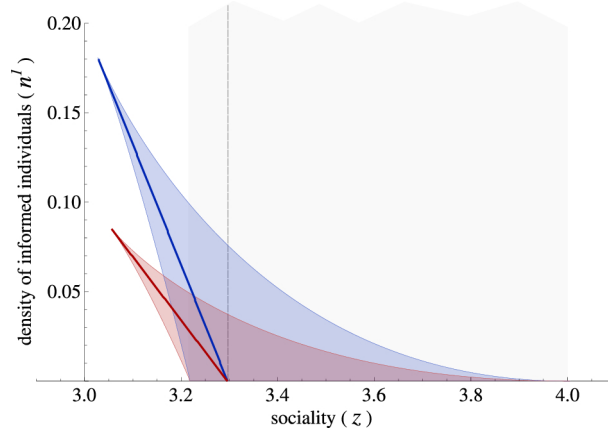

Figure 3: Phase diagram of the system with $q = 4$ possible directions. The grey area corresponds to a preference parameter $h = 0$ (no preferences) and the dashed line is the critical line. The blue area corresponds to $h = 0.5$ and the thick blue line represents the corresponding critical line. The red area corresponds to $h = 1$ and the thick red line represents the corresponding critical line as well.

3.2 Informed migration

In order to analyse the role of information in the model, we study the simplest possible case, with q destinations, a density of informed individual $n^1 = 1 - n^0$ and a preference h about a single destination.

The equation (7) again can be solved numerically to obtain prediction on schooling behaviour. Information has two main effects on the system (Figure 2 b). First, it breaks the symmetry between the q high density solutions found in the $n_0 = 1$ case, by selecting the solution with the preferred destination $\alpha = 1$ as the most likely. The $q - 1$

solutions corresponding to migration toward other destinations remain stable, but are much less likely to be selected by the population.

Secondly, the coexistence region between high and low density solutions $[\check{z}, \hat{z}]$ is reduced in the case of informed migration (Figure 2). In fact this region becomes smaller as the number of informed individuals increases (Figure 3).

Eventually, there exists a critical value of n^1 at which the region collapses into a point. This change in the behaviour of the system is equivalent to a second order phase transition in physics. For values of n^1 greater than this critical point the system has a smooth transition between low and high density states, as z increases, and a single solution is found. Moreover the coexistence region and the critical value change with h. The thick line in Figure 3 marks the point, in the coexistence region, where the two solutions are equally probable; on the right (left) of this line we expect to see the high (low) density solution.

The behaviour of the solution as the parameters h and $n^1 = 1 - n_0$ vary, at fixed z, is depicted in Figure 4. For low values of z (Figure 4a) we observe a smooth crossover from low to high density solutions as h and/or n_1 increase whereas when z is larger the system exhibits a sharp transition between the two solutions (Figure 4b). The presence of a sharp transition with coexistence in a broad range of parameters is a robust feature of this model.

For more complicated settings using competing groups with different preferred migratory destinations, it can be shown that, for large z the population coordinates towards the migratory destination that provides the largest product $n^\alpha h_\alpha$ (see Supplementary Materials). This quantity can be interpreted as the strength of the group's collective memory toward a given migration site, α.

This provides us with a vivid picture of how we expect the collective behaviour of the population to change when the parameters z, h and n_0 change. Adapting this picture to the observed behaviour of populations provides hints on the likely underlying causal effects. In brief, when z is large, i.e. for individuals with a marked pro-social behaviour, we expect abrupt transitions when either the density n^α of individuals with a given preference, or the intensity h_α of that preference varies in such a way as to cross the boundaries in the phase diagram (Figure 3).

When both the density of informed individuals and the intensity of preference h_α decrease, abrupt transition from efficient group formation to collapse of migration efficiency is visible. We note that this hysteresis cycle is consistent with observed stock collapses of migratory fish populations [25]. When the migratory population is described using a social parameter z close to the critical point, then the interplay between the memory for a given destination, h, and the fraction of the individuals informed, n^1 about this destination can produce an abrupt transition in the migration of the species.

In the case of a school migrating in direction 1, a decrease of the value of h and n^1 over years due, for example, to overfishing of both individuals and prey in the migration site, can force the system to cross the critical line reaching eventually low values of both h and n^1. When in this condition, an increase in the value of h might occur due for example to better habitat conditions or food availability, for those few vagrant fish that might still be present in the area. However this increase alone cannot bring the system back to the original state because the system may not cross again the critical line. Thus the group may not migrate in direction 1 even though previous habitat conditions are re-established.
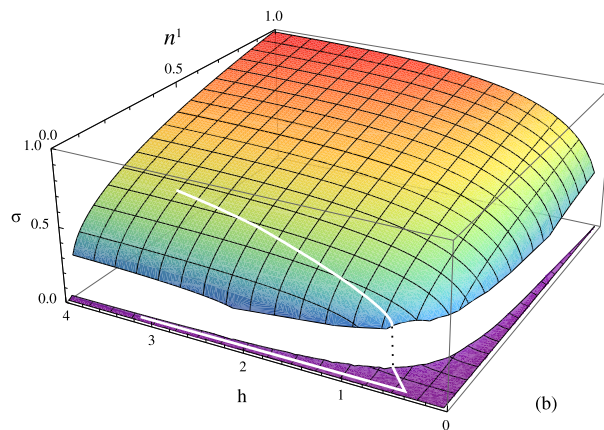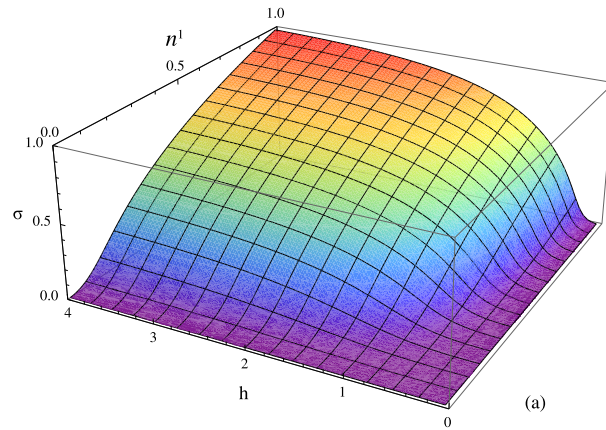
Figure 4: School efficiency σ as function of the fraction of informed individuals n^1 and strength of the preference h when the social parameter z is (a) in a non critical region $z = 2.5$ and (b) in a critical region $z = 3.1$ The white line in panel (b) is a schematic illustration of the hysteresis mechanism for a bluefin tuna population starting with high n^1 and h, then decreasing n^1 and h (overfishing of both preys and predators) and subsequently increasing h (increase of population of preys).

4 Discussion

We show that abrupt changes in migratory patterns of animal groups can be caused by removal of knowledgeable individuals from the group or by decreasing preference of the individuals towards a particular migratory destination.We demonstrate this with a robust analytical approach that allows to clearly identify the factors regulating group formation processes. Our results are consistent with previous models suggesting that a small number of informed individual can lead to large group migrations [14, 26]. Additionally we demonstrate that diminishing individual preference for a given migration site can preclude group formation and break the migration process.

4.1 The migration game

The migration process can be described as an emergent property of the population undertaking a group formation game: when the spatial density of fish is locally low, each individual moves independently, and the system is in a sparse network configuration with a value of z below the lower edge of the coexistence region. In this state uninformed individuals cannot migrate whereas informed individuals can undertake a *solitary* migration towards their preferred destination. Owing to external stimuli (water temperature, local currents, topography, etc.) the density may increase and so does the value of z, driving the system toward the coexistence region. In this region even though the local density of fish is high, a sparse network configuration with fish moving independently is still stable but an alternative and stable dense network configuration also appears. When the system reaches the upper edge of this region, further increasing the density, the sparse network state becomes unstable while the dense network state prevails and the school starts a migration toward the preferred destination. On the other hand an *hysteretic* cycle is present in this system and when the local density of fish decreases in the school, z, decreases and the system is driven back to the coexistence region. A similar effect can be reproduced in the system by lowering the preference factor, h. The schooling configuration remains stable until the system reaches the lower edge of the coexistence region: at this point, fish stop schooling and the system switches back into the sparse configuration (solitary fish).

The group formation game described above can be repeated each year naturally driving changes in the preference term h, hence in the memory of migratory fish. Likewise changes in this or in the other terms of the model may occur when the migratory population is affected by external stimuli , e.g., overfishing, habitat degradation, demographic fluctuations. Because of the hysteretic cycle, such variations may then result in *abrupt* changes in the migratory patterns.

4.2 Conflicting preferences

From the asymptotic analysis (Supplementary Materials) we demonstrate that, for large value of z, the group shall migrate toward the direction α for which the product $n^{\alpha}h_{\alpha}$ is maximal, whereas in the limit of small z, the sparse configuration is the only stable one. This suggest that our results might be extended to groups with conflicting preferences. It is relevant to note that in our model *all individuals* have a social component. For example in groups with conflicting preferences our model suggests that, for some range of the parameters, an informed individual can follow the group and migrate toward a site different from its preferred destination. This approach makes our definition of leaders not only dependent on the amount of information stored but also on the social

context in which they live. Therefore, the interaction between personal information and social effects is explicitly resolved in our model and—we note—it has been suggested to operate in living groups [5, 6].

4.3   Collective memory and breakdown of social traditions

Breakdown of social traditions, due to selected fishing on older informed individuals, has been hypothesized to have contributed to stock collapses in several large commercially important fish populations [13, 25].

Our sketch of the migration game suggests that social dynamics may lead to such collapses and that the integrity of migration pathways and spatial distributions of migratory predators might be particularly vulnerable to perturbations such as fishing or habitat degradation. Fishing out informed individuals and their prey can exacerbate the loss of collective memory up to the point where a migratory pathway is suddenly interrupted. We can assume that each year young individuals join the group: among them a fraction is able to gather information and remember a migratory route whereas the rest has a purely social behaviour. The "information-gathering-able" individuals behave as uninformed individuals ($h = 0$) but *learn* a new migratory route during the first migration(s). If the group does not succeed in starting migration, or migrates toward a different location, the young "information-gathering-able" individuals will not learn the traditional migration route of the group and the social traditions of the group will not be transmitted to the new generations. The loss of collective memory in the group will then force the system to cross the critical line and the migration toward the destination site will stop.

An example of a prey-predator collapse and subsequent abrupt disappearance of migratory route is provided by Atlantic bluefin tuna (*Thunnus thynnus* LINNAEUS, 1758) and its main prey, herring (*Clupea harengus* LINNAEUS, 1758) in the Norwegian and the North Seas. During the 1950s-1970s both species were heavily exploited in these regions resulting in the disappearances of both species [28–30]. Since then, the herring populations in both regions have recovered to moderate-high levels [28, 29], but bluefin tuna have been extremely rare during the 1980s-2000s and apparently had not migrated to these areas in large numbers since the disappearance several decades ago [30]. These hysteretic dynamics are consistent with a fishing-induced removal of predators having preference for migration to these regions and a fishing induced decline in habitat quality which then leads to the collapse of group formation and a sudden change in migratory path (cf. Figure 4).

5   Conclusions

We have presented a model that offers and elucidates a plausible mechanism for migration dynamics. By extending and generalizing previous approaches, our model shows that group formation dynamics have a critical dependence on both sociality, number of informed individuals and strength of the preference in informed individuals. For example, partial removal of knowledgeable individuals may be sufficient to interrupt the transmission of social traditions in groups of animals. Such critical dependence is consistent with abrupt transitions that are commonly observed in migration patterns of social animals such as Atlantic bluefin tuna as well as other fish populations [25].

Our findings offer deep insight into migration dynamics and suggest interesting directions both for data analysis (e.g. new interpretations of spatial temporal dynam-

ics of migratory populations) and for further theoretical development (e.g. accounting for conflicting preferences, continuous directions, different segregation policies, topological interaction). Contrary to previous Agent Based approaches [1, 15, 17–19], our model has the advantage of being analytically soluble, and thus it provides a powerful theoretical bench test for hypotheses on collective animal behaviour.

Acknowledgements

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A Supplementary materials

In these supplementary materials we provide the details of the technical calculation that are presented in the main paper and provide additional comments and details.

In the first section we detail the definition of the model. In the following section we comment on the interpretation of the parameters in terms of fish migratory behaviour. The third section contains a detailed derivation of the stationary state distribution (the invariant measure), equations (6) of the paper. From this we derive the population distribution Eq. (8).

This is then analysed in the limit of large populations (the thermodynamic limit) leading to the expression of the free energy (9) of main paper. Finally we provide details on the calculation of the equilibrium solution (10) of main paper, and of other results cited in the main paper.

A.1 Mathematical definition of the model

Let N be the number of individuals in the group and q the number of possible values for that the internal variable can take (i.e. the possible directions a fish may take).

For any finite N and q, a *state* of the system is defined by the network of interaction between individuals and by the values of the internal variables of the individuals. The processes described in the main text define a stochastic dynamics on this state space. For example, when a link is created between two individuals i and j the system will make a *transition* between a state in which the network of interaction has no link between i and j and a state in which the link between i and j is added. We use the letter ω to generically refer to a state, i.e. $\omega = (G, \mathbf{a})$ where G is the $N \times N$ adjacency matrix of the system (i.e. $(G)_{ij} = g_{ij} \in \{0, 1\}$), and $\mathbf{a} = (a_i)$ is a vector whose i-th component is the values of the internal variable of i-th node. We also use $\mathscr{S}$ to refer of all the possible states in which the system can be (i.e. the state space). $\hat{\omega}(t)$ represents the state of the system at time t which shall be equal to one of the states described above. Mathematically, our system is *a Continuous Time Markov Chain* and therefore, its evolution over time is described by a Master Equation for the probabilities:

$$\partial_t P(\omega, t) = \sum_{\omega'} P(\omega', t) \rho(\omega' \to \omega) - P(\omega, t) \sum_{\omega'} \rho(\omega \to \omega') \tag{9}$$

where

$$P(\omega, t) = \mathrm{Prob}(\hat{\omega}(t) = \omega); \tag{10}$$

and the ρ are the transition rates which correspond to the three dynamical processes described in Methods Section of the main paper. For clarity sake we describe them again here.

link creation With a rate η each node i can establish a link with another j node picked up randomly among the others. The link is established only if $a_i = a_j$

This process can connect only two states ω and ω' such that $g_{hk} = g'_{hk} \ \forall \ (h, k) \neq (i, j)$, $g_{ij} = 0$ and $g'_{ij} = 1$. The transition rate is clearly

$$\rho(\omega \to \omega') = \frac{2\eta}{N-1} \delta_{a'_i a'_j} \tag{11}$$

link destruction Each link ha a destruction rate λ.

This process can connect only two states ω and ω' such that $g_{hk} = g'_{hk} \ \forall \ (h,k) \neq (i,j)$, $g_{ij} = 1$ and $g'_{ij} = 0$. The transition rate is clearly

$$\rho(\omega \to \omega') = \lambda \qquad (12)$$

preference update Each node can update its internal state at a rate ν.

If the node is linked when an internal state update event occurs, it will conform to its neighbourhood. When an internal state update event occurs for a linked individual i, thus, the new internal state of that individual a'_i is chosen using a *majority rule*, that is :

$$a'_i = \underset{x}{\operatorname{argmax}}\left(\sum_j g_{ij}\delta_{xa_j}\right) \qquad (13)$$

This assumption is coherent with what is usually done in modelling group motion that is assuming that an individual tend to "follow" its neighbours.

Instead, when a node is not linked, it undergoes a random transition to a state a'_i; the probability of picking up one direction over another encodes the *a priori* information the individual has. Each individual has a direction preference α_i. If $\alpha_i = 0$ then each direction has the same probability($\frac{1}{q}$) of being chosen (no *a priori* information); if $\alpha_i \in \{1,...,q\}$ than the i-th individual has a higher probability of picking the direction α_i over the others. In mathematical term, this can be written as:

$$\operatorname{Prob}(a'_i = a) = \frac{e^{h_{\alpha_i}\delta_{a\alpha_i}}}{q - 1 + e^{h_{\alpha_i}}}, \quad g_{ij} = 0 \ \forall j \qquad (14)$$

where $h_{\alpha_i} > 0$ measure the strength of the preference of node i for the direction α_i. We assume that the strength of the preferences h_α does not vary among the individuals that share the same direction preference but may be different for individuals preferring different directions.

All other transition besides the three classes discussed above, have zero rates.

The model can be generalized in different ways. In particular, the creation rate η^α can be taken to depend on whether individuals are informed ($\alpha > 0$) or not ($\alpha = 0$). In general, if the propensity for forming social links among fishes with preferred direction α is η^α, then this more general model entails substituting 2η with $\eta^{\alpha_i} + \eta^{\alpha_j}$ in (11). This reflects the fact that the creation of the link between i and j may be initiated by either i or j an hence their rates add.

For the sake of simplicity, we shall focus our discussion to the case $\eta^\alpha = \eta$ for all $\alpha = 1,\ldots,q$. Indeed, the derivation proceeds along exactly the same lines and the gist of the main results is the same. We shall deal with the general case in Section A.7.

A.2 Interpretation of the parameters of the model

Our theoretical framework is a stylised representation of the migratory behaviour of fish populations. The three parameters of the model have a clear interpretation in terms of biological traits of the individuals and of the physical conditions of the environment in which they interact.

The value of η must have a dependence on the density of individuals; most of the real space models assume that individuals interact only with "close" individuals (e.g. closer than a certain radius) which is a reasonable description of the natural behaviour

of schooling fishes; thus if the local density of individuals is too low the probability of being close enough to interact with one another is small and thus the link creation rate must also be small; on the contrary the higher the density, the higher the number of "close" individuals and the higher the creation rate must be. At the same time, η quantifies also the pro-social behavior of individuals which is encoded in the genetic make-up of the species. A social fish is expected to be able to interact with other individuals of its species more effectively than a fish of a non social species: by the rules of our model, this means that at a given local density of individuals the social species will have a significantly higher link creation rate η and lower link destruction rate λ and thus a higher value of their ratio $z = \eta/\lambda$. A variation of local density may induce even significant variation of η and therefore of z. The range of these variations,however, may be seen as a *genetically determined quantity*.

The interpretation of the other parameters is easier, the value of n^α is the relative proportion of individuals in the population with preference for destination α; the value of h_α implicitly measures the strength of the preference, which in turn may encode the property of a given feeding site, such as quantity of prey, water temperature, water quality etc.

A.3 Master Equation and Invariant Measure

The derivation of the stationary state distribution, which is the solution of Eq. (9) with $\partial_t P(\omega,t) = 0$, relies on the following observations:

1. the states of the system can be classified into two sets: one $\mathscr{A}$ that contains all the states in which the network *does not contain links between different nodes – i.e. nodes that have different value of their internal variable* – and $\mathscr{T}$ containing all the states in $\mathscr{S}$ that are not in $\mathscr{A}$. In particular the states for which the network has no links are in $\mathscr{A}$;

2. transition from any state $\omega' \in \mathscr{A}$ to any state in $\omega \in \mathscr{T}$ are impossible since the rates vanish

$$\rho(\omega \to \omega') = 0, \qquad \forall \omega' \in \mathscr{A}, \ \text{and} \ \forall \omega \in \mathscr{T}. \tag{15}$$

In words, link between nodes i and j with different internal variables $a_i \neq a_j$ cannot be generated in the course of the dynamics.

3. If any such link exists at a given time t, then *i)* it must be present in the initial conditions and *ii)* it has a finite life time, because any link decays at a rate λ.

4. As a consequence, the dynamics sooner or later reaches a state $\omega \in \mathscr{A}$ where no link between different nodes exists, and from that time onwards states $\omega' \in \mathscr{T}$ where at least one link between different nodes exists, will never be reached. In formal terms, this means that states $\omega \in \mathscr{T}$ are transient and therefore they occur with zero probability in the stationary state

$$\lim_{t \to \infty} P(\omega,t) = 0, \qquad \forall \omega \in \mathscr{T}. \tag{16}$$

5. it is possible to reach any state in $\mathscr{A}$ starting from any state in $\mathscr{A}$. More precisely, for any two states $\omega, \omega' \in \mathscr{A}$ it is possible to find a sequence of transitions between intermediate states connecting ω to ω', with each transition having a positive probability. One such "path" of transitions, for example" is the one where first all the

links in the initial state ω decay, then the internal variables of each node is updated from the one prevailing in state ω to the one in ω', and finally all the links in state ω' are sequentially added. Each of the intermediate states ω'' along this path is also in $\mathscr{A}$ and each transition between consecutive states on the path occurs with a strictly positive rate. Since the number of states on the path is finite, this means that the probability $P\{\hat{\omega}(t) = \omega | \hat{\omega}(t_0) = \omega'\}$ to find the system in ω at time t given that it was in state ω' at an earlier time $t_0 < t$ is strictly positive.

6. Since the process can reach any state in $\mathscr{A}$ from any other state in $\mathscr{A}$ this proves that the dynamics is *ergodic* when restricted to $\mathscr{A}$. This implies that the stationary state exists and is unique (see e.g. [2]).

7. it is easy to verify, by direct substitution, that the probability distribution

$$\pi(\omega) = \frac{1}{\mathscr{Z}} \begin{cases} e^{\sum_i h_{\alpha_i} \delta_{a_i \alpha_i}} \prod_{j<i} \left(\frac{2\eta}{\lambda(N-1)} \right)^{g_{ij}} & \omega \in \mathscr{A} \\ 0 & \omega \in \mathscr{T} \end{cases} \tag{17}$$

where $\mathscr{Z}$ is the normalization constant ensuring $\sum_\omega \pi(\omega) = 1$, satisfies the detailed balance condition

$$\pi(\omega)\rho(\omega \to \omega') = \pi(\omega')\rho(\omega' \to \omega). \tag{18}$$

Indeed, for each ω, ω' for which $\rho(\omega \to \omega') = 0$ we have either that $\rho(\omega' \to \omega) = 0$ also or that $\rho(\omega' \to \omega) > 0$ but $\omega' \in \mathscr{T}$, and therefore Eq. (18) holds because $\pi(\omega') = 0$. When both $\rho(\omega \to \omega') > 0$ and $\rho(\omega' \to \omega) > 0$, then either $\omega, \omega' \in \mathscr{T}$ and then Eq. (18) holds because $\pi(\omega) = \pi(\omega') = 0$, or $\omega, \omega' \in \mathscr{A}$. In the latter case ω differs from ω' either for the presence of one link or for the value of the internal variable of a single isolated node. In both cases, one can check that Eq. (18) holds. This means that if $P(\omega, t) = \pi(\omega)$ then $\partial_t P(\omega, t) = 0$, i.e. $\pi(\omega)$ is a stationary distribution of the process.

8. Since the stationary state is unique we conclude that

$$\pi(\omega) = \lim_{t \to \infty} P(\omega, t) \tag{19}$$

is the invariant distribution.

The fact that a process satisfies detailed balance is related to the existence of a potential function $\mathscr{H}(\omega) = -\log \pi(\omega)$ such that each transition can be interpreted as either "climbing" or "descending" the landscape of $\mathscr{H}$. In order to gain intuition on why the process satisfies detailed balance one can argue that such a function $\mathscr{H}$ exists for this process. Indeed, notice that the process links states which differ by one link (with the profile **a** of nodes' variables constant) or states with the same graph G, which differ only by the attribute a_i of a single isolated node. In the fist case, the transition rate is the same, so the process, at fixed **a**, can be described as "climbing" or "descending" a step of a function $\mathscr{H}$ that depends only on the number of links added. In the second case, the dynamics of **a** at fixed G involve rates that depend only on whether a node is updated so that his attribute a_i equals the preferred value α_i or not. This can be captured by a potential $\mathscr{H}$ that takes two different values depending on whether $a_i = \alpha_i$ or not.

We note that $\pi(\omega)$ is the invariant distribution under a broader set of choices of the internal state update rule. Indeed Eq. (13) can be replaced by any rule by which

the choice of the internal state a_i' is limited to the values a_j of the neighbours of node i. For example, if Eq. (13) is replaced by a rule where node i takes the value a_j of a randomly chosen neighbour j, as in the voter model, the process converges to the same invariant distribution π. This is because once the process reaches a state $\omega \in \mathscr{A}$, the link creation/destruction policy ensures that local uniformity that characterizes states in $\mathscr{A}$ will be preserved.

We may expect, however, that the choice of the internal state update rule may influence the transient behaviour of the system (e.g. average time to reach the stationary state, structure of the metastable states).The analysis of those behaviour, albeit very interesting, is beyond the scope of this work.

A.3.1 The population distribution

In order to take the thermodynamic limit we need to obtain an expression in which the number of nodes N is explicit. That is we need to infer from the invariant measure (17) an expression for the probability distribution function of the populations involved.

Let's consider a partition of the entire population (i.e. the number of nodes) N into classes. Let $N_a^\alpha = |\{i|(a_i = a) \wedge (\alpha_i = \alpha)\}|$ be the number of nodes with preferred state α that are in the state a. Moreover we define a class of uninformed individuals and define $N_a^0 = |\{i|(a_i = a) \wedge (\alpha_i = 0)\}|$ as the number of nodes with state a that have no preference (i.e. $\alpha = 0$). We denote by $\mathbf{N} = \{N_a^\alpha, a = 1, \ldots, q, \alpha = 0, 1, \ldots, q\}$ the profile of population occupation states. Obviously

$$\sum_{a,\alpha} N_a^\alpha + \sum_a N_a^0 = N \tag{20}$$

We define $\hat{\Omega}(\mathbf{N}) = \{\omega \in (G, \mathbf{a}) : (|\{j : (a_j = a) \wedge (\alpha_j = \alpha)\}| = N_a^\alpha) \wedge (\{j : (a_j = a) \wedge (\alpha_n = 0)\}| = N_a^0)\}$ as the subset of states ω with profile $\mathbf{N}$. The probability to observe $\mathbf{N}$ is clearly given by

$$p(\mathbf{N}) = \pi(\hat{\Omega}(\mathbf{N})) = \sum_{\omega \in \hat{\Omega}(\mathbf{N})} \pi(\omega). \tag{21}$$

For sake of simplification we shall use the following notation: $N_a = \sum_\alpha N_a^\alpha + N_a^0$ which denotes the number of nodes in actual state a, $N^\alpha = \sum_a N_a^\alpha$ which denotes the number of nodes with preferred state α, $N^0 = \sum_a N_a^0$ which denote the number of uninformed nodes. Clearly N^α, N^0 are known and fixed.

For each configuration of the internal variables, the equilibrium dynamics allows $\sum_a 2^{\frac{N_a(N_a-1)}{2}}$ different network configurations with non-zero probability. The weight of all network structures with a given number m_a of links in a given preference class is the same (since only networks with links between coordinated nodes carry non zero contribution). Calculating their contribution to $p(\mathbf{N})$ reduces to counting how many different network structure are there with a given number of links m_a in each component a. The answer is trivially $\binom{\binom{N_a}{2}}{m_a}$ The network contribution to $p(\mathbf{N})$ is then

$$\sum_{m_1, \ldots, m_q} \prod_{a=1}^q \binom{\binom{N_a}{2}}{m_a} \left[\frac{2\eta}{\lambda(N-1)}\right]^{m_a} = \prod_a \left[1 + \frac{2\eta}{\lambda(N-1)}\right]^{\binom{N_a}{2}} \tag{22}$$

Concerning the statistical weight coming from individual preferences, we notice that:

$$\sum_i h_{\alpha_i} \delta_{a_i \alpha_i} = \sum_\alpha h_\alpha \sum_i \delta_{\alpha_i, \alpha} \delta_{a_i \alpha} = \sum_\alpha h_\alpha N_\alpha^\alpha$$

Thus this results in a statistical weight given by $\exp(\sum_a h_a N_a^a)$.

In order to compute $p(N)$ we notice that there are exactly $\frac{N!}{\prod_a N_a^0! \prod_{a\alpha} N_a^{\alpha}!}$ configuration with the same weight and thus we can write

$$p(\mathbf{N}) = \frac{1}{\mathscr{Z}} \frac{N!}{\prod_a N_a^0! \prod_{a\alpha} N_a^{\alpha}!} e^{\sum_\alpha h_\alpha N_\alpha^\alpha} \prod_a \left[1 + \frac{2\eta}{\lambda(N-1)} \right]^{\frac{N_a}{2}(N_a-1)} \tag{23}$$

Where $\mathscr{Z}$ is the normalization constant.

The measure is defined over the multisymplex defined by:

$$0 \le N_a^\alpha \le N^\alpha \tag{24}$$

and

$$\sum_a N_a^\alpha = N^\alpha \tag{25}$$

A.4   Thermodynamic limit and equilibrium solution

Once we have a form for the $p(\mathbf{N})$ we look for the asymptotic behavior for large N.

Let us denote the densities with $n_a^\alpha = \frac{N_a^\alpha}{N}$ and consequently $n_a = \sum_\alpha n_a^\alpha$ and $n^\alpha = \sum_a n_a^\alpha$ for $\alpha = 0, 1, \ldots, q$ and $a = 1, \ldots, q$.

Next, we expand $\log p(\mathbf{N})$ in a large N limit, using Stirling approximation($\log(N!) \simeq N\log(N) - N$, $\log(1+x) \simeq x$ for small x and normalization :

$$\sum_a n_a^\alpha = n^\alpha. \tag{26}$$

We then obtain :

$$\log(p(\mathbf{N})) = N\log(N) - N - \sum_{a\alpha}(Nn_a^\alpha \log(N) + Nn_a^\alpha \log(n_a^\alpha) - Nn_a^\alpha)$$

$$+ N\sum_{a\alpha} h_\alpha \delta_{a\alpha} n_a^\alpha + N\frac{\eta}{\lambda}\sum_a \left(\frac{N}{N-1}(n_a)^2 + \frac{N}{N-1}\frac{1}{N}n_a \right) - \log \mathscr{Z} \tag{27}$$

$$= -N\left[\sum_{a\alpha} n_a^\alpha \log(n_a^\alpha) - \sum_{a\alpha} h_\alpha n_a^\alpha \delta_{a\alpha} - \frac{\eta}{\lambda}\sum_a (n_a)^2 + O(1/N) \right] - \log \mathscr{Z}$$

This expression is reminiscent of Gibbs distribution in statistical physics

$$p(N) = \frac{1}{\mathscr{Z}} e^{-N\left[F(\mathbf{n}; \frac{\eta}{\lambda}, h) + O(1/N) \right]}. \tag{28}$$

where the *free energy* is given by

$$F(\mathbf{n}; \frac{\eta}{\lambda}, \mathbf{h}) = \sum_a n_a^0 \log n_a^0 + \sum_{a\alpha} n_a^\alpha \log(n_a^\alpha) - \sum_{a\alpha} h_\alpha n_a^\alpha \delta_{\alpha a} - \frac{\eta}{\lambda}\sum_a (n_a)^2 \tag{29}$$

In the limit of very large N the invariant measure concentrates on the global minimum $\mathbf{n}^*$ of the function $F(\mathbf{n}; \frac{\eta}{\lambda}, h)$. Any state $\mathbf{n}$ with a value of F that is larger by δF than the minimum, will have a probability $p(\mathbf{n}) \sim e^{-N\delta F}$ which is exponentially small compared to $\mathbf{n}^*$, i.e. will virtually never occur for large N.

A.4.1 Minimization of Free Energy

We then have to minimize the free energy $F(\mathbf{n}; \frac{\eta}{\lambda}, \mathbf{h})$ of the system, over the variables $\mathbf{n}$ subject to the constraints:

$$n^\alpha = \sum_a n_a^\alpha \tag{30}$$

and

$$n^0 = \sum_a n_a^0 \tag{31}$$

We introduce then Lagrange multiplier $\beta_\alpha - 1$ for the first constraints and $\beta_0 - 1$ for the second one and impose first order conditions (FOC):

$$\nabla \left\{ F(\mathbf{n}; \frac{\eta}{\lambda}, \mathbf{h}) - \sum_\alpha (\beta_\alpha - 1) \left[-n^\alpha + \sum_a n_a^\alpha \right] - (\beta_0 - 1)(n^0 - \sum_a n_a^0) \right\} = 0 \tag{32}$$

obtaining

$$\log(n_a^0) - \frac{2\eta}{\lambda} n_a - \beta_0 = 0 \tag{33}$$

and

$$\log(n_a^\alpha) - h_\alpha \delta_{a\alpha} - \frac{2\eta}{\lambda} n_a - \beta_\alpha = 0 \tag{34}$$

and thus

$$\begin{cases} n_a^0 = e^{\frac{2\eta}{\lambda} n_a} e^{\beta_0} \\ n_a^\alpha = e^{h_\alpha \delta_{a\alpha} + \frac{2\eta}{\lambda} n_a} e^{\beta_\alpha} \end{cases} \tag{35}$$

If we define :

$$Q = \sum_a e^{z n_a} \tag{36}$$

we can write

$$n^0 = e^{\beta_0} Q \tag{37}$$

and

$$n^\alpha = e^{\beta_\alpha} e^{\frac{2\eta}{\lambda} n_\alpha} (e^{h_\alpha} - 1) + e^{\beta_\alpha} Q \tag{38}$$

Equation (37) allows us to eliminate one Lagrangian multiplier:

$$e^{\beta_0} = \frac{n^0}{Q} \tag{39}$$

Equation (38) instead allows us to eliminate the quantity

$$e^{\beta_\alpha} = \frac{n^\alpha}{(e^{h_\alpha} - 1) e^{\frac{2\eta}{\lambda} n_\alpha} + Q} \tag{40}$$

We then have also the normalization constraint:

$$\sum_i n^i = 1 - n^0. \tag{41}$$

We can then write the FOC for our system in the following way

$$\boxed{n_a = e^{\frac{2\eta}{\lambda} n_a} \left[\frac{n^0}{Q} + W + \frac{(e^h - 1) n^a}{(e^h - 1) e^{\frac{2\eta}{\lambda} n_a} + Q} \right]} \tag{42}$$

where

$$Q = \sum_{i=1}^{q} e^{\frac{2\eta}{\lambda} n_i} \tag{43}$$

and

$$W = \sum_{i=1}^{q} \frac{n^i}{(e^{h_i} - 1)e^{\frac{2\eta}{\lambda} n_i} + Q} \tag{44}$$

These equations can be solved numerically to any preassigned degree of precision.

A.5 The $n^1 = 1 - n^0$ case

When we consider systems where only one direction is preferred, some simplification can be made.

To ease the notation we shall write $z = \frac{2\eta}{\lambda}$, $x = n_1$ and $y_i - 1 = n_i$ for $i \in \{2, .., q\}$.

In this case equation (42) take the simplified form:

$$\begin{cases} xe^{-x} = z\frac{n^0}{Q} + ze^h \frac{1-n^0}{(e^h-1)e^x+Q} \\ y_i e^{-y_i} = zP = z\frac{n^0}{Q} + z\frac{1-n^0}{(e^h-1)e^x+Q} \quad \text{q-1 times} \end{cases} \tag{45}$$

with the conditions

$$x + \sum_{i=0}^{q-1} y_i = z \tag{46}$$

$$Q = e^x + \sum_{i=0}^{q-1} e^{y_i} \tag{47}$$

and

$$P = \frac{n^0}{Q} + W = \frac{n^0}{Q} + \frac{1-n^0}{(e^h-1)e^x+Q}. \tag{48}$$

Solving equation (48) with respect e^x, calling $\Gamma = PQ = n^0 + WQ$ we get:

$$\frac{e^x}{Q} = \frac{1-\Gamma}{\Gamma - n^0} \frac{1}{e^h - 1} \tag{49}$$

and thus, plugging it in the first equation of (45), we obtain:

$$x = \frac{z}{e^h - 1} \frac{1-\Gamma}{\Gamma - n^0} \left[(1 - e^h)n^0 + e^h\Gamma \right] \tag{50}$$

Plugging the previous result in (49), we get Q. On the other hand form equation 1 in (45) we obtain

$$\frac{1-n^0}{(e^h-1)e^x+Q} = P - \frac{n^0}{Q} \tag{51}$$

plugging everything in equation (45) we obtain the following system of equations written in term of Γ :

$$\begin{cases} xe^{-x} = \frac{z}{e^h-1} \left[(1-e^h)n^0 + e^h\Gamma \right] \frac{1-\Gamma}{\Gamma-n^0} e^{-\frac{z}{e^h-1} \frac{1-\Gamma}{\Gamma-n^0} \left[(1-e^h)n^0 + e^h\Gamma \right]} \\ ye^{-y} = \frac{z}{e^h-1} \Gamma \frac{1-\Gamma}{\Gamma-n^0} e^{-\frac{z}{e^h-1} \frac{1-\Gamma}{\Gamma-n^0} \left[(1-e^h)n^0 + e^h\Gamma \right]} \quad \text{q-1 times} \end{cases} \tag{52}$$

From previous equation (52) we can infer the structure of the solutions.

Both equations have the same shape:

$$xe^{-x} = c \tag{53}$$

where c is a constant to be determined auto-consistently.

If c is negative the equation has only one negative (thus unphysical) solution, if c is greater than e^{-1} it has no solution otherwise it admits solution which can be expressed in terms of Lambert W functions [1]:

$$x_- = -W_0(-c) \tag{54}$$

and

$$x_+ = -W_{-1}(-c) \tag{55}$$

where W_0, W_{-1} represents the two real branches of Lambert W function (using the notation of [1]). It is trivial to check $x_- < 1$ whereas $x_+ > 1$ and that for small values of c, $x_+ > z$ and thus is to be discarded.

In our case c is a complicate function of Γ but, as above, once Γ (and z) is fixed we know that x and y can take only two values $x_\pm$ and $y_\pm$ as defined above and thus we can label all the solutions using two integers α which counts the number of x in + state (which of course is either 0 or 1) and L_+ which counts the number of y in + state.

If we define, for notational ease:

$$B(\Gamma) = \frac{z}{e^h - 1} \Gamma \frac{1-\Gamma}{\Gamma - n^0} e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]} \tag{56}$$

and

$$A(h,\Gamma) = \left[(1-e^h)n^0 + e^h\Gamma\right] \tag{57}$$

it is easy to check that solutions have the following hierarchy in the admissible range $\Gamma \in [n^0, 1]$:

$$y_-(A(0,\Gamma)B(\Gamma)) \le x_-(A(h,\Gamma)B(\Gamma)) \le 1 \le x_+(A(h,\Gamma)B(\Gamma)) \le y_+(A(0,\Gamma)B(\Gamma)) \tag{58}$$

The normalization equation (46) will then become, given integers α and L_+:

$$
\begin{aligned}
&\alpha x_+ \left(\frac{z}{e^h-1}\left[(1-e^h)n^0+e^h\Gamma\right]\frac{1-\Gamma}{\Gamma-n^0}e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]}\right) \\
&+(1-\alpha)x_-\left(\frac{z}{e^h-1}\left[(1-e^h)n^0+e^h\Gamma\right]\frac{1-\Gamma}{\Gamma-n^0}e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]}\right) + \\
&L_+y_+\left(\frac{z}{e^h-1}\Gamma\frac{1-\Gamma}{\Gamma-n^0}e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]}\right) \\
&+(q-1-L_+)y_-\left(\frac{z}{e^h-1}\Gamma\frac{1-\Gamma}{\Gamma-n^0}e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]}\right) = z.
\end{aligned} \tag{59}
$$

Its solutions will give the Γ auto-consistently.

Since the previous substitution is valid only when (50) is assumed we can rewrite the equation as:

$$
\boxed{
\begin{aligned}
&L_+y_+\left(\frac{z}{e^h-1}\Gamma\frac{1-\Gamma}{\Gamma-n^0}e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]}\right) \\
&+(q-1-L_+)y_-\left(\frac{z}{e^h-1}\Gamma\frac{1-\Gamma}{\Gamma-n^0}e^{-\frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]}\right) \\
&=z - \frac{z}{e^h-1}\frac{1-\Gamma}{\Gamma-n^0}\left[(1-e^h)n^0+e^h\Gamma\right]
\end{aligned}
} \tag{60}
$$

A.5.1 Stability

When $n^\alpha = 1 - n^0$ all the values $n_a^\alpha = 0$ for $\alpha > 1$ because of the normalization constraints; the Lagrangian function, thus, becomes (here $z = 2\frac{\eta}{\lambda}$):

$$L(\mathbf{n}; z, \mathbf{h}) = (\beta_1 - 1)\left(n^1 + \sum_a n_a^1\right) - (\zeta_0 - 1)(n^0 - \sum_a n_a^0) - h_1 n_1^1$$
$$+ \sum_a n_a^0 \log(n_a^0) + n_a^1 \log(n_a^1) - \frac{z}{2}(n_a)^2 \tag{61}$$

To check the stability and the nature of these stationary points we have to check the Hessian L of the Lagrangian restricted to the tangent space $\mathcal{T}$ to the constraints manifold in the stationary point.

The stationary point will be a (local minimum) if and only if:

$$\mathbf{y}^T L \mathbf{y} > 0 \text{ for any } \mathbf{y} \in \mathcal{T} \tag{62}$$

In our case the constraint are linear; therefore the tangent space $\mathcal{T}$ is a $2q - 2$ dimensional space and it can be easily seen to be spanned by the orthonormal base:

$$(\mathbf{e}_i)_j = \frac{1}{\sqrt{2}}(\delta_{ij} - 2\delta_{2q+1+j \pmod 2, j}) \tag{63}$$

where $i \in \{1, .., 2q\}$ and $j \in \{1, .., 2q+2\}$. The projection operator then is given by the matrix

$$M_{ij} = (\mathbf{e}_i)_j \tag{64}$$

Any vector $\mathbf{y}$ of $\mathcal{T}$ can be expressed by a general vector $\mathbf{v}$ of $\mathbb{R}^{2q}$ as $\mathbf{y} = M\mathbf{v}$. Equation (62) can be then expressed as:

$$\mathbf{v}^T M^T L M \mathbf{v} > 0 \tag{65}$$

Thus in order to check the stability of a stationary point in the constrained problem we can simply apply the usual Hessian criteria to the "effective Hessian $H_{\text{eff}} = M^T L M$

A.6 Asymptotic Expansion of the solutions of FOC for $z \to \infty$

In the case of $z \to \infty$ case it is easy to see that the minimum of $F(\mathbf{n}; \frac{\eta}{\lambda}, \mathbf{h})$ must correspond to states $\mathbf{n}_a^*$ corresponding to $n_a = 1$ and $n_b = 0$ for $a = 1, \ldots, q$ and $\forall b \neq a$.

In order to gain some insight on which of these solutions is the true minimum of the free energy for large but finite z we have to make and asymptotic expansion around $z = \infty$.

An asymptotic expansion of $n_a(z)$ can be derived from equation (42) for large z. It is easy to verify that the leading correction is extremely small, i.e.

$$n_b(z) \simeq \delta_{ab} + O(e^{-z}) \tag{66}$$

The detailed calculation of the leading order correction is carried out in Ref. [3]. Here we remark that *i)* given the size of the correction, the asymptotic limit is representative also of the regime where z is only moderately large. *ii)* the free energy for z large is approximately given by

$$F \simeq -\frac{z}{2} + \sum_{b=0}^{q} n^b \log(n^b) - n^a h_a + z e^{-z}\left(-n^a h_a e^{h_a} + \sum_{b \neq a} n^b h_b e^{h_b}\right) + o(e^{-z}). \tag{67}$$

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For this expression it is clear that the global minimum for large z is the solution with the maximum $n^a h_a$. In the case in which two or more direction have the same value of $h_i n^i$ the solution with the bigger value of h_i will prevail.

A.7 Tradeoff

Let us now discuss the generalization of the above results to cases where informed individuals might be *less social* then their co-specific uniformed fellows. Several works, for example [4], have assumed that there is a trade-off between sociality and the ability of individuals to store, gather or process information. There is no conclusive evidence that such trade-offs exist, to the best of our knowledge. Evidences are mounting that individual-level information and social processes can be both present in collective decision processes in fish groups [5, 6]. However, since this aspect has been included as an important ingredient in other models, it is important to explore its reelvance in the present context.

Our theoretical framework can be extended to account for this aspect in two different ways: either by making informed individuals promote the formation of links at a lower rate or by generalizing the choice behavior to a stochastic probabilistic model. Here we show that the qualitative results discussed in the main paper are kept significantly unchanged in both cases.

A.7.1 Heterogeneous link formation rates

A natural way to introduce a tradeoff between sociality and information is to assume that *informed individuals shall promote link creation at a lower rate*.

Under this assumption it is possible to calculate the exact invariant distribution and to proceed with the same calculations of the simpler case discussed in the main article. In particular the large z and small z solutions are the same. Here we report the main results, without repeating lengthy derivations.

We assume that individuals that are informed about direction α shall promote link creation with rate η^α whereas uninformed individuals shall promote link creation with rate η^0. While we keep the dependence on α in η, it is reasonable to assume that $\eta^\alpha = \eta^1$ takes the same value, irrespective of the preferred direction $\alpha \neq 0$, for all informed individuals.

In particular we have that the link creation rate for the creation of a link between nodes i and j is :

1. $\frac{\eta^{\alpha_i} + \eta^{\alpha_j}}{N-1}$ if $a_j = a_j$ (here $\alpha_i = 0$ denotes uninformed individuals)

2. 0 otherwise

The invariant measure therefore reads

$$\pi(\omega) = \frac{1}{\mathscr{Z}} e^{\sum_i h_{\alpha_i} \delta_{a_i \alpha_i}} \prod_{j<i} \left(\frac{\delta_{a_i a_j} (\eta^{\alpha_i} + \eta^{\alpha_j})}{\lambda(N-1)} \right)^{g_{ij}}. \tag{68}$$

In order to obtain the distribution in term of population we have to distinguish between two different types of links. Let us define $M_a^{\alpha\beta}$ denote the number of links between individuals that are in state a but would prefer to be in state α and individuals that are in state a but would prefer to be in state β. For simplicity we shall extend the notation described above denoting with preference 0 the individuals with no preference.

Let N_a^α denote the number of individuals that are in state a but would prefer to be in state α.

It is trivial to infer from eq. (68) that, in term of these quantities, the invariant distribution reads

$$\pi(\mathbf{N},\mathbf{M}) = \frac{1}{\mathcal{Z}} \frac{N!}{\prod_a N_a^0! \prod_{a\alpha} N_a^\alpha!} e^{\sum_a h_a N_a^a} \prod_{a\in S, \alpha\in S\cup\{0\}} \binom{\frac{N_a^\alpha(N_a^\alpha-1)}{2}}{M_a^{\alpha\alpha}} \left(\frac{2\eta^\alpha}{\lambda(N-1)}\right)^{M_a^{\alpha\alpha}}$$

$$\prod_{\beta\in S\cup\{0\}, \beta\neq\alpha} \binom{N_a^\alpha N_a^\beta}{M_a^{\alpha\beta}} \left(\frac{\eta^\alpha+\eta^\beta}{\lambda(N-1)}\right)^{M_a^m}.$$

$$(69)$$

Summing over M's and taking the logarithm we get that

$$\log(\pi) = \sum_{a\alpha} N_a^\alpha \log(N_a^\alpha) - \sum_a h_a N_a^a - \left(\sum_{a\alpha\beta} N_a^\alpha N_a^\beta \frac{\eta_\alpha+\eta_\beta}{\lambda(N-1)}\right) - \sum_{a\alpha} N^\alpha \frac{2\eta_\alpha}{\lambda(N-1)} \quad (70)$$

thus leading to a free energy in the thermodynamic limit:

$$F(\mathbf{n}; z^\alpha, h_\alpha) = \sum_{a\alpha} n_a^\alpha \log(n_a^\alpha) - \sum_a h_\alpha n_a^a - \frac{1}{2}\sum_a \left(\sum_\alpha z^\alpha n_a^\alpha\right) n_a \quad (71)$$

The saddle point equations can be derived in a straightforward manner, following the steps outlined above for the homogeneous case.

The numerical solution of these equations can be studied as a function of the parameters. In particular, in the extreme case where $\eta^\alpha = 0$ for all informed individuals ($\alpha > 0$) exhibits the same hysteric behavior of the homogeneous case discussed above. The limit $z^0 = \eta^0/\lambda \gg 1$ can also be studied in exactly the same way as above, with the same conclusion, that corrections to the coordinated solutions $n_b^* = \delta_{ab}$ are exponentially small in z_0. From Eq. (71) it is clear that again the dominant solution for z^0 large is the one with the largest product $n^a h_a$, exactly as in the homogeneous case. This conclusion also extends to the case where $z^\alpha = z^1 > 0$ for $\alpha \neq 0$.

A.7.2 Generalized internal update rule

A different way to introduce a tradeoff between sociality and preferences is to modify the update rule (13), by assuming that individuals weight their preferred choice and the choice taken by neighbors when updating their choices. One way to do this is to assume that individual i, when an internal state update event occurs, will pick up randomly an internal state with a probability proportional to:

$$P_i(a) \propto e^{h\alpha_i \delta_{a\alpha_i} + \beta_i \sum_j g_{ij} \delta_{aa_j}}. \quad (72)$$

The parameter β_i measures to what extent individual i takes into account the choices of the social group in making his decision. The effect of this choice is mostly evident by discussing the limiting cases:

1. if $\beta_i \to 0$, individual i will make its choices selfishly, without considering the choices of its neighbouring individuals;
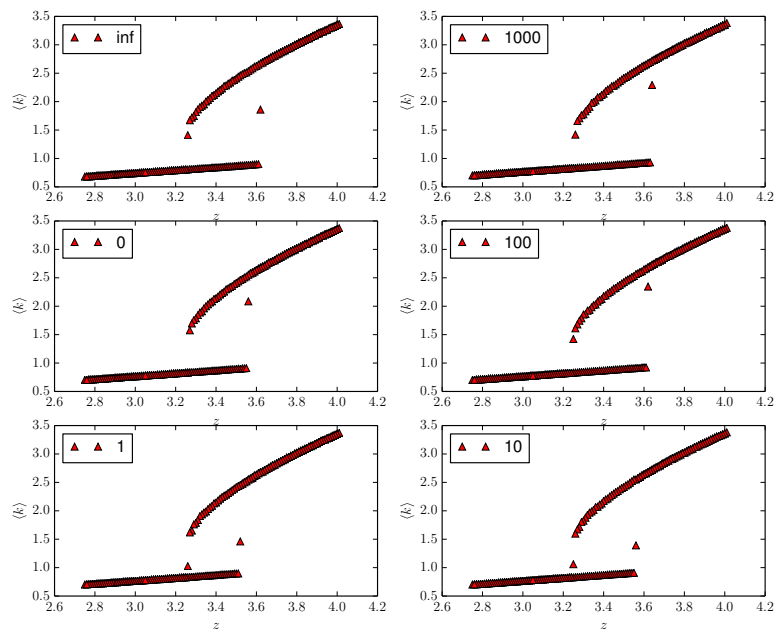
Figure 5: Plot of the average degree obtained in numerical simulations of the model with stochastic choice update. These are based on 100 runs, with $N = 5000$ nodes and parameter $n^0 = 0.99$, $n^1 = 0.01$ and $h_1 = 0.05$ for different values of β (the value is written in the legend) for the informed individuals (the uninformed ones have $\beta_i = \infty$).

2. if $\beta_i \rightarrow \infty$, individual i will make its choices always conforming to its neighbourhood, if ths is not empty. Only when his neighborhood is empty, his choice will reflect the pieces of information it possesses: this is exactly the case discussed in the main paper.

As one can see, β_i interpolates between a fully pro-social behaviour and a completely individualistic one; the tradeoff may be simply introduced assuming that uniformed individuals have $\beta_i = \infty$ whereas informed individuals have lower β_i.

The drawback of this extension of the model is that, as soon as $\beta_i < \infty$, the system is not analytically solvable and can only be investigated by numerical stochastic simulations. Fig. A.7.2 reports a series of numerical simulations of this extended model. This shows that introducing a trade-off between sociality and preference does not qualitatively change the behaviour of the system; the only appreciable difference being the fact that the symmetric solution becomes unstable at lower values of z. Therefore, even though quantitative results differ, the qualitative picture described in the article holds true also in this more general model.

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