# Adaptive network dynamics and evolution of leadership in collective migration

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## HIGHLIGHTS

- Analytically tractable, two-timescale, network-dependent collective migration model.
- Bifurcations explain hysteresis in migration recovery in fragmented environments.
- Minimum connectivity for evolutionary branching into leaders and followers.
- Social interaction graph influences emergence and location of leaders.

## ARTICLE INFO

## ABSTRACT

The evolution of leadership in migratory populations depends not only on costs and benefits of leadership investments but also on the opportunities for individuals to rely on cues from others through social interactions. We derive an analytically tractable adaptive dynamic network model of collective migration with fast timescale migration dynamics and slow timescale adaptive dynamics of individual leadership investment and social interaction. For large populations, our analysis of bifurcations with respect to investment cost explains the observed hysteretic effect associated with recovery of migration in fragmented environments. Further, we show a minimum connectivity threshold above which there is evolutionary branching into leader and follower populations. For small populations, we show how the topology of the underlying social interaction network influences the emergence and location of leaders in the adaptive system. Our model and analysis can be extended to study the dynamics of collective tracking or collective learning more generally. Thus, this work may inform the design of robotic networks where agents use decentralized strategies that balance direct environmental measurements with agent interactions.

## 1. Introduction

A great variety of species including birds, fish, invertebrates and mammals engage in collective migration [1–4]. The migratory process is often an adaptive response to conditions such as competition for resources in a dynamic environment, seasonal variability, and selection of new habitats for breeding [1,5–7]. On the one hand, animals perform migratory tasks by leveraging environmental cues such as nutrient and thermal gradients, magnetic fields, odor cues, or visual markers [8–10]. Measuring these stochastic environmental signals is complicated and requires the investment of time and energy, as well as the development of necessary physiological and sensory machinery such as vision in insects and vertebrates [2] and chemical signaling in bacteria [11]. On the other hand, animals can

perform migrating tasks by leveraging social cues from neighbors (nearby conspecifics) [5–7]. By imitating invested neighbors (or neighbors of invested neighbors, etc.) using consensus processes such as cohesion and alignment, some animals in a group can migrate well without paying the costs associated with directly measuring and processing the environmental signal.

The interplay between costly information acquisition from the environment and relatively less expensive social interactions with the group raises two important questions regarding leadership and social interactions in migratory populations. Here, leadership means the influence of individuals who are informed about the environmental signal, e.g., by investing time and energy in taking a measurement. Although these informed individuals are referred to as "leaders" and the remaining uninformed individuals as "followers", it is *not* assumed that leaders can be identified or can signal their information to others.

The first important question relates to the migratory performance of large groups in the presence of a limited number of leaders, i.e., can a subset of informed individuals effectively lead a large

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group? Couzin et al. [12] address this question using individual-based simulations (involving social forces of attraction, repulsion and alignment among individuals) and demonstrate that in a group of socially interacting individuals, a small fraction of informed leaders can effectively determine the direction of travel of a large group of uninformed followers.

The second important question relates to the evolution of leadership in collective migration, i.e., under what conditions is the coexistence of invested leaders and social followers stable in an evolutionarily sense? This question is especially relevant when the cost of investing in signal acquisition is sufficiently high; followers can leverage the investments made by leaders using social interactions without having to pay the investment costs themselves, but not all individuals can be followers if the group is to migrate successfully. Guttal and Couzin [5] address this question (also see related commentary [13]) using evolutionary simulations and an individual-based model similar to that used in [12]; they show that the specialization of groups into coexisting leaders and followers (also known as branching) is a stable evolutionary outcome.

Motivated by these questions and results, we develop an analytically tractable model of collective migration with which we can rigorously study the adaptive network dynamics associated with the evolution of collective migration and the emergence of leadership when leadership is costly and social interaction is relatively cheap. We investigate the influence on group-level outcomes of the (evolving) network topology, i.e., who is sensing and responding to whom within the group, as a function of the cost of investing in the environmental signal. Our model can be generalized to a broader set of adaptive network dynamics associated with a collective task, such as collective tracking or collective learning of a noisy, unknown signal [14,15], carried out by agents with decentralized strategies that balance direct environmental measurements with social interactions.

Torney et al. [6] derive a mean-field approximation to the evolutionary model studied in [5], and using tools from evolutionary adaptive dynamics [16,17] prove conditions for the branching of a migrating population into leader and follower groups. The mean-field approach effectively prescribes an all-to-all social interaction topology between the individuals in order to reduce dimensionality, critical to the analysis in [6]. However, the approach ignores the potentially important role of limited social interactions; indeed, it has been shown that network topology plays a critical role in determining outcomes in collective dynamics [14,15,18–21]. Our model derives directly from the model of [6] with a key generalization to the case of limited interaction networks and a modification that allows individual fitnesses to be computed from a linear matrix equation as a function of the network topology encoded by a directed graph.

In our model each agent $i$ has a scalar strategy $k_i(t) \in [0, 1]$ at time $t$ which defines how much it invests in the environmental signal; $k_i = 0$ means no investment and $k_i = 1$ means full investment. The strategy also determines how much it attends to social interaction: a higher $k_i$ implies a lower attention to measurements of neighbors, equivalently, the associated edges of the network graph are scaled by $(1 - k_i)^2$. The network dynamics have two timescales. In the fast timescale the strategies $k_i$ are fixed, such that the stochastic migration dynamics and the fitnesses depend on a fixed interconnection topology. In the slow timescale the strategies $k_i$ change according to evolutionary (or adaptive) dynamics and with them the investments and graph edge weights.

We present three main results that leverage the extension of the migration model of [6] to directed, limited social interaction topologies and the corresponding matrix equation for fitnesses (which replaces extensive Monte-Carlo simulations as used in [6, 5]). Our first main result is a complete bifurcation analysis of the

two-timescale dynamics as a function of investment cost in the case of a large population with an underlying network topology that is all-to-all; our results explain previous observations that are initial condition dependent and demonstrate the hysteretic effect associated with losing and then recovering migration ability as described in [5,22]. Our second main result addresses the two-timescale dynamics in the case of a large population with an underlying network topology that is limited; we find a relatively small threshold in connectivity above which there is evolutionary branching and emergence of leaders.

Our third main result addresses the case of a small population in which the slow evolutionary dynamics of strategies $k_i$, based on replication and mutation, are replaced with individual greedy adaptive dynamics. We show the critical role that the structure of the underlying network topology plays in determining the location of leaders in the adaptive network and in influencing bifurcations in the dynamics as a function of increasing cost. This analysis is motivated in part by an interest in leveraging the mechanisms of evolved natural collectives in the design of decentralized protocols for collective motion and decision-making in robotic groups [18,23].

The paper is outlined as follows.[1] In Section 2 we present our evolutionary migration model. We derive analytical results for fitnesses on the fast timescale in Section 3. We study the slow timescale dynamics in the all-to-all limit in Section 4 and for limited interconnections in Section 5. We focus on adaptive dynamic nodes in small networks in Section 6 and conclude in Section 7.

## 2. Model description

Our model is derived from the mean-field migration model in [6] with two key modifications; we explicitly account for a limited social interaction graph topology in the dynamics and we introduce a slightly modified social noise model to allow for analytical fitness computations as a function of graph topology and individual investments. In the remainder of the paper we will refer to individuals, agents and nodes interchangeably, and likewise population and network.

Consider a set of $N$ agents indexed by $i \in \{1, \ldots, N\}$. Let $x_i(t) \in \mathbb{R}$ be the direction of migration of agent $i$ at time $t$, and let $\mu \in \mathbb{R}$ be the "true" desirable direction of migration. Accurate tracking of the direction $\mu$ over time may correspond to benefits such as improvement in environmental conditions for foraging, predator evasion, early access to breeding grounds, etc. Following [6], the stochastic dynamics of each agent are given by

$$dx_i = k_i dx_{Di} + (1 - k_i) dx_{Si}, \qquad (1)$$

where $dx_{Di}$ and $dx_{Si}$ are the driven tracking and social consensus stochastic processes, respectively. The adaptive strategy $k_i \in [0, 1]$ tunes the level of investment made by agent $i$ in the driven and social processes. When $k_i = 1$, agent $i$ is fully invested in the tracking process and ignores social cues, while when $k_i = 0$ agent $i$ exclusively leverages social cues without tracking the environmental signal.

The driven process $dx_{Di}$ is modeled as an Ornstein–Uhlenbeck stochastic process [25,26] of the form

$$dx_{Di} = -k_{Di}(x_i - \mu)dt + \sigma_D dW_{Di}. \qquad (2)$$

The parameter $k_{Di} \geq 0$ corresponds to the gain associated with tracking, $\sigma_D > 0$ is the noise intensity associated with measuring the environmental signal $\mu$, and $dW_{Di}$ represents the standard

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[1] See [24] for related text and figures.