

Specialization and evolutionary branching within migratory populations

Colin J. Torney¹, Simon A. Levin, and Iain D. Couzin

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544

Contributed by Simon A. Levin, September 28, 2010 (sent for review April 30, 2010)

Understanding the mechanisms that drive specialization and speciation within initially homogeneous populations is a fundamental challenge for evolutionary theory. It is an issue of relevance for significant open questions in biology concerning the generation and maintenance of biodiversity, the origins of reciprocal cooperation, and the efficient division of labor in social or colonial organisms. Several mathematical frameworks have been developed to address this question and models based on evolutionary game theory or the adaptive dynamics of phenotypic mutation have demonstrated the emergence of polymorphic, specialized populations. Here we focus on a ubiquitous biological phenomenon, migration. Individuals in our model may evolve the capacity to detect and follow an environmental cue that indicates a preferred migration route. The strategy space is defined by the level of investment in acquiring personal information about this route or the alternative tendency to follow the direction choice of others. The result is a relation between the migratory process and a game theoretic dynamic that is generally applicable to situations where information may be considered a public good. Through the use of an approximation of social interactions, we demonstrate the emergence of a stable, polymorphic population consisting of an uninformed subpopulation that is dependent upon a specialized group of leaders. The branching process is classified using the techniques of adaptive dynamics.

collective behavior | evolutionary dynamics | social information

As a generalized process, animal migration is observed over a broad range of temporal and spatial scales, from the diurnal, vertical migration of lake dwelling algae (1), to the annual inter-oceanic movements of the humpback whale (2). Animals typically navigate these routes through the use of environmental cues and various sensory modalities, responding to nutrient or thermal gradients, magnetic or electric fields, odor cues, or visual markers (3). Detecting and processing these sources of information is nontrivial and doing so requires an investment either in time and energy or in the physiological cost of developing cognitive or sensory capacity (4).

The potential cost associated with the acquisition of information raises several issues in the context of leadership dynamics and social interaction. Previous works have shown how sociality can facilitate or even enable the use of environmental cues, both theoretically (5–7) and empirically (8, 9). In ref. 10, Couzin et al. demonstrated that small groups of individuals can affect the direction choice of large numbers of uninformed followers, indeed it was shown that for a fixed proportion of leaders the accuracy in terms of the group direction increases as the size of the group grows. If considering collective migration alongside these studies of social interaction, the relation between the costly acquisition of personal information, which drives the migration, and the uninformed following of others may be mapped to a producer-scrounger dynamic (11). In this situation the commodity being generated is information (12) and it is available via two sources, directly from the environment (personal information) or through observations of the behavior of conspecifics (social information) (4).

In a recent study (13) this process was examined using an individual based model governed by localized rules of attraction, alignment etc., with differing degrees of independence and sociality. This work showed that, under certain conditions, specialized groups of leaders form. The challenge in understanding and classifying models of this type lies in identifying an appropriate methodology for the abstraction of interindividual interactions (i.e., amenable to analysis of the evolutionary process but still able to capture the higher level effects of low level behavior). This abstraction is required if complex, interacting systems are to be mapped to a framework that is compatible with the mathematical study of evolutionary dynamics. In this work we employ a unique mean-field approximation of these social interactions to analyze the frequency dependent selection dynamics created via the collective migratory process.

Model Description

In our model, individuals are able to access an imperfect source of information indicating the correct migration route. It is assumed that the effective utility of the environmental cue is an increasing, but saturating, function of the level of investment made in its detection. This represents the diminishing returns that may be associated to variable behavioral or physiological parameters, such as the frequency direction choice is evaluated, or the exploration of alternative routes. The distance travelled in the correct direction over a fixed time interval is then continuously mapped to a linear fitness benefit, which may result from long range improvements in mean abiotic conditions or nutrient availability, reduced risk from nocturnal predators by reaching safe havens earlier, first access to preferred breeding or grazing grounds etc.

A lone individual is then faced with the simple challenge of optimizing the level of return versus cost of investment, however an individual within a group may also choose to follow others and it is assumed that imitation of direction choice incurs no cost. (Note: The validity of this assumption is dependent on the cost to sociality being less than the cost of obtaining personal information but not necessarily zero.)

To describe and quantify the social information source we note an equivalence between the interacting, migratory population defined by an infinite-dimensional system of orientation headings, and a collection of coupled chemical or biological oscillators. This leads us to an approach proposed by Kuramoto (14, 15) in his study of the onset of synchronization in large-scale coupled oscillator systems. By using Kuramoto's method, the population is described by two key properties; the average heading of the group and the degree of coherence; i.e. the level of consensus around the average heading.

The result is two well-defined sources of information, an external fixed source that represents an environmental cue, and

Author contributions: C.J.T., S.A.L., and I.D.C. designed research; C.J.T. performed research; C.J.T., S.A.L., and I.D.C. analyzed data; and C.J.T., S.A.L., and I.D.C. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: ctorney@princeton.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1014316107/-DCSupplemental.

a social source dependent on the behavior of the population. Individuals can then freely evolve sociality, meaning aggregation and the imitation of others, or leadership, the tendency to acquire information and respond autonomously.

For simplicity we assume that if θ defines an individual's orientation relative to a fixed axis and it moves at a constant speed in this direction, the orientation $\theta = 0$ corresponds to the heading associated with maximum benefit; i.e. along the defined migration route. The quality of the environmental cue is controlled by a noise term in the dynamics of an individual's orientation heading, representing fluctuating external fields or internal errors in their detection. Increased investment in detection reduces this noise and brings the orientation toward the optimal direction $\theta = 0$. This leads to an Ornstein–Uhlenbeck process of the form

$$d\theta_g = -x_g \theta dt + \sigma dW_t, \quad [1]$$

where x_g is the evolutionarily tunable parameter that defines the degree of investment into gradient detection, dW_t is a standard Wiener process and σ encompasses the noise inherent in detecting the gradient. Hence, increasing the amount of investment made means greater average migration speed.

Considering first the situation for a single individual, we use a Fokker–Planck (16) representation of Eq. 1,

$$\frac{\partial \rho}{\partial t} = x_g \frac{\partial}{\partial \theta} (\theta \rho) + \frac{\sigma^2}{2} \frac{\partial^2 \rho}{\partial \theta^2}, \quad [2]$$

from which it is possible to obtain the probability density function $\rho(\theta)$ that defines the time averaged distribution in θ for a given value of investment. A stationary solution to Eq. 2 can be found if it is assumed $\rho(\pm\pi) \rightarrow 0$; i.e., an individual spends a vanishingly small amount of time moving opposite to the desired direction. In this case the periodic boundary conditions due to the angular rotation may be neglected and an analytical approximation of the probability density function can be obtained as

$$\rho(\theta) = \sqrt{\frac{x_g}{\pi \sigma^2}} e^{-\frac{x_g \theta^2}{\sigma^2}}. \quad [3]$$

This equation represents an approximation of the distribution only. It is exact in the limit of $x_g/\sigma^2 \rightarrow \infty$, however it remains a good approximation even for small values of x_g (see Fig. 1 for a comparison of the average migration speed calculated using this approximation and the numeric values, and *SI Text* for comparisons of Eq. 3 to the actual distribution). Effectively, by using Eq. 3, we are neglecting the periodic boundaries, assuming $\rho(\theta)$ is defined on an infinite domain, and then extracting the only region that is meaningful to our system $\theta \in [-\pi, \pi]$.

Using this density function, the distance traveled within a given period can be calculated by projecting the density at each point on to the optimum directional vector. This is then normalized to give a mean velocity along the migration route that lies in the interval (0,1)

$$\int_{-\pi}^{\pi} \rho(\theta) \cos(\theta) d\theta \approx \exp\left[\frac{-\sigma^2}{4x_g}\right]. \quad [4]$$

If $\rho(\theta)$ were defined by a Dirac delta function then the individual would spend all its time perfectly aligned along the correct heading and the average migration speed would be maximized. In the absence of any cost for personal information $x_g = \infty$ is an evolutionary attractor and all individuals increase their investment so that $\rho(\theta) \rightarrow \delta(\theta)$. In our model the average migration speed is scaled by a reducing factor dependent on the level of investment x_g . The fitness, F associated to a given strategy is

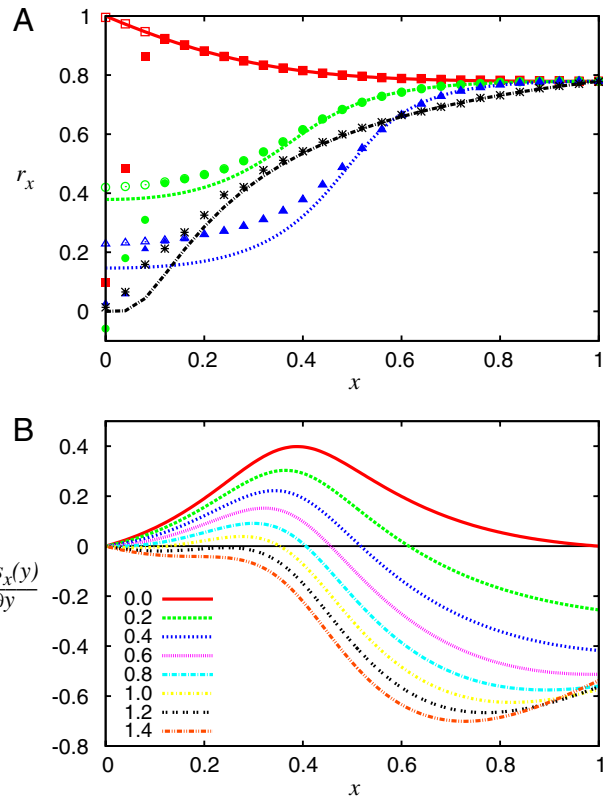


Fig. 1. (A) Phase coherence r_x as a function of x , lines are analytical result, points are from the numerics, black dash-dot (asterisk) is for a lone individual (the asocial case of Eq. 4), red solid (square) $\eta = 2$, green dash (circle) $\eta = 2.5$, blue dot (triangle) $\eta = 3$. Outline shapes, average migration speed; filled shapes, population order parameter modulus r , which may not be centered around the correct direction. (B) Local fitness gradient $\frac{\partial s_x(y)}{\partial y}$ as a function of x . Lines are different values of cost, negative values indicate the population will move toward the left, positive to the right.

$$F = \exp\left[\frac{-\sigma^2}{4x_g}\right] \exp[-cx_g^2], \quad [5]$$

where a reducing factor has been introduced with a strength defined by c and a quadratic dependence on x_g so that higher values of investment become increasingly costly. As an additive fitness differential (i.e., in units of fitness), this cost is defined as $\exp\left[\frac{-\sigma^2}{4x_g}\right](1 - \exp[-cx_g^2])$. Our choice of this cost function is motivated by analytical tractability; the results do not appear to depend on its exact form. For example, numerical simulations with linear additive cost demonstrate equivalent behavior (see also ref. 13).

Because individuals in the asocial case are noninteracting, the optimum value of x_g can be easily found as

$$x_g^* = \left(\frac{\sigma^2}{8c}\right)^{\frac{1}{3}}. \quad [6]$$

In the absence of any social interaction, there can be no frequency dependent effects and x_g^* represents an evolutionary stable strategy that all initial strategy values will evolve toward. However social interactions dramatically alter this situation as the directional choice of others is another source of information that can be exploited through copying, without expending energy in detecting environmental cues directly.

Exactly how this second source of information will be accessed is dependent on the system in question, but for many migratory systems the degree of ordering and the average orientation within

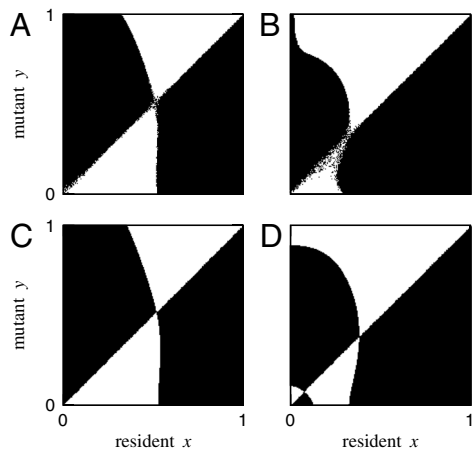


Fig. 3. Pairwise invasibility plots. Dark regions represent positive differential fitness (mutant will invade), light regions negative (mutant will not invade). (A, B) Numerical result, (C, D) Analytical approximation. For (A) and (C) $c = 0.4$ (no branching). For (B) and (D) $c = 0.9$ (branching occurs). The population resides on the diagonal, mutations occur along the vertical axis and the sign of the fitness differential determines if it will invade. Invasion results in this mutant becoming the resident and the population shifts along the line $y = x$ until it reaches a convergence stable strategy, x^* . If branching is to occur once a CSS is reached, it is required that a line drawn vertically from x^* will immediately encounter a region of positive differential fitness. Numerical results are obtained by evaluating the average fitness of a single individual in the resident population, analytical results stem from Eq. 13.

value, x^* is greater or less than the value required for branching to occur (SI Text). If

$$r_{x_c} - \exp\left[-\frac{x_c^* \sigma^2 + (1 - x_c^*)^2 \eta^2 (1 - r_{x_c^*})}{4(2x_c^* - 2x_c^* + 1)}\right] < 0, \quad [19]$$

then the singular strategy lies to the left of the critical value and the population will branch. After some manipulation the condition for the emergence of a polymorphic population reduces to

$$\eta^2 < \frac{k_1 c + \sigma^2}{(1 - \exp[-\frac{\sigma^2}{4} - k_2 c])}, \quad [20]$$

where $k_1 = \frac{224\sqrt{7}-544}{27}$ and $k_2 = \frac{4\sqrt{7}-2}{27}$. The key to interpreting this condition lies in its influence on the location of the convergence stable strategy. If the cost c or the environmental noise value σ are low the CSS is found at higher values of x . Individuals are then locked into a high investment strategy because they are predominantly asocial and the advantage to exploitation through imitation is weak compared to the loss of environmental information. Lower values of the social noise term η moves the fixed point to the left where individuals are more social and the advantage of imitation is greater. As individuals invade the social information source is weakened, effectively increasing η and shifting the attracting strategy to the right for those that are more informed. The population therefore diverges.

Parameter values that lie either side of this condition are used in the simulations shown in Fig. 2 with the critical value x_c plotted

as a red line. In Fig. 3, we include pairwise invasibility plots that show how the evolutionary dynamics shift as the parameters of the model are changed. The condition for branching is illustrated by the presence of positive differential fitness on the vertical line through x^* .

It should be noted the branching condition described is valid for any small but finite mutation rate. Larger mutations result in a relaxation of this condition as greater variance in the phenotype trait frequency means populations more readily evolve into a polymorphic state.

Discussion

The principle of natural selection appears to define a homogenizing force, leading to the survival of only a few well adapted species whose members compete fiercely for resources. This image, however, is inconsistent with the observed abundance of species diversity and fails to explain the cooperation, division of labor and specialization that facilitates cohesion across multiple biological scales, from human social groups (25) to the unicellular colonial origins of multicellularity (26). Much progress in reconciling these discrepancies has come through the mathematical analysis of evolutionary dynamics (23, 27–30); however, a major difficulty for the study of evolving populations arises from their inherent complexity. Often they consist of many interacting components that display emergent, collective-level phenomena that cannot be predicted or explained by an analysis of individuals in isolation (31–33).

Insight into the behavior of these systems has been gained by using techniques developed in areas such as statistical physics (17, 34, 35), but the focus has largely been on the proximate cause of behavior (i.e., from a mechanistic, functional perspective) and not the ultimate cause (i.e., how natural selection at lower levels has shaped these systems or how collective-level phenomena feeds back on the fitness of individuals). In this work we have shown that the influence of collective interactions on evolution can be dramatic, and in the framework presented results in the formation of a subpopulation of specialized leaders that drive a population level migration.

The catalyst for the evolutionary divergence in our model can be found in the creation and exploitation of information about an optimal migration route. As the production of information is often costly, and through imitation or social facilitation may be inadvertently shared with others, it can be equated to a public good. The key difference to a standard public goods game (36), is the self-dependence of the social information source (illustrated by the implicit definition of the ordering parameter of Eq. 11) that causes a steep transition to a high migration ability once a threshold level of investment is reached. It is this nonlinearity, arising from collective interactions, that creates the selection gradients required for evolutionary branching to occur, and ultimately leads to the stable coexistence of two discrete, interdependent populations.

ACKNOWLEDGMENTS. We thank Vishwesh Guttal, Michael Neubert, Zoltan Neufeld, and an anonymous referee for helpful comments on the manuscript. This work was supported by Searle Scholars Award 08-SPP-201 (I.D.C.), National Science Foundation Grant PHY-0848755 (I.D.C.), Office of Naval Research Grant N00014-09-1-1074 (I.D.C.), and Defense Advanced Research Projects Agency Grant HR0011-09-1-0055 (Princeton University).

- Sommer U, Gliwicz ZM (1986) Long range vertical migration of Volvox in tropical lake Cahora Bassa (Mozambique). *Limnol and Oceanogr* 31:650–653.
- Pomilla C, Rosenbaum HC (2005) Against the current: an inter-oceanic whale migration event. *Biol Letters* 1:476–479.
- Gould JL (2004) Animal navigation. *Curr Biol* 14:R221–R224.
- Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193.
- Grünbaum D (1998) Schooling as a strategy for taxis in a noisy environment. *Evol Ecol* 12:503–522.
- Torney C, Neufeld Z, Couzin ID (2009) Context-dependent interaction leads to emergent search behavior in social aggregates. *Proc Natl Acad Sci USA* 106:22055–22060.
- Codling EA, Pitchford JW, Simpson SD (2007) Group navigation and the many wrongs principle in models of animal movement. *Ecology* 88:1864–1870.
- Tamm S (1980) Bird orientation: Single homing pigeons compared with small flocks. *Behav Ecol Sociobiol* 7:319–322.
- Steele CW, Scarfe AD, Owens DW (1991) Effects of group size on the responsiveness of zebrafish, *Brachydanio rerio* (hamilton buchanan), to alanine, a chemical attractant. *J Fish Biol* 38:553–564.

