Original Research Article

Basic model of purposeful kinesis

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A B S T R A C T

The notions of taxis and kinesis are introduced and used to describe two types of behaviour of an organism in non-uniform conditions: (i) Taxis means the guided movement to more favourable conditions; (ii) Kinesis is the non-directional change in space motion in response to the change of conditions. Migration and dispersal of animals has evolved under control of natural selection. In a simple formalisation, the strategy of dispersal should increase Darwinian fitness. We introduce new models of purposeful kinesis with diffusion coefficient dependent on fitness. The local and instant evaluation of Darwinian fitness is used, the reproduction coefficient. New models include one additional parameter, intensity of kinesis, and may be considered as the *minimal models of purposeful kinesis*. The properties of models are explored by a series of numerical experiments. It is demonstrated how kinesis could be beneficial for assimilation of patches of food or of periodic fluctuations. Kinesis based on local and instant estimations of fitness is not always beneficial: for species with the Allee effect it can delay invasion and spreading. It is proven that kinesis cannot modify stability of homogeneous positive steady states.

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1. Introduction

The notions of taxis and kinesis are introduced and used to describe two types of behaviour of an organism in non-uniform conditions:

- Taxis means the guided movement to more favourable conditions.
- Kinesis is the non-directional change in space motion in response to the change of conditions.

In reality, we cannot expect pure taxis without any sign of kinesis. On the other hand, kinesis can be considered as a reaction to the local change of conditions without any global information about distant sites or concentration gradients. If the information available to an organisms is completely local then taxis is impossible and kinesis remains the only possibility of purposeful change of spatial behaviour in answer to the change of conditions. The interrelations between taxis and kinesis may be non-trivial: for example, kinesis can facilitate exploration and help to find non-local information about the living conditions. With this non-local information taxis is possible.

In this paper, we aim to present and explore a simple but basic model of purposeful kinesis. Kinesis is a phenomenon observed in

a wide variety of organisms, down to the bacterial scale. *Purposeful* seems to imply a sort of intentionality that these organisms are incapable of. The terms 'purpose' and 'purposeful' are used in mathematical modelling of biological phenomena in a wider sense than in psychology. 'Purpose' appears in a model when it includes optimisation. The general concept of purposeful behaviour (Rosenblueth and Wiener, 1950) of animals requires the idea of evolutionary optimality (Parker and Smith, 1990). In many cases this optimality can be deduced from kinetic equations in a form of maximization of the average in time reproduction coefficient – Darwinian fitness (Gorban, 2007; 1984; Metz et al., 1992). Application of this idea to optimization of behaviour is the essence of evolutionary game theory and its applications to population dynamics (Hofbauer and Sigmund, 1998).

There are three crucial questions for creation of an evolutionary game model:

1. Which information is available and usable? Dall et al. (2005) proposed a quantitative theoretical framework in evolutionary ecology for analysing the use of information by animal. Nevertheless, the question about information which can be recognised, collected and used by an animal requires empirical answers. Answering this question may be very complicated for analysis of taxis, which involves various forms of non-local information. For kinesis the situation is much simpler: the pointwise values of several fields (concentrations or densities) are assumed to be known (Sadovskiy et al., 2009).

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2. What is the set of the available behaviour strategies? All the organisms, from bacteria to humans have their own set of available behaviour strategies, and no organism can be omnipotent. It is necessary to describe constructively the repertoire of potentially possible behaviours.
3. What are the statistical characteristics of the environment, in particular, and what are the laws and correlations in the changing of environment in space and time? It is worth mentioning that all the changes in the environment should be measured by the corresponding changes of the reproduction coefficient.

We use a *toy model* to illustrate the idea of purposeful kinesis. Assume that an animal can use one of two locations for reproduction. Let the environment in these locations can be in one of two states during the reproduction period, *A* or *B*. The number of survived descendants is r_A in state *A* and r_B in state *B*. After that, their further survival does not depend on this area. Assume also that the change of states can be described by a Markov chain with transition probabilities $P_{A \to B} = p$ and $P_{B \to A} = q$. These assumptions answer Question 3.

The animal is assumed to be very simple: it can just evaluate the previous state of the location where it is now but cannot predict the future state. There is no memory: it does not remember the properties of the locations where it was before. This is the answer to question 1.

Finally, there is only one available behaviour strategy: to select the current (somehow chosen) location or to move to another one. There exists resources for one jump only and no 'oscillating' jumps between locations are possible. This means that after the change of location the animal selects the new location for reproduction independently of its state. Thus Question 2 is answered.

Analysis of the model is also simple. If the state of the location is unknown then the probability of finding it in state *A* is $\frac{q}{p+q}$ and the probability of finding it in state *B* is $\frac{p}{p+q}$; these are the stationary probabilities of the Markov chain. The expectation of the number of offsprings without arbitrary information is

$$r_0 = \frac{qr_A + pr_B}{p + q}.$$

If an animal chooses for reproduction the location with the previous state *A* then the conditional expectation of the number of offsprings is $r|_A = (1 - p)r_A + pr_B$. If it chooses the location with the previous state *B* then the expected number of offsprings is $r|_B = (1 - q)r_B + qr_A$.

If the animal is situated in the location with the previous state *A*, and $r|_A < r_0$, then the change of location will increase the expected number of offsprings. Analogously, if it is situated in the location with the previous state *B*, and $r|_B < r_0$, then the change of location will increase the number of offsprings.

We have obtained the simplest model with mobility dependent conditionally expected reproduction coefficient $r|_\bullet$ under given local conditions: if $r|_\bullet$ is less than the value r_0 expected for the indefinite situation then jump, else stay in the same location. This is the essence of purposeful kinesis for this toy model.

It is very difficult to find realistic space and time correlations in the environment during the evolution of animals under consideration. The answers to Questions 1 and 2 for real animals are also non-obvious, but the main idea can be utilised for the modelling of kinesis. We expect that the dynamics of the models could provide insight, regardless of whether parameters were obtained from optimization of real Darwininan fitness or just the structure of equations was guessed on the basis of this optimization.

In this paper, we study PDE models of space distribution. We start from the classical family of models. Patlak (1953), and Keller and Segel (1971) proposed a PDE system which is widely

used for taxis modelling (Hillen and Painter, 2009).

$$\partial_t u(t, x) = \nabla(k_1(u, s)\nabla u + k_2(u, s)u\nabla s) + k_3(u, s)u,$$
$$\partial_t s(t, x) = D_s \nabla^2 s + k_4(u, s) - k_5(u, s)s, \quad (1)$$

where

$u \geq 0$ is the population density,
$s \geq 0$ is the concentration of the attractant,
$D_s \geq 0$ is the diffusion coefficient of the attractant,
coefficients $k_i(u, s) \geq 0$.

Coefficient $k_1(u, s)$ is a diffusion coefficient of the animals. It depends on the population density u and on the concentration of the attractant s. Coefficient $k_2(u, s)$ describes intensity of population drift.

Special random processes were introduced for 'microscopic' theory of dispersal in biological systems by Othmer et al. (1988). They consist of two modes: (i) position jump or kangaroo processes, and (ii) velocity jump processes:

- The kangaroo process comprises a sequence of pauses and jumps. The distributions of the waiting time, the direction and distance of a jump are fixed;
- The velocity jump process consists of a sequence of 'runs' separated by reorientations, after which a new velocity is chosen.

Eq. (1) can be produced from kinetic (transport) models of velocity–jump random processes (Othmer and Hillen, 2000, 2002) in the limit of large number of animals and small density gradients under an appropriate scaling of space and time. The higher approximations are also available in the spirit of the Chapman–Enskog expansion from physical kinetics (Chapman and Cowling, 1970). Chalub et al. (2004) found sufficient conditions of absence of finite-time-blow-ups in chemotaxis models. Turchin (1989) demonstrated that attraction (and repulsion) between animals could modify the space dispersal of population if this interaction is strong enough. Méndez et al. (2012) derived reaction-dispersal-aggregation equations from Markovian reaction-random walks with density-dependent transition probabilities. They have obtained a general threshold value for dispersal stability and found the sufficient conditions for the emergence of non-trivial spatial patterns. Grünbaum (1999) studied how the advection-diffusion equation can be produced for organisms ("searchers") with different food searching strategies with various *turning rate* and *turning time* distributions, which depend on the density of observed food distribution.

The family of models (1) is rich enough and the term $\nabla(k_1(u, s)\nabla u)$ can be responsible for modelling of kinesis: it describes non-directional motion in space with the *diffusion coefficient $D = k_1(u, s)$*. This coefficient depends on the local situation represented by u and s. In some sense, the family of models (1) is even too rich: it includes five unknown functions k_i with the only requirement, the non-negativity.

Cosner (2014) reviewed PDE reaction–advection–diffusion models for the ecological effects and evolution of dispersal, and mathematical methods for analyzing those models. In particular, he discussed a series of optimality or evolutionary questions which arose naturally: Is it better for the predators to track the prey density, the prey's resources, or some kind of combination? Is it more effective for predators to slow down their random movement when prey are present or to use directed movement up the gradient of prey density? Should either predators or prey avoid crowding by their own species? Cosner (2014) presented also examples when diffusion is harmful for the existence of species: if the average in space of the reproduction coefficient is negative for all distributions of species then for high diffusion there is no steady state with positive total population even if there exist steady states