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Original Research Article

Mobility cost and degenerated diffusion in kinesis models

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ABSTRACT

A new critical effect is predicted in population dispersal. It is based on the fact that a trade-off between the advantages of mobility and the cost of mobility breaks with a significant deterioration in living conditions. The recently developed model of purposeful kinesis (Gorban & Çabukoğlu, Ecological Complexity 33, 2018) is based on the "let well enough alone" idea: mobility decreases for high reproduction coefficient and, therefore, animals stay longer in good conditions and leave quicker bad conditions. Mobility has a cost, which should be measured in the changes of the reproduction coefficient. Introduction of the cost of mobility into the reproduction coefficient leads to an equation for mobility. It can be solved in a closed form using Lambert *W*-function. Surprisingly, the "let well enough alone" models with the simple linear cost of mobility have an intrinsic phase transition: when conditions worsen then the mobility increases up to some critical value of the reproduction coefficient. For worse conditions, there is no solution for mobility. We interpret this critical effect as the complete loss of mobility that is degeneration of diffusion. Qualitatively, this means that mobility increases with worsening of conditions up to some limit, and after that, mobility is nullified.

1. Introduction

The study of two basic mobility mechanisms, *kinesis* and *taxis*, is concerned with responses of organisms motions to environmental stimuli: if such a response has the form of directed orientation reaction then we call it taxis, and the change in the form of undirected and random locomotion is called kinesis. These 'innocent' definitions cause many problems and intensive conceptual discussion (Dunn, 1990). One of the problems is: how to select the proper frame for discussion of the directed motion and separate the directed motion from the motion of the media. If the frame is selected unambigously then in the PDE (partial differential equations) approach to modelling taxis corresponds to change of *advection* terms, whereas kinesis is modeled by the changes of the *mobility coefficient*.

The notion of 'mobility coefficient' (or simply 'mobility' for brevity) was developed by Einstein (1956) (for historical review we refer to Philibert (2005)). It is summarised by the Teorell formula (Gorban et al., 2011; Teorell, 1935)

Flux = mobility × concentration × specific force.

Teorell studied electrochemical transport and measured specific force as force per 'gram-ion'. For ecological models (Lewis et al., 2013) concentration of animals u is used. The "diffusion force" is $-\nabla(\ln u) = -\frac{\nabla u}{u}$ (the "physical" coefficient RT is omitted).

The most important part of Einstein's mobility theory is that the mobility coefficient is included in the responses to *all forces*. For the applications of the mobility approach to dispersal of animals this means that intensity of kinesis and taxis should be connected: for example, decrease of mobility means that both taxis and kinesis decrease proportionally.

The kinesis strategy controlled by the locally and instantly evaluated well-being can be described in simple words: Animals stay longer in good conditions and leave more quickly bad conditions. If the well-being is measured by the instant and local reproduction coefficient then the diffusion model of kinesis gives for mobility μ_i of ith species (Gorban and Çabukoğlu, 2018):

$$\mu_i = D_{0i}\mathrm{e}^{-\alpha_i r_i(u_1,\dots,u_k,s)} \tag{1}$$

The corresponding diffusion equation is

$$\partial_t u_i(x,t) = \mathrm{div}[\mu_i(u_1,\dots,u_k,s)\nabla u_i] + r_i(u_1,\dots,u_k,s)u_i, \tag{2}$$

where:

k is the number of species (in this paper, we discuss mainly the simple case $k = 1$),
u_i is the population density of ith species,
s represents the abiotic characteristics of the living conditions (can be multidimensional),
r_i is the reproduction coefficient of ith species, which depends on all

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u_i and on s,
$D_{0i} > 0$ is the equilibrium mobility of ith species ('equilibrium' means here that it is defined for $r_i = 0$),
The coefficient $\alpha_i > 0$ characterises dependence of the mobility coefficient of ith species on the corresponding reproduction coefficient.

This model aimed to describe the 'purposeful' kinesis (Gorban and Çabukoğlu, 2018) that helps animals to increase there fitness when the conditions are bad (for low reproduction coefficient mobility increases and the possibility to find better conditions may increase) and not to decrease fitness when conditions are good enough (for high values of reproduction coefficient mobility decreases). The instant quality of conditions is measured by the local and instant reproduction coefficient.

Gorban and Çabukoğlu (2018) demonstrated on a series of benchmarks for models (2) with mobilities (1) that:

- If the food exists in low-level uniform background concentration and in rare (both in space and time) sporadic patches then purposeful kinesis (2) allows animals to utilise the food patches more intensively;
- If there are fluctuations in space and time of the food density s then purposeful kinesis (2) allows animals to utilize these fluctuations more efficiently.
- If the presence of the Allee effect the kinesis strategy formalised by (2) may delay the spreading of population
- The "Let well enough alone" strategy (1), (2) can prevent the effects of extinction caused by too fast diffusion and decrease the effect of harmful diffusion described by Cosner (2014).

The 'let well enough alone' assumption (1), (2) provides the mechanism for staying in a good location because mobility decreases exponentially with the reproduction coefficient. High mobility for unfavorable conditions allows animals to find new places with better conditions and seems to be beneficial. Nevertheless, it is plausible that increase of mobility in adverse conditions requires additional resources and, therefore, there exists a negative feedback from higher mobility to the value of the reproduction coefficient. This is the 'cost of mobility.' In the next section we introduce the cost of mobility and analyse the correspondent modification in the mobility function.

2. Cost of mobility

The 'cost of mobility' has been introduced and analysed for various research purposes. It is a well known notion in applied economic theory (Tiebout, 1956). The 'psychic cost of mobility' and it influence on the human choice of occupations has also been discussed (Schwartz, 1973). Analysis of evolution of social traits in communities of animals demonstrated that the cost of mobility has a major impact on the origin of altruism because it determines whether and how quickly selfishness is overcome (Le Galliard et al., 2004). Different costs of mobility on land and in the sea is considered as an important reason of higher diversity on land that in the sea (Vermeij and Grosberg, 2010). It was mentioned that the energy cost of mobility may lead to surprising evolutionary dynamics (Adamson and Morozov, 2012).

The optimality paradigm of movement is the key part of the modern movement ecology paradigm (Nathan et al., 2008). Movement can help animals to find better conditions for foraging, thermoregulation, predator escape, shelter seeking, and reproduction. That is, movement can result in increase of the Darwinian fitness (the average in time and generations reproduction coefficient). At the same time, movement requires spending of resources: time, energy, etc. This means that movement can decrease fecundity. The trade-off between fecundity loss and possible improvement of conditions is the central problem of evolutionary ecology of dispersal. In general, it is hardly known if and how mobility transfers to fitness costs. The fecundity costs of mobility in some insects was measured in field experiment (in non-migratory, wing-monomorphic grasshopper, *Stenobothrus lineatus*) (Samietz and Köhler, 2012). For some other insects (the Glanville fritillary butterfly *Melitaea cinxia*) the fecundity cost of mobility was not found (Hanski et al., 2006). These results challenge the hypothesis about dispersal–fecundity trade-off. A physiological trade-off between high metabolic performance reduced maximal life span was suggested instead. Another source of the cost of mobility may be increase of the rate of mortality due to the losses on the fly.

From the formal point of view, all types of 'mobility cost' can be summarised in the negative feedback from the mobility to the reproduction coefficient: increase of mobility decreases the reproduction coefficient directly. On the other hand, the change of conditions can increase the fitness. Form this point of view, there is trade-off between the direct loss of fitness due to mobility and probable increase of fitness due to condition change.

In our previous model (1), (2) the trade-off between the cost of mobility and the possible benefits from mobility was not accounted (Gorban and Çabukoğlu, 2018). Let us introduce here the cost of mobility as a negative linear feedback of the mobility μ on the reproduction coefficient r:

$$r = r_0 - C\mu, \tag{3}$$

where r_0 depends on the population densities and abiotic environment, C is the cost coefficient and $C\mu$ is the cost of mobility.

According to 'let well enough alone' assumptions (1), $\mu = D_0\exp(-\alpha r)$. Let us introduce $\mu_0 = D_0\exp(-\alpha r_0)$, that is the mobility (1) for the system with the reproduction coefficient r_0 instead of the coefficient r (3) with the cost of diffusion. Obviously, $\mu_0 \geq \mu$ and $\mu/\mu_0 = \exp(-C\mu)$.

Simple algebra gives:

$$-\alpha C\mu_0 = \alpha(r - r_0)\exp(\alpha(r - r_0)).$$

Therefore,

$$\mu = -\frac{W(-\alpha C\mu_0)}{\alpha C}, \tag{4}$$

where W is the Lambert W-function (Corless et al., 1996). The Lambert W-function is the inverse function to $x\exp(x)$, Fig. 1. Function $W(x)$ is defined for $x > -1/\mathrm{e}$. Therefore, the mobility μ (4) exists for

$$\alpha C\mu_0 \leq \frac{1}{\mathrm{e}}. \tag{5}$$

The argument of the function W in (4) belongs to the interval $[-1/\mathrm{e}, 0)$. The dependence of the dimensionless variable $\alpha C\mu$ on the dimensionless variable $\alpha C\mu_0$ (Fig. 2) is universal for all models of the form (1), (2) with the cost of mobility (3).

The universal limit (5) can be represented in terms of the

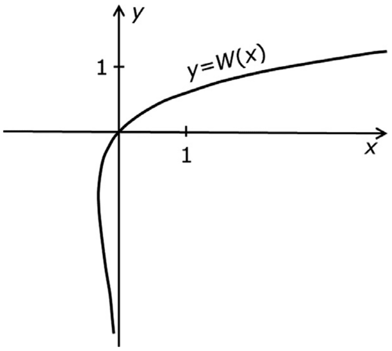

Fig. 1. The Lambert function $y = W(x)$ is defined for $x \geq -1/\mathrm{e}$. For negative x, the upper branch of W is used, the so-called W_0, which is real-analytic on $(-1/\mathrm{e}, \infty)$.

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