

KINESIS IN ANIMAL DISPERSAL: DEPENDENCE OF DIFFUSION ON REPRODUCTION COEFFICIENT

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by

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Abstract

Migration and dispersal of animals has evolved under the control of natural selection. In a simple formalisation, the strategy of dispersal should increase Darwinian fitness. In this dissertation, we aim to introduce and analyse new models of purposeful kinesis with diffusion coefficient dependent on fitness. New models include one additional parameter, intensity of kinesis, and may be considered as the *minimal models of purposeful kinesis*. It is demonstrated how kinesis could be beneficial for assimilation of patches of food or of periodic fluctuations. Nevertheless, kinesis, based on local and instantaneous estimations of fitness, is not always beneficial in the long-term and spatially global perspective: for example, 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.

In the proposed basic model, mobility decreases for high reproduction coefficient. Therefore, animals stay longer in good conditions and leave quicker bad conditions. Accounting for the cost of mobility in the reproduction ratio leads to an equation for mobility. It can be solved in a closed form using Lambert Wfunction. These 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 bifurcation as the complete loss of mobility that is degeneration of diffusion. Mobility increases with worsening of conditions up to some limit, and after that, mobility nullifies.

We analyse the impact of the purposeful kinesis model on running waves. Both monotonic and non-monotonic (the Allee effect) dependence of the reproduction coefficient on the population density are studied. The possible benefits of the purposeful kinesis are demonstrated: with the higher diffusion, while the population without kinesis ends up with extinction, the population with kinesis stays alive and has the running wave behaviour.

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To my dear father and mother for your endless love and unconditional support

Chapter 1

Introduction

1.1 General overview of animal movement, random walk and animal adaptation to survive

Change and motion describe the world's behaviour, from the molecular to the global levels. Molecules change their place, collide and react to produce new molecules. Elements of cells provide molecular places, and in these places, molecules participate in, and maintain, life processes. Change and motion give rise to rich natural phenomena, and this shows itself in spatial and temporal systems [103].

Chemistry makes the study of such pattern-forming systems start, and it is a discipline described by both change and motion. By the end of the 19th century, the main rules of the kinetics of chemical reactions and molecular migration had been formally presented. In 1896, the German chemist Raphael Liesegang [125]conducted a series of experiments that demonstrated that when certain inorganic salts move and react in a gel matrix, they produce periodic lines. Leisegang recognized that the manner in which molecules move affects other molecules. However, he could not explain the cause. In 1910, the French chemist Stephane Le Duc [114] highlighted the fact of substantial biological structures. After several decades, his approach was applied to space and time, therefore the form of living systems become perceptible. Chemistry has been combined with biology, physics, mathematics, and engineering to understand the reactions. Nonlinear chemical kinetics and dynamic system theory have been established. Mathematical models and computational biology have been developed together to explore a wide range of previously puzzling phenomena. For example, the skin patterns of animals and the functions of their skeleton have been revealed through such means. More recent studies have considered reaction-diffusion systems which have been accepted as a key element of an evolving world [103].

In the environment, organisms either move randomly or with purpose. The terms 'purpose' and 'purposeful' have been widely considered to be biological phenomena. Rosenblueth and Wiener proposed the general concept of purposeful behaviour, namely that animals require evolutionary optimality [162]. In 1990, Parker and Smith proposed the idea that the purposeful behaviour of animals is indicative of evolutionary optimality [162]. Sadovsky et al. [184] introduced a station model, where in a population will move according to local information. This indicates kinesis movement, which is more simplistic than taxis movement, since taxis requires non-local information (see Chapter 2.6).

Darwin, Wallace and Weismann [46, 227, 230] introduced optimization theory through the explanation of the natural selection. Evolutionary optimality also gives rise to the concept of adaptation, where Darwinian fitness can be used to define what traits might actually be maximized; it should be noted that Darwinian fitness can be defined as the capacity to survive and reproduce (see Chapter 2.4).

In 1930, Fisher, for the first time, pointed out that Darwin's quantitative ideas can be considered to be the measures of fitness in [60]. Moreover, Darwin [132] also improved Malthus' ideas quantitatively, and Fisher named the index of Darwinian fitness the 'Malthusian parameter'. Gause studied the struggle for existence of Darwin's idea in [70], and demonstrated his ideas in a laboratory environment using bacteria. He then stated the principle of 'competitive exclusion'. Darwin demonstrated that there is a competition between animals as a result of the destruction one another.

In general, 'fitness' has been defined in many studies as the average reproduction rate, for instance, by Haldane in 1932, Maynard-Smith in 1982, Metz et al. in 1992 and Gorban in 2007 [75, 91, 134, 142].

Haldane first introduced dynamics systems with inheritance in [91]. Then, Maynard-Smith defined Evolutionary Stable Strategy (ESS) in [134]. In 2007, Gorban, studied non-linear kinetic systems with conservation. 'Inheritance' presents this conservation of support [75].

If the reproduction coefficient is not a monotonic function of the population density, this is referred to as the Allee effect. Gorban, in 1989, demonstrated that if the average population density is less than optimal density, then the evolutionary optimal strategy for individuals when the Allee effect is life in clumps with optimal density [81]. Petrovskii et al. described the patchy invasion with the predatorprey model in [171]. Lewis and Pacala [123] studied the spread of invasive species and Petrovskii et al. presented a mathematical model to describe that study. Moreover, Morozov et al. proposed a means of population invasion through such patchy dynamics via irregular motion and interaction of different species in [143].

1.1.1 Animal movement

Animal movement depends on the associated physiological and psychological conditions [145, 232]. Animals need to eat, find the proper habitat in which to survive, find mates, and escape life-threatening conditions or severe competition. The type of movement can change according to habitat such as the availability of food sources, the quality of location, or invasion by predators or competitors. Therefore, this moment-based behaviour can be considered as related to three processes: the animal's internal state, movement behaviour, and external factors [145].

If the habitat is high quality, such as having a rich food source or no lifethreatening conditionality, animals will spend less time attempting to find food compared to lower quality habitats. This type of habitat affects the animal's movement path. If the local habitat is larger than average patch size, searching food desire can transform across multiple patches. For instance, in North America, raccoon home range sizes enlarged when extent of forests and number of water sources decrease [13]. When the raccoons had larger home ranges, their hourly movement rates were higher and they occupied small patches. They had to move huge distances to survive, for instance to find food sources.

In this thesis, we present a number of animal movement terms: kinesis and taxis. Fraenkel and Gunn, in 1940, defined 'kinesis' and 'taxis' terms as follows "Undirected locomotory reactions, in which the speed of movement or the frequency of turning depend on the intensity of stimulation, we call kinesis." and "The term taxis is used today for directed orientation reactions. Thus, positive and negative photo-taxis mean respectively movement straight towards or straight away from the light. We use the word only for reactions in which the movement is straight towards or away from the source of stimulation." [66].

Keller et al. used the term kinesis to describe chemical effects on cell locomotion [108]: "Chemokinesis. A reaction by which the speed or frequency of locomotion of cells and/or the frequency and magnitude of turning (change of direction) of cells or organisms moving at random is determined by substances in the environment. Chemokinesis is said to be positive if displacement of cells moving at random is increased and negative if displacement is decreased."

Kinesis can be defined as having two forms. One is *ortho-kinesis*. This is a reaction whose speed is determined by the intensity of some given stimulus. Kline-kinesis is a reaction in which the frequency is determined by the intensity of the stimulus [108].

1.1.2 Random walk

The random walk theory was first studied by Brown in 1828 [22], and helps to describe a phenomenon that became known as Brownian motion. Random walk theory can be expressed as the irregular motion of individual pollen particles in a fluid. Although scientists had been studying probability theory for centuries, random walk theory only entered the literature at the beginning of the twentieth century; when Pearson and Rayleigh published a discussion in the journal of Nature in 1905. Uhlenbeck and Ornstein developed random walk theory with the mean-reversion process in 1930 [218]. The first, basic model of random walks is uncorrelated and unbiased. Here, 'uncorrelated' indicates that the direction of movement in any given instant is unrelated to any previous directions of motion; the location of the next movement is only related to the previous location. 'Unbiased' indicates that the movement is completely random, in the sense that there the direction or location is unrelated to the previous location. For example, if a given movement is allowed to proceed in any direction, then this can be referred to as Brownian motion. This type of movement is also described by the standard diffusion (heat) equation.

Random walk can be broadened in three ways: correlated random walks (CRW), biased random walks (BRW) and both correlated and biased random walks (BCRW). Correlated random walks (CRWs) allow for some form of correlation between successive steps [165] such that the direction has a local bias; that is, each step tends to be in roughly the same direction, though the influence due to the initial direction decreases over a long period. Most animals show CRWs, and this type of random walk has been frequently used to model animal movement (e.g. [20, 105, 200, 201, 214]).

CRW introduces a correlation between the orientations of successive steps, where this orientation includes a local bias: any step is related to the previous one in the same direction, but the initial point of the movement effect vanishes, the movement will be uniformly distributed in the long term. Since animals have the necessity to perform curvilinear movements; they have aimlessly motion as steps or turns. Any step length distribution can be used; however, the mean step should be considered carefully [20].

If the movement is consistently bias in the direction of the preferred direction or towards some given target, then this random movement is referred as a biased random walks (BRW). BRW and BCRW present consistent bias in the preferred direction. These two random walks refer two type of motions: taxis and klino-kinesis. Other kinesis forms were not considered, since they are space-use mechanisms [14, 20]. Bias factor can be related to the external [97]. Othmer et al. (1988) [158] claimed that jump positions can determine the type of uncorrelated random walks. Generally, CRW and BCRW can be considered to be velocity jump processes, since this process includes random changes in velocity [158, 159].

1.1.3 Animal adaptation to survive

Adaptation can be defined as an "effective design for reproductive survival". The adaptation, 'fitness', can have an alternative definition as Medawar stated in 1960 [139] "The genetical usage of 'fitness' is an extreme attenuation of the ordinary usage: it is, in effect, a system of pricing the endowments of organisms in the currency of offspring, i.e., in terms of net reproductive performance. It is a genetic valuation of goods, not a statement about their nature or quality."

Animal adaptation can be measured by net reproductive performance. We can obtain this measure by counting past and present individuals. Medawar's definition is important since it emphasizes reproductive success as the basis of natural selection [192]. Animal survival is certainly the result of the reproduction. If the reproduction is explained entirely on the individual adaptation, the survival of a species could in fact be considered to be an incidental effect. Survival can be accepted as a group or individual.

There is a correlation between the reproduction and mortality rate. Low death rates bring low reproduction. There are two reasons for such an effect of mortality on reproduction: the population size and resources. Although one species is well adapted, the carrying capacity of the environment will limit the numbers this species can reach. Once these limits have been reached, the individuals will start to die.

Environmental conditions affect animal reproduction and mortality. Environmental change typically has a negative influence on biological systems in terms of the well-being and survival of a given species. Organisms will react to abnormal conditions such as invading organisms or harmful weather effect. If animals are being adversely affected by environmental conditions, then they will search for better habitats. However, if suitable areas are already occupied by other species, competition will occur as a result.

Moving from one habitat to the other one is caused not only by individual fitness but also the population dynamics, genetics and species distribution [39, 53, 92, 93]. It is important to understand the relationship between dispersal and population dynamics to manage and predict a given population's response to the environment; for instance, the reactions to habitat fragmentation, climate change, and the invasion and spread of alien species can be discussed to such ends [21].

The evolutionary reasons for dispersal strategies can also be considered. We can give examples of animal migration or survival reasons such as kin competition, in-breeding, resource competition and environmental stochasticity. Dispersal may vary with species depending on their life histories and their reaction to the environment. Dispersal also results in certain costs, or consequences which can be paid during the dispersal movements or by investing resources ito influence dispersal capacity. Costs and benefits of dispersal will depend on space and time, and indeed individuals within the species itself.

In its extreme, dispersal might also carry the risk of extinction for a population. This might be minimized by colonizing an empty habitat, and indeed such colonization can balance the loss of other populations [92, 93].

1.1.4 Insect migration as an example of animal movement

A widely used example of animal migration is insect migration. Further, in these subsections, we will consider the insect movement problem.

Global changes give rise to various ranges of natural environment. These natural changes, such as climatic and weather, affect the locations of insect, their population dynamics, abundance, and feeding behaviour. Recent studies, for instance, suggest that the Asian Longhorn Beetle distribution is affected by various factors including the anthropogenetic, biotic and a-biotic [19, 197]. High or low temperature effects often govern insect reproduction, diapauses, emergence, flight and dispersal rates. The high-temperature threshold can affect population size, although cold temperatures can also plays a significant role. For example, insects can be affected by cold weather and it will cause dark body colour compare to living in a hot climate. In addition to a-biotic causes, biotic factors can affect insect adaptation physiologically, behaviourally and morphologically, and also affect their populations.

1.1.4.1 A-biotic factors

A-biotic factors are non-living features which can influence the places in which plants or animals live. Certain factors such as the thermal factor affects changing the position of pest by stimulating genetic potential, fertility rate, and mortality [59, 178]. It was observed that the young rice leaf folder can be affected at 35 °C, and they cannot even lay eggs.

1.1.4.2 Insect populations at high-temperatures

In general, the length of time that insects can live for increases or decreases with temperature factors [178]. For instance, the *Helicoverpa armigera* egg period has been determined as 7.9 days at 28 °C; however, it can be as long as 10.4 days at 25 $^{\circ}C$ [95, 96]. In coastal regions, a-biotic factors such as soil salinity can greatly affect the survival of terrestrial insects. For instance, the influence of global warming and meteorological factors on rice insect pests were studied between 1992 and 2008 in Korea [112]. There is another case study of the effects of climatic change, such as global warming, on European forests. Ectothermic organisms demonstrate an important response against mortality, reproduction, fecundity and community interactions [148]. These insects can die in the temperatures 9-55 °C. Many species of insects (99%) will die at 50 °C under 2.5 hours, their survival is generally dependent on being in more optimal temperatures. On the other hand, for the management of insect pest population fluctuation, there are various factors like physiological and environmental temperature which have an important relation [67]. In addition to that ants soil temperature is 45.8 ± 1.3 , and this temperature is higher than their thermal limit [5].

1.1.4.3 Insect response to low-temperature

Low-temperatures can affect many kinds of insect physiologically, mechanically and behaviourally. The physiological and behavioural responses of insect to abiotic factors were first discussed in [199].

Let us consider, insects live on the hills. They cannot survive in winter, since the cold weather on the hills. Insects run to leave their eggs on the hills; however, there is density control. The concentration may be too much. Then they can leave these eggs in the down places. That is, late insects laid their eggs to down. However, an unexpected winter comes and some of these eggs die because of the environmental effect. Then summer comes, and the downside eggs will survive with the less winter effect.

Thermal effects on reproduction have been studied, and also the survival rate of insects were first discussed in [106, 178]. Researchers observed that insects cannot endure particularly high and low temperatures. Mortality was found increase and reproduction was significantly affected away from optimal temperature ranges.

1.1.4.4 Insect responses to genetic factors

The immune system of some insects can be affected by environmental stress via neurohormone or the stress hormone. Insects can reduce stress by some biological functions, though stress itself plays a key role in survival [47]. Respiration and metabolism in insects can increase at high temperatures. The endocrine and nervous systems of insects can be affected by temperatures which are above or below certain critical thermal points; also such extremes of temperature can influence their development and behaviour [1, 149, 161].

1.1.4.5 Gas effects on insect population

Insects are affected by certain gases, frequently in a concentration-dependent manner. Extremely low or high levels of the gas can have an impact on insects' bodies, such as hypoxia or hyperoxia; namely, athe lack of oxygen or high excess of oxygen, respectively [175].

1.2 The general aim of the study

The main aim of this study is to present a new reaction-diffusion model that includes purposeful kinesis. Taxis and kinesis movements describe two types of behaviour: taxis is a guided movement, whilst kinesis is an undirected movement. In this proposed model, diffusion coefficient depends on the reproduction coefficient. The well-being of the population is measured by the local and instant values of the reproduction coefficient. The animal movement, or dispersal to the new area to survive, evolves under the control of natural selection. This strategy should increase Darwinian fitness. Therefore, the new model should include the kinesis parameter, as we initially proposed in the basic reaction-diffusion model, and then introduced to the *minimal models of purposeful kinesis*. We explore the properties of the population using numerical experiments. We observe that the new kinesis model is beneficial for the assimilation of patches of food or periodic fluctuations. Furthermore, we analyse the non-monotonic behaviour of the reproduction coefficient. Through the Allee effect, we understand that this model may not be always beneficial; the spreading and invasion can delay.

1.3 Methodological and theoretical basis

In mathematical modelling, the reaction-diffusion equations have been studied in several fields, and have been the subject of intense research. Flux was first studied by Maxwell in 1881 with regards to electromagnetism in [136]. Flux, J, depends on motion with speed V and concentration C, advection is flux with a given velocity V:

$$\frac{\partial C}{\partial t} = -V\nabla C + D\nabla^2 C. \tag{1.1}$$

where $-V\nabla C$ describes advection and $D\nabla^2 C$ describes diffusion with the diffusion constant D. For example, we can imagine a river. Animals flow through the river with a given velocity and 'concentration', C.

Fick's first law is the diffusion equation. This law states that if D is the diffusion and C is the concentration on a space x, then the flux is:

$$J = -D\frac{\partial C}{\partial x}.$$
(1.2)

The time derivative of concentration is the negative divergence of the flux

$$\frac{\partial C}{\partial t} = D \frac{\partial^2 C}{\partial x^2}$$

This equation is Fick's second law. Gauss-Ostrogradskii theorem states that:

$$\iiint_V \operatorname{div} J \, dV = \iint_S Jn \, ds$$

the left-hand side of the equation is the integral over the volume, V, the right-hand side of is the surface integral, and n is the outward pointing unit normal field of the boundary of the volume V. This theorem was first presented by J.L. Lagrange in 1762, then in 1813 was independently discovered by C.F. Gauss [71], in 1828 by G. Green [86] and in 1831 by M.V. Ostrogradsky [157]. Hence, with this theorem, the diffusion equation is just a conservation law which indicates that flux is the cause of all concentration changes.

Fick used the conservation law and the combination of the diffusion and Fourier's law for heat conduction in his work in 1822 [65], and Ohms law for electricity in 1827 [153]. The fundamental patterns of diffusion were developed by Graham for the diffusion of salts in water [85], where in these studies he made an analogy between the diffusivity of various salts. Before diffusion in liquids, in 1833, he explored diffusion in gases. After this study, in 1863, J.C. Maxwell used Graham's data to calculate diffusion coefficients of gases. Hence, Maxwell's diffusion theory is based on gas kinetics [135]. In 1871, Boltzmann generalized the Maxwell equation and restated it as the Maxwell-Boltzmann distribution in [18].

Einstein introduced the theory of the diffusion coefficients of liquids which includes diluted particles. In addition, he discussed particle motion in liquids under a constant extrinsic force and diffusion in [57]. Einstein's kinetic theory connects the diffusion coefficient and mobility,

$$D = \mu k_B T$$

where D is the diffusion constant, μ is the mobility, k_B is the Boltzmann constant, and T is the absolute temperature.

In 1935, Teorell [210] studied the mobility-based approach. He presented his theory on the diffusion of ions through a membrane and defined flux as:

$Flux = mobility \times concentration \times force.$

This is called the Teorell formula. Diffusion force as a result of concentration gradient is given by:

$$F = -RT\frac{1}{C}\nabla C = -RT\nabla \left(\ln\left(C/C^{eq}\right)\right).$$

Here R is the universal gas constant, T is absolute temperature, C is the concentration, and C^{eq} is the equilibrium concentration. In the population dynamics, kinesis is modelled by modification of the mobility, and taxis is modelled by adding new forces.

Predator-prey models were introduced as space and time representations in [131, 163, 194] and investigated by Lee et al. [115]. Taxis can appear when individuals start to change their pattern of movement [115] according to external conditions, for the formulation of such systems describe the prey-taxis systems. Taxis is a function of force; that is, taxis is a directional movement. Force changes the direction. For instance, when you put a plant in the window during the summer, it will grow towards the light, i.e., towards the window. This effect is referred to as positive phototaxis since it is a directional movement towards the light (in contrast to a non-directional or random movement). Negative phototaxis can be considered to be a directional movement away from the light. Therefore, taxis can occur either towards or away from a stimulus, as subject to the organism and stimulus in questions. On the other hand, kinesis is mobility. V is the speed which depends on the direction x. Flux is proportional to the concentration. If there is a greater concentration in a given position, then the prey or predator will move in this direction. Therefore, this describes taxis as a directional movement towards (positive) or away from (negative) a given stimulus. Let us consider a system with food concentration. Flux then can be introduced with taxis as follows:

$$J = -D\nabla C + VC,$$

$$\frac{\partial C}{\partial t} = -\nabla J = \nabla \left(-D\nabla C + VC \right)$$

Moreover, it was determined that a continuous travelling wave can appear for prey-taxis in a model that includes the Allee effect. The model for prey-taxis that is under biological control was presented with a reaction-diffusion-advection in [190]. Spatial patterns of random movement in plankton populations with different velocities were investigated in [130]. Additionally, in a plankton community model, the directional movement of zooplankton leads to the generation of patterns; zooplankton move through the high density of phytoplankton [129]. It has recently become clear that it is important to investigate whether the spatial heterogeneity of species is related to the stability and coexistence of them in ecological systems [219]. The movement of animals cannot purely be explained through random movements. They have directional or non-directional movement. Modelling the rapid dispersal of predators through random diffusion shows a certain stabilization of the the associated population dynamics. Prey-taxis can occur with spatial heterogeneities such as prey density gradients [26, 27, 35, 62, 102].

Kareiva and Odell presented a prey-taxis model in [104], and they derived predator accumulation data in regions of the high prey population levels. In addition to this study, to reach the prey population as a resource, the mean time for travel of the predators was explored in [87]. Chakraborty et al. conducted numerical analyses that indicated that prey-taxis can affect biological control. Furthermore, the spatial pattern-formula was investigated between two spider mites in [29, 30, 31].

Animals usually try to find suitable environments to escape from predators or in which to find mates; and they also stock food using their sense of smell. Predators follow this kind of smell to discover the prey [179].

On the other hand, kinesis is a type of movement made in response to a stimulus [100], whereas taxis is a directional movement. Therefore, kinesis is a migration type with undirected responses. For instance, orthokinesis can be defined as changing the speed of movement, or klinokinesis as the frequency of directional changes in response to the intensity of some stimulation relative to an elected habitat [66]. The response of the animal can grow (positive kinesis) or decrease (negative kinesis) [121]. Using partial differential equations, Fraenkel and Gunn's model [66] was applied to various analytical forms in [66, 88, 154, 214]. Moreover, computer simulations were used in [23, 101, 104, 147] to model these equations.

In this thesis, we have investigated kinesis in animal diffusion with a system of partial differential equations for the reaction-diffusion-advection equation. When predators start to eat prey, the prey population start to decrease. The prey will also try to escape from its predators. On the other hand, the predator population depends on its reproduction and death rates; that is, the reproduction coefficient affects diffusion. For instance, woodlice like wet conditions. If the environment is too dry, they usually move away in a random direction, or directions, until they find a damp environment. They will then move less often to try and stay in that environment. It may be noted that the movement is nondirectional; instead, the organism simply moves more or less in response to stimuli. Consequently, we are studying kinesis which refers a non-directional movement in response to a stimulus. Therefore, flux with a kinesis effect which is equal to

$$J = -D(C, V) \nabla C. \tag{1.3}$$

D does not purely depend on concentration, space or time; but also includes a kinesis effect inside itself which will give non-directional random movements in response to a stimuli. Volume, V, can depend on concentration, prey, predator, etc.

For example, bacteria move towards sources of sugars to survive. If the region into which they move has a high concentration of sugar, then the bacteria will effectively cease their movement. As the bacteria eating the sugar, the sugar concentration will become lower. Therefore, they will feel the need to find another place in which to feed themselves.

1.4 Reproduction coefficient and diffusion

In the population dynamics, when we want to define the density of a population, the random motion of individuals can be described in terms of diffusion, and their reproduction in reaction terms. Reaction forms can be chosen in different ways. Lotka and Volterra presented these forms as the interaction of populations and the concentrations or densities of reacting elements in [222].

Reaction-diffusion equations are used to describe concentration and temperature distributions in chemical physics. In this context, the diffusion term describes heat and mass transfer and the rate of heat and mass production is described by the reaction term [222]. Modelling population dynamics is important for biological communities. Volterra's studies [223, 224] are the fundamental work of mathematical ecology, as the modelling of the population dynamics (see also [127, 215]). In brief, the Volterra model is continuous, in the same manner as chemical kinetics. By analogy, the population defines a kind of chemical reactor, whereby various 'chemical' reactions take place. Births, deaths and other types of interaction are possible examples of these reactions [183].

One can match a differential equation (or a system of differential equations, either ordinary or partial differential equations) to the dynamic behaviour of any observed real-life system in the environment. The founder of the mathematical biology of populations, Volterra, explained biological systems through mathematical expressions. Later, the limitations of this methodology were realised. Basically, spatially distributed models were constructed with the reaction-diffusion systems [3, 15, 16, 17, 35, 50, 56, 73, 127, 144, 164, 183, 202, 211, 215]. Kolmogorov, Petrovsky, and Piscounov (KPP) studied such types of equation in detail [110].

The modelling of biological populations is a serious problem: one must assume that the organisms question move over a space randomly and aimlessly [113, 138]. Obviously, such assumptions are not realistic (see, for example, [40, 133, 205]), even for microorganisms [78, 120, 185, 208]. Generally, there are three levels of information patterns. Generally, the first of these is global information access. This information means that the organism knows everything about the conditions, i.e., the environmental conditions, subpopulation densities, main characters in the residence, immigration habitat and immigration costs. The second is a total lack of information; the organism does not have any information with which to make a decision regarding residence or migration areas. The last is local information access. With this pattern, the organism has information about the environmental and reproduction conditions in the locale and its immediate neighbourhood. This is the most debatable pattern since there can be too much available information [186].

The existence of a homogeneous environment characterizes the reactiondiffusion systems in space equilibria where the reaction terms vanish. The waves of animals provide the transition between equilibria. There are some examples of such waves: tumour growth, migration of biological species or propagation of flames [222].

The wave equation was first introduced by Jean-Baptiste le Rond d'Alembert [44] in 1747. He presented a 1-dimensional form:

$$\frac{\partial^2 u}{\partial t^2} = c^2 \frac{\partial^2 u}{\partial x^2},\tag{1.4}$$

where u is the population size and c is a constant.

The scalar reaction-diffusion equation was introduced as

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + F(u). \qquad (1.5)$$

Reaction-diffusion equations were introduced in [61, 110] for a specific reaction term

$$F\left(u\right) = u\left(1-u\right).$$

A population can be defined as a community which lives in the same region and uses the same resources. Let us suppose the population has a size 'u', i.e. the total number of individuals, then the impact of space on the population can be considered unimportant. The size of the population may change with time when births and deaths are changing. Therefore, the population size can be presented as a time-dependent function u = u(t). Changes in population size with time can depend on the environmental or biological conditions and the behaviour of the species. For populations with non-overlapping generations, a natural mathematical technique is a difference equation:

$$u(t+T) = F(u(t)).$$
 (1.6)

Here, the population size with time is u(t) and the size of the next generation with time will be u(t + T), where T is the time between the two generations and F is a function describing reproduction. For insects and plants, species with nonoverlapping generations are indeed observed [222]. Usually, however, generations do overlap, and the population size is a continuous function of time. The mathematical equation for such can be written as an ordinary differential equation:

$$\frac{du}{dt} = F\left(u\right),\tag{1.7}$$

where the function F can be given as the form

$$F\left(u\right) = r\left(u\right)u,\tag{1.8}$$

where r(u) is the so-called reproduction coefficient. Moreover, for u = 0 and $\frac{du}{dt} = 0$. That is, if there are no animal, then there will be no migration. Therefore, if the population does not exist, $\frac{du}{dt} = 0$. If we define mortality as m, m_1 is predicted death and m_2 is not. Then, mortality will be equal to

$$m = m_1 + m_2.$$

The reproduction coefficient r, which can be defined as follows:

$$r = b - m = b - m_1 - m_2,$$

where b is the birth rate and r depends on space x and time t. Globally informed animals have all available information about the reproduction coefficient. However, it is possible that some components of the information are known whilst others remain unknown. Mortality can be the result of a lack of food or death; but, for instance, winter mortality cannot be predicted.

When the conditions are not uniform, then there can be flux and the reproduction coefficient that are dependent on the flux itself. On the other hand, when external conditions change, population density can result in flux. Flux depends on both the environmental and population densities. Hence, the reproduction coefficient can depend on the environment such as forest, river, desert, city, etc. Moreover, it is related to how much information individuals have. Animals can have some information, such as about food. On the other hand, animals cannot predict how cold the weather will be.

When we are considering space, the heterogeneity of the spatial distribution

of a given population cannot be neglected. That is, if the population size is not sufficiently large, one must use the population density u(x,t) instead. The movement of individuals determines the redistribution of the density in space. This movement can be approximated as a random walk; therefore, the diffusion equation can be used to describe the dynamics of the population [155, 156, 201].

Let us define the flux of u by the diffusion, D

$$J = -D\frac{\partial u}{\partial x}.$$
(1.9)

Therefore, the population model concentration is equal to the summation of flux and advection

$$\frac{\partial u(x,t)}{\partial t} = -\frac{\partial J}{\partial x} + F(u), \qquad (1.10)$$

which is equivalent to

$$\frac{\partial u\left(x,t\right)}{\partial t} = -\frac{\partial}{\partial x}\left(-D\frac{\partial u}{\partial x}\right) + F\left(u\right). \tag{1.11}$$

Therefore, when D is constant, this can be rewritten as:

$$\frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + F(u).$$
(1.12)

Here, u(x, t) is the population density, and D is the diffusion coefficient [222].

Instead of this non-spatial model (1.12), we can consider a reaction-diffusion equation by combining the population via diffusion and reproduction (1.11). We can write the model as follows:

$$\frac{\partial u}{\partial t} = r(u)u + \nabla \cdot (D(r(u))\nabla u).$$

where r(u) is the reproduction coefficient, D is the diffusion coefficient and the population size u depends on space. Here, the diffusion coefficient depends on the reproduction coefficient. When reproduction is increasing, D become smaller. The diffusion coefficient changes with mobility and decreases when well-being is greater. The boxed reaction-diffusion equation is the main model of in this study, and we will use this for our own experiments. When the reproduction coefficient is increasing, the diffusion coefficient will decrease monotonically, though it will not drop to zero. Then, we can rewrite the above equation as the following form:

$$\frac{\partial u}{\partial t} = r\left(u\right)u + D_0 \frac{\partial}{\partial x} \left(e^{-\alpha r} \frac{\partial u}{\partial x}\right), \qquad (1.13)$$

where r, u depend on space and α is the kinesis parameter, $D = D_0 e^{-\alpha r}$. In this form, when r is increased, diffusion will decrease monotonically. That is, the mobility drops.

1.5 Thesis outline and main results

In this thesis, we have studied the reaction-diffusion model with kinesis. We introduced the diffusion coefficient as being dependent on the reproduction coefficient. This means that the diffusion will depend on species well-being. This thesis is organized as follows:

Chapter 1 gives a general description of the reaction-diffusion systems. We explained the approaches adopted by previous studies, and also the mathematical and theoretical backgrounds they describe.

In Chapter 2, we describe purposeful and non-purposeful movement. Animal movement can be dependent on a purpose, for instance the animal may have a purpose to run to an exact place, or otherwise they can undergo random movement to leave a region of adverse conditions. We explained evolutionary optimality, which gives rise to the concept of adaptation. Darwinian fitness, which represents the capacity to survive and reproduce, will also be discussed. In this study, we attempt to understand how animals survive. Darwin explained his ideas about the struggle for existence in his book, whilst and Gause gave the quantitative expressions for the competition of two populations. Our study considers animal movement with kinesis. There are similarities and differences between taxis and kinesis movement. Therefore, taxis and kinesis movement were introduced as concepts. Animals use a number of behavioural strategies to survive, and we discussed how the characteristics of the environment can affect these strategies. Finally, we proposed a new model describing a reaction-diffusion model with kinesis. Chapter 3 gives our main results, which were published in 2018, [79]. The proposed model can be expressed as a "Let well enough alone model". The population with kinesis and without kinesis were analysed. We demonstrate that while the population without kinesis is dying, by contrast the population with kinesis was able to survive. If there are periodic fluctuations in space and time of the food density, then purposeful kinesis, defined by the instant and local reproduction coefficient, is evolutionarily beneficial. Moreover, we discussed how these populations can survive in the same environment. The Allee effect was presented in lower and higher diffusion cases, where the behaviour of the populations was illustrated. With the Allee effect, the strategy can delay the spreading of the population. The "Let well enough alone" strategy with too rapid a rate of diffusion can prevent the extinction of the population. At the end of this chapter, we give an example of a predator-prey diffusion model with kinesis.

In Chapter 4, we propose the model which includes the simple cost of mobility. This model has an intrinsic phase transition. When fatal conditions are increasing, then the mobility increases up to some critical value of the reproduction coefficient. That is, mobility will increase to some limit, and after that, will vanish. These results were published in 2018, [80].

In Chapter 5, we analyse the impact of purposeful kinesis on travelling waves. While the coherence between the diffusion coefficient and reproduction coefficient is increasing, the travelling wave speed monotonically decreases, and at some point stabilizes. The Allee effect parameter and velocity were also found. We can see that as the Allee effect increases, the waves' travelling speed decreases. The waves in the model with kinesis run slower than without kinesis. This can lead to an extinction in the invaded area. This study was submitted recently as [43].

Chapter 6 presents conclusions which give an overall summary of the results of the above chapters. We proposed a new reaction-diffusion model. This thesis will encourage possible future work into the field of the population dynamics, animal movement and reaction-diffusion problems.

1.6 Publications

Main results of thesis were published as

- Gorban, A.N. and Çabukoğlu, N., 2018. Basic model of purposeful kinesis. Ecological Complexity, 33, pp.75-83.
- Gorban, A.N. and Çabukoğlu, N., 2018. Mobility cost and degenerated diffusion in kinesis models. Ecological Complexity, 36, pp.16-21.
- Çabukoğlu, N., 2018. Impact of the purposeful kinesis on running waves. arxiv.

Chapter 2

Fitness and Kinesis

2.1 Introduction

In this chapter, we present the main reaction-diffusion model. We aim to present and explore a simple but basic model of purposeful kinesis. In the environment, animals move in two ways: taxis and kinesis. Taxis is a directed movement; kinesis, by contrast, is an undirected movement. Kinesis movement, generally requires that animals have local information and want to move away from fatal conditions. Taxis also requires a knowledge of non-local information. Escaping from death occurs with natural selection. This strategy should increase Darwinian fitness. We have presented a new model that includes kinesis movement. These can be considered to be the *minimal models of purposeful kinesis*. To analyse this model, numerical experiments have been used. The mean by which kinesis could be beneficial for the assimilation of patches of food or of periodic fluctuations has been introduced. This model cannot be always beneficial, however, such as when the Allee effect is in operation. This can affect the population spread and invasion in the form of a delay to such. We have demonstrated that kinesis will not change positive uniform steady states.

2.2 Purposeful and Non-Purposeful behaviour

Kinesis is a phenomenon observed in a wide variety of organisms, down to the bacterial scale. Purposeful seems to imply a form 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 [181] of animals requires the idea of evolutionary optimality [162].

We can separate purposeful and non-purposeful behaviour from each other in most scientific analyses by selecting goals. We can give the example of a radarcontrolled gun, for instance. The purpose of the gun is to find the enemy. However, if the gun tries to find the main commander, and destroys it, then this means that the purpose of the gun has been changed accordingly. This is an example of cross-purposes.

Weighted roulette acts as purposeful behaviour. The movement of the wheel should include the fact that it ends in a specific place. The aim of the mechanism differs in the inside of the structure since the behaviour of the latter is active, but the wheel and magnetized needle are not.

We can give an example of purposeful behaviour as the behaviour of the mechanical hare. The mechanism will not change except for any effect on its motion or path. We cannot think about the hare without the hounds; that is, the hounds follow the hare. Therefore, the behaviour this describes is purposeful.

We define the clock's behaviour as non-purposeful. In the mechanical system, if we stop it and start the time after half an hour, it will not try to make up for the lost time. We will not consider as a goal or purpose the place or time that the clock stopped since this will not affect the running of the clock. On the other hand, the photo-tropic mechanism has purposeful behaviour, since it reacts to turn a plant toward a source of light [181].

We aim to illustrate some of the differences between purposeful and nonpurposeful behaviour:

(a) For an object, if it forms of a larger system, then its behaviour is purposeful. That is, an object changes others behaviour in the environment. In this manner, an active clock is purposeless, because it is independent of the environment, as is roulette for the same reason.

(b) The object should act together with the goal of purposeful behaviour. In other words, the object gets some, but not all, messages from the environment. (c) Purposeful behaviour refers to the behaviour that the object should move toward or away from the goal. If the goal is static, then the object will have a relationship with the goal in a specific time or space. The goal can also be dynamic; in this instance, the object should reduce the error risk with the relation to the goal. From the above example, the light-seeking mechanism is purposeful.

(d) Purposeful behaviour requires several observations with different initial and subsequent conditions. Some repetitions can occur with random coincidences. Moreover, it is necessary to understand that the relationship between the acting object and the goal of the independent development at a specific time.

(e) The acting object and goal do not have a one-way relationship. The purposeful behaviour of the hounds is the fact that hounds follow a mechanical, and purposeless hare. However, if the hounds pursue a hare that is deliberately avoiding the hounds, then this is a two-way relationship with purposeful behaviour.

(f) Passive behaviour can be purposeful. For instance, the magnetic compass is diverted from its position on purpose. That is, it shows purposeful behaviour, and the goal is the resting orientation. Moreover, in some conditions passive behaviour cannot be purposeful. If the passive behaviour couples with the environment then it is purely energetic and it is expected in the non-purposeful behaviour.

(g) It is not necessary to have complex structures to be purposeful behaviour. For example, while a steam locomotive which runs without a crew is non-purposeful as a complex machine, a magnetic compass is purposeful.

(h) It is important to study whether the behaviour of the object or organism allows an understanding of all complicated levels. The behaviour cannot be described through instantaneous changes in the levels, for example, when an animal's motion is directed towards, in the target direction.

As a result, an acting object usually couples with the environment. The behaviour of an object cannot be precisely decided if it is in an isolated place since it is just a small part of the system. The object coupling with the environment can have purposeful behaviour. That is, the behaviour has a directed goal. A sudden interaction between an object and environment does not change the associated behaviour. Objects have been used to understand the behaviour of an organism. The question arises as to whether the machines can be like men or animals. It has been supposed that humans and animals are like machines from a scientific perspective since their systems can be applied to the machines as well. Therefore, the main reason is accepted choosing objects that in a scientific consideration humans do not have any difference from machines [181].

In this study, we are interested in the biological meaning of purposeful and non-purposeful movement. Animals more frequently move with purposeful behaviour than in a random walk manner. For example, Euglena requires light to survive as an energy source, and the movement of Euglena is direct towards the light. Hence, Euglena displays positive phototaxis. The movement of the animal is not random, as it has the purpose of survival. On the other hand, woodlice prefer moist conditions since their gills can dry out in dry conditions. They move away from such potentially fatal conditions in a random manner. Therefore, they show kinesis behaviour. We will explain taxis and kinesis movement in detail in Chapter 2.6.

2.3 Evolutionary optimality

In recent years, field biologists in particular used optimization and game theory to analyse evolutionary adaptation. Scientists supported the idea that animals and plants are optimally adapted, or at least that they try to live in such a way [84].

Optimization theory starts with Darwin, Wallace, Weismann and evolutionary optimality includes the adaptation idea. To construct the model, we need to define what is being maximized and Darwinian fitness was used for this purpose (see Chapter 2.4). The usual direct criteria are fitness, and expected lifetime can be assumed as a survival strategy. However, many scientists prefer to use the criteria described by Euler-Lotka increasing rate per individual of the population. Otherwise, in most cases, reproduction will be main strategic criteria. Group selection (non-Darwinian criteria) will decrease the extinction to minimum rate and species selection, which is adaptation, refers to the differential extinction of different species [162].
As a fitness measurement, optimization can be accepted as being indirect. For instance, Smith and Savage [203] assumed energy loss to be kept to a minimum when they analysed animal movement. It was assumed that natural selection will maximise in take of energy [162].

2.4 Darwinian fitness

Darwin defined fitness as the capacity to survive and reproduce. In other words, Darwinian fitness was presented as the invading and displacement of several kinds of population in a competitive manner with regards to any remaining food sources. This dynamical process suggests that competitive results are determined by the population growth rate, as measured by the so-called Malthusian parameter. Recent studies show that growth rate decides invasion success in the dynamics of competition for infinite-sized populations. For a population with finite size, the competition has a stochastic process outcome. This process is determined by the rate at which the population reaches its steady-state condition after random perturbations in the number of individual births and deaths. This return rate, which represents the population stability, is referred as the measure of robustness which is analytically characterized by the demographic parameter, evolutionary entropy, and a measure of the uncertainty in the age of the mother of a randomly chosen newborn [49].

Darwinian fitness covers some behavioural factors which represents the animal's experiences of the environmental conditions. In the competition for food, fitness can be considered to be foraging ability; when animals respond to predators, fitness appears in this instance as visual acuity and in the competition for mates, whilst the capacity to intimidate might represent a new dominant trait.

Fisher pointed out that Darwin's qualitative ideas can be transformed to selective measures of fitness in 1930 [60]. Fisher claimed that the demographic components of age-specific fecundity and death rates must overlap. Mortality rates and the rate of individual reproduction shows us the rate of increase in population size. Fisher presented this quantity as an index of Darwinian fitness and named it the Malthusian parameter; it is the fact that Maltus presented important studies on the population dynamics. Fisher's study is accepted as a cornerstone of ecology and the population genetics [34, 180, 207].

Gause was the first, historically, to propose the number 'dimension of the environment'. This number refers to the connection between the number of species and food. He proposed this famous principle named 'the Gause principle'. However, according to him, Gause developed Darwin's idea of the struggle for existence [70, 75].

Evolutionary ecology has been facing unrelated approaches for many years. However, over the last 10-20 years, the mathematical ecology has changed this approach in that there was now a general fitness measure. This fitness gives an indication of the overall timescale for potential invasions. Characterizing this invasion give rise to the idea of evolutionary stable life strategies (ESSs) that can be assumed to be traps for the evolutionary random walk [142].

The well-being of an organism can be measured by individual fitness. Moreover, this can be defined for every moment, since it is an instant value. 'Fitness' was defined in mathematical biology as an average reproduction rate over a long period [75, 91, 134, 142]. This refers to Darwinian fitness. Since taking the average of the reproduction coefficient over many generations and not a momentary state of individuals, it is non-local in time [76].

The instant individual fitness (well-being) can be defined as the behaviour of the current state of an organism, and this reflects the nonoptimality of performance. The well-being can be measured as being between 0 (death) and 1 (maximum performance). If the organism lives at some level of well-being, then this can be considered as a factor in the lifetime fitness. The organism, to determine fitness, acts independently of other factors. Fisher, in 1930, presented these ideas in [60]. Haldane analysed Fisher's basic model in [91]. The term 'independence' in this instance is presented as being multiplicative. Individual fitness appears in particular aspects of performance such as answering environmental problems. The instant individual fitness connects all different performances into one quantity.

Haldane first studied dynamics systems with inheritance in [91]. In the pioneering book 'The Causes of Evolution' (1932), he gave the relationship between inheritance and optimality. He later continued with evolutionary strategies and evolutionary games. Maynard introduced the Evolutionarily Stable Strategy (ESS).

In many cases, optimality can be deduced from kinetic equations in a form of maximization of the average time reproduction coefficient – Darwinian fitness [75, 142]. The application of this idea to optimization of behaviour is the essence of evolutionary game theory, as is its applications to the population dynamics [99].

According to Metz et al., evolution does not maximize fitness when various simplifying assumptions are made. Rather, they discussed a number of complex ecological scenarios. We can think about short-term interactions between individuals, for instance. Invader dynamics can be represented with linear equations, and the coefficients can be represented by time-dependent variables. They are mainly focussed on a finite dimensional and discrete time model. The infinite dimension model was studied in [142].

We can suppose a finite-size population and that the population has finite number of '*i*-states', or physiological differences. For instance, different ages of individuals or nutrition differences. '*x*-states' represent the spatial location. The '*h*-state' is the combination of i - x states. The population size at time *t* and location *x* (*h*-state) is defined as N(t), and the total population size is |N(t)|[142].

When the population migrates or gives birth or dies, then what happens next? Or what happens when it changes *h*-status? If we refer to the overall condition of the environment as E(t), such as temperature or predation effects, it can be assumed that E(t) is density-independent function [142]. Then,

$$N(t+1) = B(E(t))N(t),$$

where B(t) is a matrix depending on E(t) as

$$N(t) = B(E(t-1))B(E(t-2))\dots B(E(0))N(0).$$

The theorem shows that N will be independent from N(0) with time. Moreover, the long-term growth rate is a constant. This quantity can be expressed as taking a maximum value as time tends towards infinity. It is equal to

$$s = T^{-1} \{ \ln |N(T)| \ln |N(T) - \ln |N(0)| \}.$$

This value represents the selection coefficient and it is known as the Lyapunov exponent of B(E(t)). When it is smaller than 0, the population will be extinct. s can be defined as 'the fitness of a life history phenotype in a given environment'. We cannot say that 's' has all the properties of the fitness of a population, but it still gives a certain connection between the population genetics and evolutionary ecology.

We can construct a model to see the matrix form of the population models with density dependence and also to see the Lyapunov exponents [142] in the population dynamics, as described in [10].

Suppose cannibalistic population consisting of juveniles with density $N_j(t)$ and adults with density $N_A(t)$. Every year an adult gives birth to r children and pe^{-bN_A} of them become adults in the following year. Then we can write the matrix B as follows:

$$B(E(t)) = \begin{bmatrix} 0 & r \\ pexp(-bN_A) & p \end{bmatrix}$$

with

$$E(t) = N_A(t).$$

The Lyapunov exponent of the infinite matrix $B(E(0)), B(E(1)), B(E(2)), \ldots$ is 0. If we linearise the bounded orbit as $\overline{N}(0), \overline{N}(1), \overline{N}(2), \ldots$ and define

$$M(t) = N(t) - \overline{N}(t).$$

Then the first approximation can be written as

$$M(t+1) = D(t)M(t)$$

with

$$B(E(t)) = \begin{bmatrix} 0 & r \\ pexp(-b\overline{N}_A(t)) & -bpexp(-b\overline{N}_A(t))\overline{N}_j(t) + q \end{bmatrix}$$

 $D(0), D(1), D(2), \ldots$ defining the stability of orbit, where at least one of them has to be positive [142].

Metz et al. stated that we can find the best available fitness using nonlinear analysis with Lyapunov exponents. Evolution can be limited by mutation. Moreover, ESSs can be considered as the final stage in a complicated genetic structure. It was considered that this study can be extended to structured populations, but only for a dynamical equilibrium population. Fluctuations in the environment can be important, but are generally also hard to study [142].

Haldane first expressed the study of dynamical systems with inheritance and generated basic forms such as steady-state distributions. His study can be assumed as the first to consider selection systems. In this study, the population was observed as having asymptotic behaviour. In 1932, he published the book 'The Causes of Evolution' and explained the connection between inheritance, the conservation of distribution support and species' optimality [91]. Haldane, Semevsky and Semenov generalized the model for a discrete time in 1982 [195] and also Gorban for a continuous time period in 1984. Gorban developed the theory of systems with inheritance and expressed some applications to mathematical ecology problems in [75, 77].

Gorban studied the finite-dimensional asymptotic behaviour of infinitedimensional dynamic systems. Finite-dimensional asymptotic behaviour generally represents a non-linear kinetic system with conservation. These systems can be seen in many areas of biology, chemistry and physics. 'Inheritance' defines this conservation of support. The finite-dimensional asymptotic appears in the 'natural' selection form. It was observed that, after some time, conservation of support is a finite set of narrow peaks which over time become increasingly narrow and slow. When the time approaches infinity $t \to \infty$, these peaks do not stabilize and the path covered tends to infinity. He presented the drift equations as the observation of the motion and stability of these peaks in [75]. The common equation is the distribution support, which does not increase over time as per the following:

$$\frac{d\mu}{dt} = k_{\mu} \times \mu \tag{2.1}$$

 μ represents each distribution and k_{μ} is the reproduction coefficient. The operator $\mu \to k_{\mu}$ is non-linear. μ_i are positive vectors and $X = \{x_1, \ldots, x_n\}$ is a finite set, therefore we can write the above as a system of equations:

$$\frac{d\mu_i}{dt} = k_i \left(\mu_1, \dots, \mu_n\right) \times \mu_i.$$

We can transform the equation to the following biological form: μ defines the distribution over inherited species, organisms or genes. In Eq. (2.1), conservation of support can be considered a form of inheritance and this system has been referred to as 'systems with inheritance'. The system transforms biological information into inheritance and mutations.

The systems with inheritance were first applied to the population dynamics and genetics. Eq. (2.1) presents the distribution of animals or genes. x can be introduced as the inherited variations, species or genes. Inherited generations of animals give appropriate results about the modelling of changes in the community under specific conditions.

Gorban [75] presented the general results of systems of inheritance i.e., the optimality principles for limit distributions, the points of the limit distribution support, and selection efficiency. He developed this simple model for 'reproduction + small mutations' systems.

w-limit sets were used to describe systems with inheritance. The solution to the above system is

$$\mu(t) = \mu(0) \exp \int_0^t k_{\mu(t)} d\tau.$$

The equation can be rewritten as the dependence of μ and the reproduction coefficients k on x:

$$\mu(t) = \mu(0) \exp\left(t \langle k_{\mu(t)} \rangle_t\right),$$

 $\langle k_{\mu(t)} \rangle_t$ as the average reproduction coefficient.

Let's μ^* be the *w*-limit point of the solution $\mu(t)$. Then, when $t_i \to \infty$, there exists $\mu(t_i) \to \mu^*$. The optimality principle is

 $k^{*}(x) = 0$ if $x \in supp\mu^{*}$, $k^{*}(x) \leq 0$ if $x \in supp\mu(0)$. When $\mu(t)$ has limit cycle behaviour, then all $\mu^{*}(t)$ have the same support. These points are the maximum averaged over the reproduction coefficient on the support of $\mu(0)$:

$$k^* = \langle k_{\mu(t)} \rangle_T = \frac{1}{T} \int_0^T k_{\mu^*(\tau)} d\tau.$$

 k^* defines the functions of support of *w*-limit distributions. Therefore, we can write the optimality principle for the reproduction coefficient $k_{\langle \mu \rangle}$ of $\langle \mu \rangle$

 $k_{\langle \mu \rangle}(x) = 0$ if $x \in supp\mu^*$, $k_{\langle \mu \rangle}(x) \leq 0$ if $x \in supp\mu(0)$. This is known as the generalized Volterra averaging principle [225].

Gorban presented two main theorems about selection efficiency. This principle represents the first application for w-limit sets. When the time approaches infinity, $t \to \infty$, it is necessary to have a selection for the system with inheritance. There is a 'best' choice for the selection. Gorban studied the theorem of selection efficiency and the basic formula for the selection effects is presented in [75]. Suppose that X is a compact metric space without isolated points.

- **Theorem 2.1.** 1. For system 2.1, the w-limit distribution is nowhere dense in X-compact metric space.
 - 2. Suppose that ϵ_n is an arbitrary positive sequence. For system 2.1, finite sets can approximate the support of any w-limit distribution uniformly and faster than $\epsilon_n \to 0$.

To this point, only the individual *w*-limit distribution has been presented. When $t \to \infty$, the peaks can get narrow and move slower, and do no reach to the fixed points. Gorban proposed the first drift equations in [74].

Let $\{x^{\alpha}\}$ set be the finite support, and where the distribution is $\mu = \sum_{\alpha} = N_{\alpha} \delta(x - x^{\alpha})$. The dynamics can be written as follows:

$$\frac{dN_{\alpha}}{dt} = k_{\alpha} \left(N \right) N_{\alpha}, \tag{2.2}$$

where N refers to the component vector of N_{α} . $k^*(\{x^{\beta}\})(x)$ is the reproduction coefficient of the support $\{x^{\alpha}\}$

$$\sum_{j} q_{ij}^{\alpha} \frac{dx_{j}^{\alpha}}{dt} = \frac{\partial k^{*} \left(\left\{x^{\beta}\right\}\right)(x)}{\partial x_{i}}|_{x=x^{\alpha}};$$

$$\frac{dq_{ij}^{\alpha}}{dt} = -\frac{\partial^{2} k^{*} \left(\left\{x^{\beta}\right\}\right)(x)}{\partial x_{i} \partial x_{j}}|_{x=x^{\alpha}};$$
(2.3)

Let us switch the equation to logarithmic time as $\tau = \ln t$ and

$$b_{ij}^{\alpha} = \frac{1}{t} q_{ij}^{\alpha} = -\frac{\partial^2 \langle k\left(\mu\right)_t \rangle}{\partial x_i \partial x_j} |_{x=x^{\alpha}}$$

We can derive equation (2.3) for large t:

$$\sum_{j} b_{ij}^{\alpha} \frac{dx_{j}^{\alpha}}{d\tau} = \frac{\partial k^{*} \left(\left\{x^{\beta}\right\}\right)(x)}{\partial x_{i}}|_{x=x^{\alpha}};$$

$$\frac{db_{ij}^{\alpha}}{d\tau} = -\frac{\partial^{2} k^{*} \left(\left\{x^{\alpha}\right\}\right)(x)}{\partial x_{i} \partial x_{j}}|_{x=x^{\beta}} - b_{ij}^{\alpha};$$
(2.4)

The drift Eqs. (2.3, 2.4) indicate the peaks of this finite set $\{x^n\}$ and q_{ij}^{α} . Moreover, the distribution density can be described as the sum of Gaussian peaks:

$$\mu = \sum_{\alpha} N_{\alpha}^* \sqrt{\frac{\det Q^{\alpha}}{\left(2\pi\right)^n}} exp\left(-\frac{1}{2}\sum_{ij} q_{ij}^{\alpha} \left(x_i - x_i^{\alpha}\right) \left(x_j - x_j^{\alpha}\right)\right),$$

where Q^{α} is the covariance matrix (q_{ij}^{α}) .

2.5 The struggle for existence

Darwin expressed his studies on the struggle for existence in a broad manner that he pioneered the destruction of one another in addition to the competition between organisms. He presented a study that indicated animals and plants are connected to each other through a complex relationship in order to survive. The main question is that a life of battle results in the variety of organisms and indicates why one species should achieve 'victory' over another. Thus, we understand that one species has an advantage over another. We can see that not all the organisms have a mutually beneficial relationship. It is a fact that we should keep in mind that each organism will be attempting to increase its size in a geometrical ratio. That is, each species, during some period in its lifespan, whether this be each generation or at intervals, suffers from considerable great destruction and has to strive to survive ([46], pp. 56-57).

Organisms have a complex relationship with nature and they have a particular process in the struggle for existence. This elementary process indicates that one species beats another for a place in a limited environment. Some researchers have observed such systems in the struggle for existence. The results were presented in detail that included laboratory experiences. Through such experiments, it becomes clear that we can answer the question: 'Why has one species been victorious over another in the great battle of life?'. We still cannot definitely explain this complex process and its properties. It is also probable that the total struggle for existence will be similarly unexplained. There is considerable, and quite extraordinary competition in nature which we cannot properly attempt to discuss. Therefore, we can only highlight the main processes required to survive in life. The various parts of body systems have been studied separately, but then to understand them they need to be considered as a whole.

A number of scientists scientists discussed the struggle for existence in the last century. In such research, a large number of processes have been discussed, but we will only focus on the struggle between groups of organisms differing in structure and mode of life. This competition can be considered to be either indirect or direct in nature. The direct struggle for existence indicates that one species undertakes the destruction of another. For example, fox and rabbit, viruses and human, bear and fish. Another example of the direct form of struggle for existence is that the case where a plant acts as a parasite of another. Indirect competition is also considerable among animals, however. This occurs when two organisms live and share the same place, and need the same food and light to survive.

Gause studied the struggle for existence among animals. He expressed his idea that it is not necessary to ask questions such as 'what are we going to observe in the future as a result of competition among animals' and 'what are the real differences in competition between plants and animals'. He was interested in what these methods, as studied by botanists, actually are, and what do these methods require in the field of zoology? Botanists recognized that experimentation was necessary in order to investigate the competition between animals. According to Clements: "The opinions and hypotheses arising from observation are often interesting and suggestive, and may even have permanent value, but ecology can be built upon a lasting foundation solely by means of experiment. In fact, the objectivity afforded by comprehensive and repeated experiment is the paramount reason for its constant and universal use." [38].

Botanists have performed extensive experiments into plant competition for many years. This relation begins when the newborn plant starts to compete with another, and this competition continuous through all the subsequent stages of development. Therefore, the question arises as to what kind of physiological and morphological reasons brings a victory of one plant over another in their normal environment? The question was answered in this manner. Initial competition starts when the plants are so spaced that one species limits another at the beginning of the reaction. Cumulation firstly increases the advantage, since even a small amount of energy can satisfy a further response and reaction. Plants can preserve or gain access to water via a larger, deeper or more active root system. Moreover, the stems and leaves react to light by absorbing, and this will allow an increase in the amount of food for the next stage of growth in the root system [38].

We need to perform experiments to examine the elementary process of the struggle for existence. We want to discuss the process of destruction and, indeed, the process of replacing one species with another. Gause analysed the mixed population as an experimental study via a large number of environmental factors. That is, we need to examine not just the groups of population growth but also the interaction between the associated individuals. This experiment was conducted as follows: a test tube was filled with a nutritive medium and several species of Protozoa were added which consume the same food or eat each other. Therefore, a number of generations were analysed with numerous experiments to examine the change in the individual population sizes, and also to determine the direct effects of these alterations. Thus, we should be able to gain an objective idea of the main processes of the struggle for existence. The relation between the individuals of the mixed population is a problem, and the struggle for existence among animals should be studied in terms of their movement.

We can see the struggle for existence in animals through an appropriate experiment. We can put some nutrient medium into a tube and we will include two species of animals. We cannot add any other food or change the concentrations of the species. Then, under these conditions, we should see that these species will grow over time. Afterwards, there will be competition between them due to their common food source, but over time the food will be consumed by these animals or the food will rot away. As a result, the population of the animals will not grow after this time. When the population growth stops, we can analyse the amount of energy that has been distributed between the animals during this competition. Moreover, this experiment can be tested as adding a species of 'prey' under the conditions of a limited energy 'predator'. When we follow the process one species will devour the other or we can otherwise maintain the energy at a fixed level or change the food level at certain intervals. Thus, we can learn the kind of situations that can occur through these natural conditions, which level energy is maintained and also we can discuss the competition for the common food to survive.

We can try to understand the main steps in the struggle for existence through experiments, through which a mathematical description of the process can be established. Consequently, we can determine the coefficients for the struggle for existence. In 1874, Nageli made the first attempt to introduce the suppression of one plant by another through a mathematical expression. He started to check the annual increase in size of the plants until they were destroyed. However, this study was not appropriately recognized. Research into plant competition come through lately and still it cannot be properly explained but only the beginning process. Historically, various scientists have conducted in-depth studies in the attempt to set up a mathematical structure describing the struggle for existence in this field. They studied different aspects of such, but in the end came to the same conclusion.

The scientists who studied for the struggle for existence experienced significant difficulties due to lack of data. This data problem was solved in the next years. What are the preliminary studies to make it come through this stage? The rational for the study of the struggle for existence among animals starts after questioning the exact quantitative analysis of the multiplication of organisms. It was noted that studying a mixture of populations is harder than other methods of study. We first need to study a single population group and the competition between them. 'Equations of multiplication' were presented in the following manner:

reproduction coefficient - the destruction coefficient = population size.

However, all these variables could not be formulated exactly. Recently, Vernadsky presented a broad study on the multiplication of organisms. According to this author, the multiplication of organisms can be explained via a geometric progression. This can be expressed as a new formula:

$$2^{b_t} = N_t.$$

t is time, b_t is the exponent of progression (every kind of individual), and N_t is the population size at a certain time t. Also, these variables have no limits. That is, this expression was formulated in terms of infinite progress.

This infinite process can be interrupted purely by external factors. For example, the population dies when temperature is low, or stops increasing due to a lack of food or insufficient space in which to live. According research presented by Linnaeus, Buffon, Humboldt, Ehrenberg and von Baer, if there are no external effects, all the organisms can live but at a different time cover the whole universe due to their reproduction. The growth rate is always different for each kind of organisms and is also related to their size. Small organisms can reproduce faster than large organisms. These generalizations have not been considered in geometrical homogeneous time and space. In real life, we cannot separate time and space. Organisms live in a specific place and in a gas environment or in a liquid. In addition, time cannot, of course, be infinite. The obvious result of this assumption is to set limits to all the parameters, will establish the phenomenon of multiplication of organisms in the biosphere.

There is always a maximal capacity for every species and this number cannot be exceeded. This maximum is observed when the species invade the entire living space, and can be expressed as 'the stationary number of the homogeneous living matter'. The population reproduction gets slower as time progresses and finally reaches this stationary number. In 1920, Pearl and Reed [167] introduced these general ideas mathematically in the form of the logistic curve. This mathematical form indicates that under limited conditions organisms can only reach a limited level when growing geometrically. This was demonstrated by laboratory studies. We note that for the further study of competition in mixed population, a same species mathematical expression can be beneficial.

In 1911, Ronald Ross [182] studied the first step of this theory. He was interested in the struggle for existence between malaria and man through the participation of the mosquito. Ross stated a mathematical form based on this experience. Volterra, in 1926, studied a similar subject independently to Ross. While Ross was working on malaria [182], Lotka, on the other hand, was studying the theoretical chemical reactions. Then, Lotka presented an equation for the interaction between hosts and parasites in his book 'Elements of Physical Biology' in 1925 [127]. Volterra, in 1926, determined similar equations for the struggle for existence without any knowledge of those previous studies in [223]. Therefore, three important scientists stated almost identical results from entirely different studies. After the theoretical structure, experimental studies were prepared and the same results were observed in physics and physical chemistry as the mechanical equivalent of heat (which we will Gibbs' investigations).

We can be sure that the struggle for existence will be studied in the future and will progress through biologists and mathematicians. This problem can be expressed as a biological one, and should be solved using appropriate laboratory experiments. However, in order to understand the problem in more depth, we need to combine theory and experiment, as was presented by Lotka and Volterra. According to Allee [2], mathematical formulations are an important means by which to study population dynamics. Mathematical expressions present the logical arrangements of real-life experiments, but these assumptions can give rise to errors. We have mathematical approaches that can describe population problems. However, we also need some experimental physiology, although results cannot be exactly expressed through equations.

Let N_1 be the first population size and m the number of places the first

species can inhabit. Let N_2 be the second species population size in a mixed environment. Let α be the degree of influence of one species over another and β the influence of the first species. If K_1 and K_2 are the capacities of N_1 and N_2 , then

- $\frac{K_1 (N_1 + \alpha N_2)}{K_1}$ is the opportunity for the growth rate of the first population and $\frac{K_2 (N_2 + \beta N_1)}{K_2}$.
- $\frac{dN_1}{dt}$ and $\frac{dN_2}{dt}$ are the growth rates of the first and second population in a given time in the mixed environment.
- b_1 and b_2 are the birth rates of the populations.
- K_1, K_2 are the maximum numbers of the first and second species.
- α, β are the struggle for existence coefficients.

 b_1N_1 describes the rate of population growth of the first species. Therefore, we can set up the equation for the struggle for existence

$$\frac{dN_1}{dt} = b_1 N_1 \frac{K_1 - (N_1 + \alpha N_2)}{K_1},$$
(2.5)

$$\frac{dN_2}{dt} = b_2 N_2 \frac{K_2 - (N_2 + \beta N_1)}{K_2}.$$
(2.6)

Therefore, Gause expressed these quantitative expressions, (2.5) and (2.6), and the competition between two species in the same environment in his book. These equations suggest that each species will grow in terms of population size, and also the realization of the potentials of the two species can be identified through four processes:

- The first species can decrease its own opportunities for growth when increasing in number (accumulation of N_1),
- The first species growth opportunities can decrease because of the growth of the second population (αN_2) ,

- The second species can decrease its own opportunities for growth when increasing in number (accumulation of N_2),
- The second species opportunities for growth can decrease because of the growth of the first population (βN_1) .

In the struggle for existence, the first species might be victorious or the second could displace it. While they live separately, we consider the coefficients of increase b_1 and b_2 , and the maximum populations K_1 and K_2 . However, when we think about two species in the same environment, then the struggle for existence becomes relevant. α and β present the influence of growth of one upon the other. Therefore, competition is created in the environment.

The stationary state is $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$. This indicates that both $N_{1,\infty}$ and $N_{2,\infty}$ cannot be positive with these α and β in there. That is, one of the species will be extinct. We observe that

$$K_1 = N_1 + \alpha N_2;$$

 $K_2 = N_2 + \beta N_1.$
(2.7)

We can check the stationary state as follows;

$$N_1 - \alpha \beta N_1 = K_1 - \alpha K_2;$$

$$N_{1} = \frac{K_{1} - \alpha K_{2}}{1 - \alpha \beta};$$

$$N_{2} = \frac{K_{2} - \beta K_{1}}{1 - \alpha \beta}.$$
(2.8)

if $N_1 > 0$ and $N_2 > 0$, then

$$K_1 > \alpha K_2; \tag{2.9}$$
$$K_2 > \beta K_1.$$

Therefore, both populations cannot survive together.



FIGURE 2.1: Flow diagram showing the paths through from genotype to Darwinian fitness. Genotype in combination with environment determines the phenotype up to some individual variations. Phenotype determines the limits of an individual's ability to perform day-to-day behavioural answer to main ecological challenges (performances). Performance capacity interacts with the given ecological environment and determines the resource use, which is the key internal factor determining reproductive output and survival.

The instant individual fitness is the most local in time level in the multiscale hierarchy of measures of fitness: instant individual fitness to individual life fitness to Darwinian fitness in the chain of generations. The quantitative definition of the instant and local fitness is given by the equations. The change to the basic equation will result in a change to the quantitative definition.

2.6 Taxis versus Kinesis

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 guided movement to more favourable conditions.
- Kinesis is non-directional change in spatial motion in response to a change in conditions.



FIGURE 2.2: (a) Euglena requires light as an energy source and hence displays positive phototaxis. (b) Woodlice have gills for respiration and tend to prefer moist conditions (their gills may dry out in dry conditions): therefore show kinesis behaviour. Image has been taken from: http://ib.bioninja.com.au/options/option-a-neurobiology-and/a4innateand-learned-behav/innate-behaviour.html.

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

In this dissertation, we aim to present and explore a simple but basic model of purposeful kinesis. The general concept of purposeful behaviour [181] in animals requires an understanding of the idea of evolutionary optimality [162]. 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 [75, 142]. Application of this idea to optimization of behaviour is the essence of evolutionary game theory and its applications to population dynamics [99]. The crucial question for the creation of an evolutionary game model is: which information is available and usable? Dall et al. [45] proposed a quantitative theoretical framework for analysing animal information use in evolutionary ecology. Nevertheless, the question about information which can be recognised, collected and used by an animal requires empirical answers. Answering this question can be very complicated for analysis of taxis, which involves various forms of non-local information. For kinesis the situation is much simpler: the point-wise values of several fields (concentrations or densities) are assumed to be known [184].

In this section, we study PDE models of spatial distribution. We start with the classical family of models. Patlak [165] and Keller [108] proposed a PDE system which is widely used for taxis modelling [98].

Chemotaxis can be defined as biological cell motion or movement of organisms in response to chemical gradients. Keller and Segel's [108] study had an achievement as a result of the simple form, analytical solution and adaptable to the populations of having chemotaxis movement behaviour. This system shows the importance that the mechanism for the individual organisation of biological systems can indicate the ability to display 'autoaggregation'. This has been proposed as a finite-time blow-up and considerable work has been undertaken to determine the blow-up time and whether global solutions to this problem exist. Keller and Segel's model was explored in [98] from a biological perspective in terms of the modelling of chemotactic cell migration, contrast patterning properties, analytical results and classification of the solutions.

$$\partial_t u(t,x) = \nabla \cdot (k_1(u,s)\nabla u + k_2(u,s)u\nabla s) + k_3(u,s)u,$$

$$\partial_t s(t,x) = D_s \nabla^2 s + k_4(u,s) - k_5(u,s)s,$$

(2.10)

where

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

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

Special random processes were introduced for the 'microscopic' theory of dispersal in biological systems in [158]. 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. (2.10) can be produced from kinetic (transport) models of velocity– jump random processes [159, 160] in the limit of a 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 [33]. Chalub et al. [32] found sufficient conditions of absence of finite-time-blow-ups in chemotaxis models. Turchin [213] demonstrated that attraction (and repulsion) between animals could modify the spatial dispersal of the population if this interaction is sufficiently strong. Méndez et al. [140] derived reaction-dispersal-aggregation equations from Markovian reaction-random walks with density-dependent transition probabilities. They obtained a general threshold value for dispersal stability and found suitable conditions for the emergence of nontrivial spatial patterns.

This family of models (2.10) is rich enough and the term $\nabla \cdot (k_1(u, s)\nabla u)$ is responsible for modelling 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 senses, the family of models (2.10) is even too rich: it includes five unknown functions k_i whose only requirement, is one of non-negativity. Cosner [42] reviewed PDE reaction-advection-diffusion models describing ecological effects and the evolution of dispersal, and mathematical methods for analysing those models. In particular, he discussed a series of optimality or evolutionary questions which arose naturally:

- Is it better for predators to track the prey density, the prey's resources, or some combination of the two?
- Is it more effective for predators to slow their random movement when prey are present or to use directed movement along the gradient of prey density?
- Should either predators or prey avoid crowding by their own species?

Cosner [42] also presented examples of when diffusion is harmful to the existence of a species: if the average in space of the reproduction coefficient is negative for all species' distributions, then for high diffusion there is no steady state with a positive total population even if there exists some steady state with a positive total population for zero or small diffusion (for connected areas). The possibility of organisms moving sub- or super-diffusively, e.g. Lévy walks, fractional diffusion, etc. (for example, see [36, 141]), can be combined with the idea of purposeful mobility (see [36, 141]), but we limit analysis in this paper to classical PDE.

In this work, we study the population dispersal without taxis, therefore, the advection coefficient k_2 is set as zero. Such a dispersal strategy seems to be quite limited compared to the general kinesis+taxis dispersal system. Nevertheless, Nolting et al. [150] demonstrated that for the jump models pure kinesis (non-directional dispersal strategy) allows foragers to efficiently identify efficiently intensive search zones without the need for taxis and are more robust to changes in resource distribution.

We also assume a strong connection between the reproduction coefficient $r = k_3$ and the diffusion coefficient. The reproduction coefficient characterises both the competitive abilities of individuals and their fecundity. Darwinian fitness is the average reproduction coefficient over a series of generations [75, 91, 142]. Dynamics maximise the Darwinian fitness of survivors (this is a formalisation of natural selection). Unfortunately, evaluation of this quantity is non-local in time and requires some knowledge of the future. Therefore, we use the local in time and space estimation of fitness and measure well-being via the instant and local value of the reproduction coefficient, r. This is a typical approach, but it should nevertheless be used with caution: in some cases, the optimisation of the local

criteria can worsen long-time performance. We describe one such situation below: using a locally optimised strategy of kinesis can delay invasion and the spread of species through the Allee effect. On another hand, we demonstrate how kinesis controlled by the local reproduction coefficient can be beneficial for assimilation of patches of food or periodic fluctuations.

2.7 Three crucial questions

There are three crucial questions that must be addressed to allow the creation of an evolutionary game model: the use of information by animals, behaviour strategies and the characteristics of the environment. The animals can survive using the available information and they need to find the immigration strategy. The immigration, therefore survival, strategy also depends on the characteristics of the environment.

2.7.1 The use of information by animals

Which information is available and usable? Dall et al. proposed a quantitative theoretical framework in evolutionary ecology for analysing the use of information by animals in [45]. The accurate estimation of ecological parameters determines adaptive behaviour. The animal can develop itself with better information to stay alive when there is competition between individuals. Dall et al. [45] focussed on the decreasing of the adaptation that this can be possible by collecting information from 'passive' and 'responsive' sources. A statistical decision theory was proposed to study the use of information by animals. This theory indicates such a framework for the decision problems which naturally occur and also fits well with evolutionary and behavioural ecology. Statistical decision theory introduces an ideal framework for producing a hypothesis which is testable on animals using information that is 'explicit, quantitative and uncompromising'.

Nevertheless, the question about information which can be recognised, collected and used by an animal requires empirical answers. Answering this question can be very complicated with regards to analysis of taxis, and which involves various forms of non-local information. For kinesis, the situation is much simpler; the point-wise values from several fields (concentrations or densities) are assumed to be known [184].

Sadovsky et al. [184] stated that we need to decide which information is actually available to individuals that are making decisions with regards to migration in the local information area. The global information access model has presented the idea that the population dynamics have been considered station models as follows. The dynamics of each population at station 1 and 2 is presented by the Verhulst equation

$$N_{t+1} = N_t (a - bN_t), M_{t+1} = M_t (c - dM_t).$$
(2.11)

Here, N and M describe population sizes at station 1 and 2. $k^{I} = a - bN_{t}$ and $k^{II} = c - dM_{t}$ are net reproduction coefficients at station 1 and 2, respectively. The model has been considered as discrete time. The population migrates purely based on the possibility that they might find better conditions in another station. Therefore, the individual transition from one station to another can be described as migration. The migration from station 2 to 1 occurs if

$$c - dM < p(a - bN) \tag{2.12}$$

a - bN < p(c - dM) from the station 1 to 2, respectively. Here, p defines the cost of relocation from one station to another. The number of δ individuals will be located with this inequality. At time t, the number of relocated individuals when the migration occurs is:

$$\delta = \min\{M_t, \frac{c - dM_t + pa - pbN_t}{d + p^2b}\}, \delta = \min\{N_t, \frac{a - bN_t + pc - pdM_t}{b + p^2d}\}.$$
 (2.13)

Thus, the migration is first determined, then second the individuals move to the other station and grow according to Eq. (2.11). After migration, each station's population size will have a new form as \hat{N}_t (\hat{M}_t):

$$\hat{N}_t = N_t + p\delta, \hat{M}_t = M_t - \delta \tag{2.14}$$

or it will be:

$$\hat{N}_t = N_t - p\delta, \quad \hat{M}_t = M_t + \delta \tag{2.15}$$

depending on the previous migration decisions.



FIGURE 2.3: Migration between stations [183].

Sadovskiy et al. [184] suggested a model that the population dynamics depends on evolution optimization rather than being random and aimless. The species in question aim to maximize net reproduction. When the population makes a decision, knowledge of information about environmental conditions is important. Migratory behaviour is usually considered to be aimless motion. However, in this model, contrary flows are possible in purposeful migration. This shows optimal migration is not the discriminant effect for models of spatially distributed populations.

In this thesis, the animal is assumed to be very simple: it can only evaluate the previous state of the location given where it is at any given time, but cannot predict future states. There is no memory: it does not remember the properties of the locations where it was before. Therefore, this is the answer to Question 1.

2.7.2 Behaviour strategies

What is the set of the available behaviour strategies? All organisms, from bacteria to humans, have their own set of available behaviour strategies, and no organism can be omnipotent. It is necessary to describe the repertoire of potentially possible behaviours in a constructive manner.

Finally, there is only one available behaviour strategy: to select the current (somehow chosen) location or to move to another one. There are only available

resources to allow for one jump only, so no 'oscillating' jumps between locations are possible. This means that after the change in location the animal selects the new location for reproduction independently of its state. Thus, Question 2 is answered.

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

2.7.3 The characteristics of the environment

What are the statistical characteristics of the environment, in particular, and what are the laws and correlations in the changing of the environment in space and time? It is worth mentioning that all the changes in the environment can be measured by the corresponding changes to 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 be able to adopt one of two states during the reproduction period, A or B. The number of surviving descendants is r_A in for state A and r_B for state B. After that, their further survival does not depend on these areas. 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.

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 offspring without arbitrary information is

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

If an animal chooses the location with the previous state A for reproduction, then the conditional expectation of the number of offspring is:

$$r|_A = (1-p)r_A + pr_B.$$

However, if it chooses the location with the previous state B; then the expected number of offspring 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 in location will increase the expected number of offspring. 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 offspring.

We obtained the simplest model with mobility dependent conditionally expected and a reproduction coefficient $r|_{\bullet}$ under the given local conditions: if $r|_{\bullet}$ is less than the value r_0 expected for the indefinite situation then a jump should be performed, or otherwise the population should stay in the same location. This is the essence of purposeful kinesis for this toy model.

2.8 The standard model

We can state the main equation which the diffusion includes kinesis and the diffusion coefficient depends on reproduction coefficient; i.e. well being.

$$\partial_t u_i(x,t) = D_{0i} \nabla \cdot \left(e^{-\alpha_i r_i(u_1,\dots,u_k,s)} \nabla u_i \right) + r_i(u_1,\dots,u_k,s) u_i, \qquad (2.16)$$

where:

- u_i is the population density of *i*th species,
- *s* represents the abiotic characteristics of the living conditions (can be multidimensional),
- r_i is the reproduction coefficient, which depends on all u_i and on s,

- $D_{0i} > 0$ is the equilibrium diffusion coefficient (defined for $r_i = 0$),
- The coefficient $\alpha_i > 0$ characterises dependence of the diffusion coefficient on the reproduction coefficient.

Chapter 3

Models of Purposeful Kinesis

3.1 Introduction

In this chapter, we introduced the main reaction-diffusion model with kinesis. In the real environment, animals do not move randomly or aimlessly. We present another form of reaction-diffusion equation. In this model, diffusion depends on well-being, which is measured by the reproduction coefficient. That is, animal mobility depends on whether they are happy in their area or not. They think about their own position, and cannot think where the better place is. They can run anywhere to find a better life, and most informative will run as a gradient of the reproduction coefficient. Diffusion coefficient changes with this mobility. Moreover, mobility depends on the reproduction coefficient. This shows that while reproduction coefficient is increasing, the diffusion coefficient starts to decrease. The animals prefer to stay in a good place. This means, if they have a better condition, then they will not want to remove and reproduction will increase, therefore the action of removing to another place, the diffusion coefficient, will decrease. For animals, high death means a necessity of running to another place to survive. And this situation also refers that decreasing reproduction causes mobility, and therefore increasing the diffusion coefficient.

3.2 The "Let well enough alone" model

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 quicker bad conditions. If the well-being is measured by the instant and local reproduction coefficient then the minimal model of kinesis can be written as follows:

$$\partial_t u_i(x,t) = D_{0i} \nabla \cdot \left(e^{-\alpha_i r_i(u_1,\dots,u_k,s)} \nabla u_i \right) + r_i(u_1,\dots,u_k,s) u_i,$$
(3.1)

where:

- u_i is the population density of *i*th species,
- *s* represents the a-biotic characteristics of the living conditions (can be multidimensional),
- r_i is the reproduction coefficient, which depends on all u_i and on s,
- $D_{0i} > 0$ is the equilibrium diffusion coefficient (defined for $r_i = 0$),
- The coefficient $\alpha_i > 0$ characterises dependence of the diffusion coefficient on the reproduction coefficient.

$$\frac{\partial u(x,t)}{\partial t} = D_0 \frac{\partial}{\partial x} \left(e^{-\alpha r(u)} \frac{\partial u}{\partial x} \right) + r(u)u(x,t).$$
(3.2)

$$\frac{\partial u(x,t)}{\partial t} = D_0 e^{-\alpha r(u)} \frac{\partial^2 u}{\partial x^2} + D_0 \frac{\partial u}{\partial x} \left(\frac{\partial}{\partial x} \left(e^{-\alpha r(u)} \right) \right) + r(u) u(x,t).$$
(3.3)

Eq. (3.1) describes dynamics of the population densities for arbitrary dynamics of s. For the complete model the equations for environment s should be added. The space distribution strategy is summarised in the diffusion coefficient $D_i = D_{0i}e^{-\alpha_i r_i}$, which depends only on the local in space and time value of the reproduction coefficient. Exponential dependence $e^{-\alpha r}$ appears because of the simplest singularity-free monotone function and because of deep analogy between r and chemical potential in kinesis and taxis models. For example, the form $1/(1 + \alpha r)$ is not free of singularities and tends to infinity when αr tends to -1.

While the reproduction coefficient is increasing, the diffusion coefficient will decrease monotonically, and will not drop to 0. That is the fact that the diffusion coefficient has been chosen as an exponential function of the reproduction coefficient.

For example, we can take diffusion as following Fig. 3.1. Diffusion depends on well-being measured by this coefficient. We can see that the new models add one new parameter per species to the equations (instead of function $k_1(u, s)$ in (3.1)). This is the kinesis constant α_i . It can be defined as

$$\alpha_i = -\frac{1}{D_{0i}} \left. \frac{dD_i(r_i)}{dr_i} \right|_{r_i=0}.$$

In the first approximation, $D_i = D_{0i}(1 - \alpha_i r_i)$. The exponential form in (3.1) guarantees positivity of the coefficient D_i for all values of r_i .



FIGURE 3.1: The relationship between diffusion and reproduction coefficient, $D_0 = 1, \alpha = 1.$

For good conditions $(r_i > 0)$ diffusion is slower than at equilibrium $(r_i = 0)$ and for worse conditions $(r_i < 0)$ it is faster. Eq. (3.1) just formalise a simple wisdom: do not change the location that is already good enough (*let well enough alone*) and run away from bad location.

We analyse below how the dependence of diffusion on well-being effects patch dynamics and waves in population dynamics.

3.3 Stability of uniform distribution

The positive uniform steady state (u^*, s^*) satisfies the equation:

$$r_i(u_1^*,\ldots,u_k^*,s^*)=0.$$

The linearised equations near the uniform steady state are

$$\partial_t \delta u_i(x,t) = d_i \nabla^2(\delta u_i) + u_i \left(\sum_j r_{i,j} \delta u_j + r_{i,0} \delta s \right), \qquad (3.4)$$

where

- δu_i is the deviation of the population density of *i*th animal from equilibrium $u^*, \delta s = s - s^*,$
- $r_{i,j} = \partial r_i / \partial u_j|_{(u^*,s^*)}, r_{i,0} = \partial r_i / \partial s|_{(u^*,s^*)}$ are derivatives of r at equilibrium.

These linearised equations are the same as for the system without kinesis (with constant diffusion coefficients). Therefore, *kinesis does not change the stability of positive uniform steady states.* Moreover, near such a steady state linearised equations for a system with kinesis are the same as for the system with a constant diffusion coefficient.

There is an important difference between possible dynamic consequences of taxis and kinesis: we proved that Kinesis cannot modify the stability of positive homogeneous steady states, whereas Tyutyunov et al. [217] demonstrated that taxis can destabilise them.

3.4 Utilisation of a patch of food

As a first test for the new model, we used utilisation of a patch of food (a sketch of this gedankenexperiment is presented in Fig. 3.2). The concentration of food in patches is one of the standard ecological situations. Nonaka and Holme [151] considered 'clumpiness' as a main characteristic of the food distribution and developed an agent-based model for analysis of optimal foraging.



FIGURE 3.2: A schematic representation of a patch of food.

From our point of view, the potential of PDE models is not exhausted yet despite of growing popularity of the multi-agent models in dynamics of space distribution of populations [176]. Let us compare two models:

• A system of one PDE for population with the constant diffusion coefficient (i.e. without kinesis) and the same ODE for substrate:

$$\partial_t u(t,x) = D\nabla^2 u + (as(t,x) - b)u(t,x),$$

$$\partial_t s(t,x) = -gu(t,x)s(t,x) + d.$$
(3.5)

• A system of one PDE for population with kinesis and one ODE for substrate:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(as(t,x)-b)}\nabla u\right) + (as(t,x)-b)u(t,x),$$

$$\partial_t s(t,x) = -gu(t,x)s(t,x) + d;$$

(3.6)

These models are particular realisations of the system (2.10)

In this section, for the computations experiment, to solve partial differential equations, first MATLAB pdepe (2017) [166] function has been used for space dimension one. For two-dimensional results below, the MATHEMATICA NDSolve (2014) [146] solver with Hermite method and Newton's divided difference formula has been used.

We selected 1D benchmark (Fig. 3.2) on the interval [-50, 50] with von Neumann boundary conditions and with the initial conditions:

$$s(0,x) = Ae^{-\frac{x^2}{2}}, u(0,x) = 1, A = 4.$$

The values of the constants are: D = 10, $\alpha = 5$, a = 2, b = 1, g = 1, d = 1.

It is the first expectation that the proper kinesis should improve the ability of animals to survive in the clumpy landscape. We can see from Figs. 3.3 and 3.4 that the density burst for the system with kinesis is higher and the utilisation of substrate added goes faster than without kinesis.



FIGURE 3.3: Utilisation of a food patch. Population density burst and relaxation: a) for animals with kinesis and b) for animals without kinesis.



FIGURE 3.4: Utilisation of a food patch: a) dynamics of population density at the centre of patch, b) dynamics of the food density at the centre of patch.

The fluctuation of food decreases faster for the system with kinesis. The population density increases higher for the system with kinesis. This is an essentially non-linear effect because in linear approximation near uniform equilibrium models with kinesis Eq. (3.6) and without kinesis Eq. (3.5) coincide.

3.5 Utilisation of fluctuations in food density

For the second benchmark, we consider fluctuations of the substrate, which are periodic in space and time. Our gedankenexperimet includes two populations of animals. The only difference between them is that the first population diffuses with kinesis (population density v), whereas the second (population density u) just diffuses with the constant diffusion coefficient (no kinesis). The equilibrium values of the diffusion coefficients coincide. These populations interact by consuming the same resource as it described by Eq. (3.7) below

$$\partial_t u(t,x) = D\nabla^2 u + (as(t,x) - b)u(t,x);$$

$$\partial_t v(t,x) = D\nabla \cdot \left(e^{-\alpha(as(t,x)-b)}\nabla v\right) + (as(t,x) - b)v(t,x);$$

$$\partial_t s(t,x) = -g(u+v)s + d[1 + \delta\sin(w_1t)\sin(w_2x)],$$

(3.7)

with von Neumann boundary conditions and with the initial conditions:

$$s(0, x) = 0.5, u(0, x) = 1, v(0, x) = 1$$

The values of constants are: D = 10, $\alpha = 5$, a = 2, b = 1, g = 1, d = 1, $w_1 = w_2 = 1$.

Animals with kinesis have evolutionary benefits in the explored non-stationary condition. We observe extinction of the population without kinesis (Figs. 3.5 and 3.6). This is the concurrent exclusion of the animals without kinesis by the animals with kinesis. At the same time, the fluctuations of the population with kinesis in space and time are lager than for the population without it. It is expected: animals with kinesis rarely leave the beneficial conditions and jump more often from the worse conditions. In the conditions with the reproduction coefficient r > 0their density grows faster and in the worse condition (with r < 0) it decreases faster than for animals with the constant diffusion coefficient.



FIGURE 3.5: Dynamics of population densities in fluctuating conditions: a) growth of subpopulation with kinesis, b) extinction of subpopulation without kinesis c) fluctuating environment.



FIGURE 3.6: Dynamics of population densities in fluctuating conditions at time5 and at one point (the centre of the interval). Competitive exclusion of the population without kinesis by the population with kinesis.

3.6 Spreading of a population with the Allee effect

The reproduction coefficient of a population takes its maximal value at zero density and monotonically decays with the density growth in the simplest models of logistic growth and their closest generalisations. It is widely recognised that such a monotonicity is an oversimplification: The reproduction coefficient is not a monotonic function of the population density [2, 152]. This is the so-called *Allee effect*. The assumption of the negative growth rate for small values of the population density is sometimes also included into a definition of the the Allee effect. The Allee effect is often linked to the low probability to find mates in a low-density population but non-monotonicity of the dependence of the reproduction coefficient on the population density and existence of the positive optimal density can have many different reasons. For example, any form of cooperation in combination with other density-dependent factors could also produce a non-monotonic reproduction coefficient and the existence of optimal population density.

The simplest polynomial form of the reproduction coefficient with the Allee effect is $r(u) = r_0(K-u)(u-\beta)$. A typical dependence r(u) with the Allee effect is presented in Fig. 3.7. The optimal density corresponds to the maximal value of r (by definition). The evolutionary optimal strategy for populations with the Allee effect is life in clumps with optimal density when the average density is lower than optimal density [81]. This clumpiness appears even in homogeneous external conditions and is the clearest manifestation of the Allee effect in ecology. There are multiple dynamical consequences of the Allee effect [12, 137]. In combination with diffusion, it leads to a possibility of the spread of invasive species via formation, interaction and movement of separate patches even in homogeneous external condition [143, 171].

Petrovskii et al. studied predator-prey model with the Allee effect for prey that this can lead to a patchy invasion. The Allee effect causes some specific behaviours such as whereas the coexistence state is unstable, however, on the other hand, there exists no stable limit cycle. Lewis and Pacala [123] stated that the spread of invasive species via the dynamics and interaction of separate patches is more ordinary to see in the environment. Petrovskii et al. [171] presented the mathematical model which proves that ecological meaning. Different factors can be a reason for biological invasion; properties of the environment [4], population behaviour [198], and the stochasticity of the environment [123]. Although, studies on the comparison between stochastic and deterministic mechanism is still weak, in that study Petrovskii et al. [171] shows the patchy invasion of the fully deterministic predator-prey model with the cause of the Allee effect. For some variables of the model, at the beginning of the invasion some population forms have been observed, and then the population spreads as separate patches, and at the end, the area has been invaded by the populations. It has been obtained that as long as patchy sizes are in the same order the invasion behaviour stays the same as the patchy image. However, when predators invade the prey environment already, then the pattern of spread changes as the propagation of a smooth continuous front; on the other hand, predator has more complicated shape, and there seems no patchy invasion in that case.

It was shown in [143] that in the patchy invasion regime the population invades the area via irregular motion and interaction of separate species without showing any continuous front. That is, the space between patches becomes almost 0. This system corresponds to spatio-temporal chaos. In this regime, the spatially average prey density gets lower than the survival threshold. Moreover, with some parameters patchy dynamics cannot be observed and appear the usual invasion picture via propagation of continuous fronts or the population ends up with extinction [143].



FIGURE 3.7: Reproduction coefficient with the Allee effect.

The reaction-diffusion equations for a single population with the Allee effect in dimensionless variables are below for a system without kinesis (3.8) and for a system with kinesis (3.9).

$$\partial_t u(t,x) = D\nabla \cdot (\nabla u) + k(1-u)(u-\beta)u(t,x), \qquad (3.8)$$
$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha k(1-u)(u-\beta)} \nabla u \right) + k(1-u)(u-\beta)u(t,x).$$
(3.9)

The values of constants are: D = 1, $\alpha = 10$, $\beta = 0.2$.

We study invasion of a small drop of a population into a homogeneous environment. Equations (3.8) and (3.9) are solved for one space variable $x \in [-50, 50]$ with von Neumann boundary conditions and with the initial conditions:

$$u(0,x) = Ae^{-\frac{x^2}{2}}, A = 1.$$

The results of the numerical experiments (Figs. 3.8 and 3.9) demonstrate that kinesis may delay invasion and spread of species with the Allee effect. The delay in spreading appears because the animals with kinesis rarely leave dense clusters, whereas animals without kinesis are spreading in areas with lower values of the reproduction coefficient and populate them.



FIGURE 3.8: Evolution of a small, highly concentrated population with the Allee effect from the Gaussian initial conditions (3.10) in a homogeneous environment:
(a) for animals with kinesis (3.9), (b) for animals without kinesis (3.8). The values of constants are: D = 1, α = 5, β = 0.2.

The results of the numerical experiments (Figs. 3.8 and 3.9) demonstrate that kinesis may delay invasion and spread of species with the Allee effect. The width of the cluster grows faster for the system without kinesis (Fig. 3.8), and the total population dynamics numerically integrated over space (Fig. 3.9) also demonstrates the faster growth of population without kinesis. The delay in spreading appears because the animals with kinesis rarely leave dense clusters, whereas animals without kinesis are spreading in areas with lower values of the reproduction coefficient and populate them. This effect is also reproduced in two-dimensional case presented in Figs. 3.11 and 3.12: an initial Gaussian drop (Fig. 3.10) grows with kinesis (Fig. 3.11) slower than without kinesis (Fig. 3.12).



FIGURE 3.9: Evolution of a small, highly concentrated population with the Allee effect from the Gaussian initial conditions (3.10) in a homogeneous environment: (a) population density at the centre of the drop, (b) total population dynamics (numerically integrated over space). The values of constants are: D = 1, $\alpha = 5$, $\beta = 0.2$.

This effect of faster spreading could also lead to extinction for a population with the Allee effect. For a small population density $u < \beta$ the reproduction coefficient is negative. If diffusion is so fast that the local concentration becomes lower than the threshold β then the extinction of population follows. In Fig. 3.14 we can see how the population without kinesis vanishes for high diffusion, whereas the population with kinesis persists for the same diffusion (Fig. 3.13) because it keeps low mobility at locations with high reproduction coefficient.



FIGURE 3.10: Initial distribution (t = 0): $u(0, x) = Ae^{-\frac{x^2+y^2}{2}}, A = 1.$



FIGURE 3.11: The 2D Allee effect with kinesis D = 0.2, $\alpha = 5$, $\beta = 0.1$, with Gaussian initial distribution (Fig. 3.10).



FIGURE 3.12: The 2D Allee effect without kinesis D = 0.2, $\alpha = 5$, $\beta = 0.1$, with Gaussian initial distribution (Fig. 3.10).



FIGURE 3.13: The 2D Allee effect with kinesis, D = 0.5, $\alpha = 5$, $\beta = 0.1$, with Gaussian initial distribution (Fig. 3.10).



FIGURE 3.14: The 2D Allee effect without kinesis D = 0.5, $\alpha = 5$, $\beta = 0.1$, with Gaussian initial distribution (Fig. 3.10).

We can give an example on Predator-prey behaviour of diffusion with kinesis in the next section.

3.7 Predator-Prey diffusion with kinesis example

Lefebvre [117, 118] studied a conflict, i.e. competition, behaviour. There are various studies which include conflict behaviour [107, 231].

It was presented an approach to describe conflict behaviour of a spatially distributed biological community in [118]. In this study, two species were introduced as prey and predator communities. Therefore, it can be supposed that preys (the organisms of the first species) will be alive with the external resource, yet another species-predators will feed on the predation [187]. We present a community which consists of two species of predator-prey interaction. We assumed that there are two stations: one is environmentally bad station and these species will run from there to another station to survive. In time the diffusion reaches steady-state in the second station. Therefore, the migration is the transfer from one station to the other one. In addition to that, we assumed that there is no another effect on the population dynamics from spatial patterns are presumed when migration takes place. In Appendix A, we explained two-stations model in detail.

Species can be affected by the interactions of populations through the predator-prey system. A generic predator-prey system with diffusion can be given as the following form:

$$\partial_{t}u_{1}(x,t) = \nabla \cdot (D_{1}\nabla u_{1}(x,t)) + F(u_{1}) - E(u_{1},u_{2}),$$

$$\partial_{t}u_{2}(x,t) = \nabla \cdot (D_{2}\nabla u_{2}(x,t)) + KE(u_{1},u_{2}) - M(u_{2}).$$
(3.10)

where u_1 and u_2 describe the prey and predator densities. $\partial_t u_1(x,t)$ is the rate of increase of the number of prey, and $\partial_t u_2(x,t)$ is the rate of increase of the number of predators [69]. $F(u_1)$ is the prey population growth and E is predation, $M(u_2)$ is the predator death rate, and K is the predation efficiency or conversion rate [222]. We can write the model as following, r_1 and r_2 are the reproductions, D_1 and D_2 are diffusion coefficients, and the population sizes u_1 and u_2 depend on space:

$$\partial_t u_1(t, x) = r_1 (u_1, u_2) u_1 + \nabla \cdot (D_1 (r (u_1, u_2)) \nabla u_1),$$

$$\partial_t u_2(t, x) = r_2 (u_1, u_2) u_2 + \nabla \cdot (D_2 (r (u_1, u_2)) \nabla u_2).$$
(3.11)

Here, the diffusion depends on the reproduction coefficient. When the reproduction coefficient is higher, D will be getting smaller. Diffusion changes with mobility and decreases when well-being is higher. We can take the diffusion as

$$D_1 = d_1 e^{-\alpha r_1}$$
 and $D_2 = d_2 e^{-\alpha r_2}$. (3.12)

Then, we can write the model (3.11) as the following form:

$$\partial_t u_1(t, x) = r_1 (u_1, u_2) u_1 + d_1 \nabla \cdot (e^{-\alpha r_1} \nabla u_1),$$

$$\partial_t u_2(t, x) = r_2 (u_1, u_2) u_2 + d_2 \nabla \cdot (e^{-\alpha r_2} \nabla u_2),$$
(3.13)

where r and u depend on space. In this form, when r is increasing, i.e. the conditions become better, the diffusion will decrease monotonically.

Suppose that we have two stations which one presents good and bad conditions in the habitat (see also Appendix A). Some animals move the second station to have a better life. The growth rate of the prey population is

$$\left(w + \frac{q}{1 + \exp\left(-nx\right)}\right),\tag{3.14}$$

the carrying capacity of the prey population is

$$\left(p + \frac{v}{1 + \exp\left(-nx\right)}\right),\tag{3.15}$$

and the interaction between two populations, i.e. the attack rate is

$$\left(a + \frac{j}{k + \exp\left(-rx\right)}\right),\tag{3.16}$$

which all depend on space and time. Therefore, in this form, when x is $\pm \infty$ they will not be equal to 0. That is, in space there always will be interaction. The reproduction coefficient can be observed for prey population as

$$r_{1} = \left(w + \frac{q}{1 + exp(-nx)}\right) \left(1 - \frac{u_{1}}{\left(p + \frac{v}{1 + exp(-nx)}\right)}\right)$$
(3.17)
$$- \left(a + \frac{j}{k + exp(-\rho x)}\right) u_{2}.$$

Number of the eaten population is

$$\left(a + \frac{j}{k + \exp\left(-\rho x\right)}\right)u_1u_2,\tag{3.18}$$

then predator growth is

$$\gamma \left(a + \frac{j}{k + \exp\left(-\rho x\right)} \right) u_1 u_2, \tag{3.19}$$

and we will take predator death rate as a constant variable w_1 . Therefore the reproduction coefficient for predator population is

$$r_2 = -w_1 + \gamma \left(a + \frac{j}{k + \exp\left(-\rho x\right)}\right) u_1.$$
(3.20)

While the prey population is increasing, the diffusion to the next station will decrease. That is, if conditions are becoming better, they will not want to leave their place. The same situation occurs for the predator population as well. Therefore, there is a relation between predator-prey and the diffusion coefficient:

$$D_1 = d_1 e^{-\alpha r_1}$$
 and $D_2 = d_2 e^{-\alpha r_2}$.

From the first station, the diffusion will start, and some individuals will diffuse to the second station. Therefore, diffusion will be slower. At the end of the diffusion, the system will reach steady-state.

We used Euler Explicit method [25] to find numerical solutions using MAT-LAB with Neumann boundary conditions. That is, the boundary is sufficiently smooth such that normal derivative exists, which shows there is no flux at borders:

$$\frac{\partial u_1}{\partial x} = \frac{\partial u_2}{\partial x} = 0. \tag{3.21}$$

In Fig. 3.15 we can see the iterative solution for predator-prey equation.



FIGURE 3.15: Prey and predator populations on space for the values $d_1 = 1$; $d_2 = 1$; n = 0.1; w = 5; $w_1 = 2$; q = 1; p = 1; v = 0.3; a = 1.1; j = 0.2; $\rho = 0.2$; k = 3; $\gamma = 2$.



FIGURE 3.16: Prey without Predator, Flux and Reproduction Coefficient for these values $d_1 = 1$, $d_2 = 1$, n = 0.1, w = 5, $w_1 = 2$, q = 1, p = 1, v = 0.3, a = 1.1, j = 0.2, $\rho = 0.2$, k = 3, $\gamma = 2$.



FIGURE 3.17: Prey with Predator, Flux and for these values $d_1 = 1, d_2 = 1, n = 0.1, w = 5, w_1 = 2, q = 1, p = 1, v = 0.3, a = 1.1, j = 0.2, \rho = 0.2, k = 3.$

3.7.1 Stability analysis of predator-prey diffusion

The dynamical behaviour of the ecological system is discussed with mathematical models in ecology. Many studies in mathematical biology were related with predator-prey system [48].

The studies on predator-prey models, during the past decades, were used to introduce the relation between two species for food supply [233].

The stability properties of the reaction-diffusion system might be the most essential mathematical problem in the study of reaction-diffusion equations [126, 196, 204, 234, 235, 236].

In this subsection, we will introduce the predator-prey diffusion model with kinesis. We present a community which consists of two species with predator-prey interaction. It was assumed that there are two stations: one is environmentally bad station and these species will run from there to another station to survive. In time, the diffusion reaches to the steady-state in the second station. Therefore, the migration is the transfer from one station to the other one. In addition to



FIGURE 3.18: Reproduction Coefficient for these values $d_1 = 1, d_2 = 1, n = 0.1, w = 5, w_1 = 2, q = 1, p = 1, v = 0.3, a = 1.1, j = 0.2, \rho = 0.2, k = 3, \gamma = 2.$

that, it was assumed that there is no another effect on the population dynamics from spatial patterns are presumed when migration takes place. And therefore, the stability analysis of this model at $x = -\infty$ and $+\infty$ was presented.

Consider an ecosystem where we wish to model the interaction of predator and preys. To study these systems, we can construct the phase plane. That is, a picture of the solution trajectories can be mapped out by points $(u_1(t), u_2(t))$ as t varies over $(-\infty, +\infty)$ and u_1 prey u_2 predator population. Moreover, we can introduce the steady state of these populations as an intersection of isoclines.

 $u_1(x,t)$ and $u_2(x,t)$ denote the prey and the predator population densities at position x and time t. Let's look at these systems at $x = -\infty$. Therefore, the system of predator-prey becomes:

$$\frac{\partial u_1}{\partial t} = w \left(1 - \frac{u_1}{p} \right) - a u_1 u_2 = f_1 \tag{3.22}$$

and

$$\frac{\partial u_2}{\partial t} = -w_1 u_2 + \gamma u_1 u_2 = f_2 \tag{3.23}$$

It can be observed with these two equations, as a special condition, if we have always constant population $u_1 = costant$, then it will be satisfied that $\gamma a u_1 > w_1$.

The predator-prey populations are not constant; interacting and changing in time. We can determine the stability and dynamical behaviours of the equilibrium of this system. If we want to find nullclines of this system, then it can be expressed as the following

$$\frac{\partial u_1}{\partial t} = 0 \text{ and } \frac{\partial u_2}{\partial t} = 0.$$
 (3.24)

Therefore,

$$0 = w\left(1 - \frac{u_1}{p}\right) - au_1u_2,\tag{3.25}$$

and the system's solution is $u_1 = 0$, and the other one is $u_2 = \frac{w}{a} \left(1 - \frac{u_1}{p}\right)$. The second isocline can be observed by

$$0 = -w_1 u_2 + \gamma u_1 u_2. \tag{3.26}$$

The system's one solution is $u_2 = 0$ and the other one is $u_1 = \frac{w_1}{\gamma a}$.

Therefore, the trivial steady state is (0,0), and nontrivial steady state is $\left(\frac{w_1}{\gamma a}, \frac{w(\gamma a p - w_1)}{\gamma p a^2}\right)$.

Equilibrium points are not always stable. It can be useful to classify equilibrium points based on their stability since stable and unstable equilibriums play quite different roles in the dynamics of a system.

For these conditions $w = 5, w_1 = 2, p = 15, a = 0.3, \gamma = 2$, the positive steady state can be observed as (1, 15.55). The Jacobian matrix is

$$J = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix} = \begin{pmatrix} -\frac{w}{p} - au_2 & -au_1 \\ \gamma u_2 & -w_1 + \gamma u_1 \end{pmatrix}.$$

For the trivial steady-state $(u_1, u_2) = (0, 0)$, it can be observed that

$$J(u_1, u_2) = J(0, 0) = \begin{pmatrix} 5 & 0 \\ 0 & -2 \end{pmatrix}$$

This trivial steady state is unstable since det J < 0.

For the nontrivial steady-state (1, 15.55) and the Jacobian matrix can be observed as

$$J(u_1, u_2) = J(1, 15.55) = \begin{pmatrix} -4.87 & -0.3 \\ 30.3 & 0 \end{pmatrix}.$$

This steady state is stable, since det J > 0 and tr J < 0. The eigenvalues are complex. Then, the steady state is the stable focus, and therefore the spiral converges to the steady state in an oscillatory manner.

Now, we can check these conditions w = 5, $w_1 = 9.6$, p = 15, a = .3, $\gamma = 2$, the trivial positive steady state is (0,0). However, there will be no nontrivial positive steady state, since $\left(\frac{w_1}{\gamma a}, \frac{w(\gamma a p - w_1)}{\gamma p a^2}\right) = (16, -0.6)$. For the trivial steady state $(u_1, u_2) = (0, 0)$ it can be observed that

$$J(u_1, u_2) = J(0, 0) = \begin{pmatrix} 5 & 0 \\ 0 & -9.6 \end{pmatrix}.$$

This also trivial steady state is unstable, since det J < 0. That is, if the constant isocline $u_1 = \frac{w_1}{\gamma a}$ is the right hand side of the first isocline $u_2 = \frac{w}{a} \left(1 - \frac{u_1}{p}\right)$, then there will be no intersection. Hence, the system cannot reach the steady state. Moreover, we can conclude this result using stability theorem.

With these constants p = 15, a = 0.3, $\gamma = 2$ and increasing w_1 will make the predator-prey system unstable. $w_1 = 9$ is the bifurcation point which exchanges the system's stability (see Fig. 3.19). Therefore, if $w_1 > 9$, these isoclines will not have an intersection. That is, increasing the value of w_1 will cause bifurcation.

Second isocline cuts the x-axis at $0 = \frac{w}{a} \left(1 - \frac{u_1}{p}\right), u_1 = p.$

Therefore, if the system is $p < \frac{w_1}{\gamma a}$, then the system will not have a stable positive steady state, and it can be seen that $15 = p < \frac{w_1}{\gamma a} = 16$, then there is no intersection.

Now, we can consider equation the system as taking $x = \infty$. Then, the system can be observed as

$$\frac{\partial u_1}{\partial t} = \left(w+q\right)\left(1-\frac{u_1}{p+v}\right)u_1 - \left(a+\frac{j}{k}\right)u_1u_2 = g_1 \tag{3.27}$$



FIGURE 3.19: If we take p = 15, a = 0.3, $\rho = 2$, then the system will be transformed from stable to unstable by increasing w_1 .

and for predators

$$\frac{\partial u_2}{\partial t} = -w_1 u_2 + \gamma \left(a + \frac{j}{k}\right) u_1 u_2 = g_2, \qquad (3.28)$$

for these conditions: $p < v < \infty$ and -1 < k < 1. In addition to that, the nullclines can be introduced as the following

$$\frac{\partial u_1}{\partial t} = 0 \text{ and } \frac{\partial u_2}{\partial t} = 0$$
 (3.29)

Therefore, we can find the isoclines

$$\frac{\partial u_1}{\partial t} = (w+q)\left(1 - \frac{u_1}{p+v}\right)u_1 - \left(a + \frac{j}{k}\right)u_1u_2 = g_1.$$
(3.30)

The system's solutions are $u_1 = 0$ and $u_2 = \frac{(w+q)}{(a+\frac{j}{k})} \left(1 - \frac{u_1}{p+v}\right)$. In addition to that

$$0 = -w_1 u_2 + \gamma \left(a + \frac{j}{k}\right) u_1 u_2. \tag{3.31}$$

Hence, it can be observed that the solutions are $u_2 = 0$ and $u_1 = \frac{w_1}{\gamma(a+\frac{j}{k})}$.

The steady states of the system are (0,0) and

$$\left(\frac{w_1}{\gamma\left(a+\frac{j}{k}\right)}, \frac{(w+q)}{\left(a+\frac{j}{k}\right)} \left(1 - \frac{w_1}{\gamma\left(a+\frac{j}{k}\right)(p+v)}\right)\right).$$
 For these conditions $w = 5, w_1 = 2, p = 15,$

 $q = 10, v = 0.3, j = 0.2, k = 3, a = 0.3, \gamma = 2$ the positive steady state can be observed as (2.7, 33.6).

Using the Jacobian matrix, the trivial steady-state is unstable. the nontrivial steady state is stable focus, and therefore the spiral converges to the steady state in an oscillatory manner.

Now, we can look at the another conditions w = 5, $w_1 = 11.73$, p = 15, q = 10, v = 0.3, j = 0.2, k = 3, a = 0.3, $\gamma = 2$ the trivial steady state is (0, 0). However, there will be no nontrivial positive steady state. Therefore, trivial steady state of the system is unstable, since at least one of the eigenvalues is positive.

As we explained before, there will be two types of unstable conditions. One will appear for (0,0) steady state, the other one can be found as the following

$$u_{2} = \frac{(w+q)}{\left(a+\frac{j}{k}\right)} \left(1 - \frac{u_{1}}{p+v}\right).$$
(3.32)

For $u_1 = p + v$, it should be

$$p + v < \frac{w_1}{\gamma \left(a + \frac{j}{k}\right)}.\tag{3.33}$$



FIGURE 3.20: The nullclines of the system 3.27 and 3.28. (2.72, 33.63) is the stable steady state of this system with these conditions w = 5, $w_1 = 2$, p = 15, q = 10, v = 0.3, j = 0.2, k = 3, a = 0.3, $\gamma = 2$.



FIGURE 3.21: The nullclines of the system (1) with these conditions w = 5, $w_1 = 11.73$, p = 15, q = 10, v = 0.3, j = 0.2, k = 3, a = 0.3, $\gamma = 2$.



FIGURE 3.22: a): Prey population in time, b) Predator population in time. c) The phase portrait for predator prey for the initial condition (20, 5). (2.72, 33.63) is stable focus with these variables w = 5, $w_1 = 2$, p = 15, v = 0.3, q = 10, a = 0.3, j = 0.2, k = 3, $\gamma = 2$.

If we use the condition as $p + v < \frac{w_1}{\gamma(a+\frac{j}{k})}$, and we can see that the constant isocline will intersect with the other isocline. The steady state of the system is stable focus. Moreover, the interaction populations starts with 20 prey and 5



FIGURE 3.23: a) The phase portrait for predator prey for the initial condition (20,5) at w = 5, $w_1 = 2$, p = 15, a = 0.3, $\gamma = 2$ b) Prey population in time c) Predator population in time.

predator, then in a counter clockwise direction it is becoming a stable focus in time at (2.72, 33.63).

As we can see from Fig. 3.23, in this condition

$$p + v < \frac{w_1}{\gamma \left(a + \frac{j}{k}\right)},\tag{3.34}$$

these populations will not reach steady-state in time since there is no steady state as an intersection of two isoclines.

Moreover, one should obviously state that the basic predator-prey system is that the population of the prey species would grow unbounded, exponentially, in the absence of predators (when $u_2 = 0$). If the preys are absence (when $u_1 = 0$), the predator population would decay exponentially to zero due to starvation.

With the phase portrait of the system, it can be seen that for some conditions the system will be unstable. In some manner, predator population dies in station 1, but then in station 2, it reaches steady state because of the mobility.

It was introduced with stability analysis that for $p < \frac{w_1}{\gamma a}$, the system may not have a stable positive steady state.



FIGURE 3.24: Both systems do not extinct with $p > \frac{w_1}{\gamma a} w = 5$, $w_1 = 9$, $d_1 = 0.1$, $d_2 = 0.2$, n = 0.1, q = 10, p = 15, v = 0.3, a = 0.3, j = 0.2, $\rho = 0.2$, k = 3, $\gamma = 2$.

It can be seen from Fig. 3.24 that the system will not extinct, although the predator population is very close to dying out, since the condition pw_1 has been satisfied. Both populations will diffuse to the second station and will reach steady state.

However, as we can see from Fig. 3.25 the predator population will extinct in time in station 1 for the condition $w_1 = 9$, which is a very close value with Fig. 3.24 ($w_1 = 9.1$), but it satisfies $p < \frac{w_1}{\gamma a}$. Moreover, in station 2 because of the mobility the rest of the predator population will survive with diffusion, and the population will remain stable in station 2. The prey population will decrease in space until reaching steady state.

If the condition $p + v < \frac{w_1}{\gamma(a + \frac{j}{k})}$ has been satisfied, then the population will die also in station 2.



FIGURE 3.25: Predator extinction in station 1. $w = 5, w_1 = 9.1, d_1 = 0.1, d_2 = 0.2, n = 0.1, q = 10, p = 15, v = 0.3, a = 0.3, j = 0.2, \rho = 0.2, k = 3, \gamma = 2.$



FIGURE 3.26: Predator extinction in station 1 and 2. $w = 5, w_1 = 12, d_1 = 0.1, d_2 = 0.2, n = 0.1, q = 10, p = 15, v = 0.3, a = 0.3, j = 0.2, \rho = 0.2, k = 3, \gamma = 2.$

Fig. 3.26 shows that the predator population will die out in time and space (station 1 and 2) with the condition $p+v < \frac{w_1}{\gamma(a+\frac{j}{k})}$. When the predator population start to decrease in station 1, on the other side, the prey population will start to increase. Then, once predator population extinct, prey population will reach

its steady state. Therefore, prey population size will not change in space and time. In Fig. 3.25, to satisfy this condition w_1 has been increased from 9.1 (see Fig. 3.25) to 12. When we increase population interaction the prey population will die. Therefore, since increasing rate of predator is prey population, predator population will extinct in station 1 and 2 (see Fig. 3.27).



FIGURE 3.27: Extinction of both populations with increasing interaction. a = 7, w = 5, $w_1 = 9$, $d_1 = 0.1$, $d_2 = 0.2$, n = 0.1, q = 10, p = 15, v = 0.3, j = 0.2, r = 0.2, k = 3, $\gamma = 2$. Initial conditions for prey and predator (12, 10)

3.7.2 Extinction places and isoclines

In this section, we study predator-prey extinction places.

Fig. 3.28 has been observed for the small value of interaction of these populations.



FIGURE 3.28: Isolated predator-prey in both stations. w = 5 and $w_1 = 2$ for every 10 time steps (Blue is prey and predator is red plot).



FIGURE 3.29: Increasing predator death rate: w = 5 and $w_1 = 5$.

Increasing the predator population death rate affects first station isolation. However, then they start to be isolated in second station.

When the predator death rate is smaller than prey birth rate, and also when we decrease these interactions of populations, we are observed an isolated system in both stations (see Fig. 3.30).

When the interaction of these populations increases, they have intersections on these stations.



FIGURE 3.30: Isolated populations. w = 5 and $w_1 = 2$ and a = 0.1



FIGURE 3.31: Isolted system when increasing interaction. a = 0.5

Increasing of both populations interaction will allow non-isolated system behaviour. In time 3, both populations will overlap, and start to be separated from each other and will be isolated in time. It is important to note that after 9-time steps, their behaviour at both stations remains the same. That is, predator population will increase monotonically, and then reach steady state; on the other hand, prey population will reach steady state having an insignificant decrease. Moreover, increasing interaction allows short time overlap (see time 3, Fig. 3.31).

In time 2, prey and predator populations have a parallel increase. However, in time 3 predator population drops and prey increases at first; then, predator start to have a linear increase and prey has a linear fall after reaching the peak until the second station. Then, again in time 4, an isolated behaviour will be observed. Until the second station, the predator size will drop; on the other hand, the prey will reach its highest size at the beginning of second station. After 7 time steps, the system will have the same behaviour. In station 1, predator will increase and reach steady-state in the second station; and prey population will decrease and reach steady state in the second station as isolated from each other.



FIGURE 3.32: Isolations and non-isolations in time. a = 0.9

It can be seen that Fig. 3.32 shows increasing the interaction will affect these populations isolation. Increasing interaction can cause oscillations in time (see Fig. 3.32 time steps between 6 and 11). However, almost in 20-time steps, these oscillations will stop, predators will monotonically increase before reaching steady-state in station 2. In addition to that, the prey population growth will remain smooth in both stations. While in time, two populations are isolated, until time 5 it can be observed that a non-isolated behaviour start to appear in both stations. In time 3, the predator and prey reach the top, then the predator has a small drop, but the prey population will reach to the same state. In time 4, oscillations start, and in time 5 and 6, oscillations occur in the same behaviour. That is, in an area, while the predator is increasing, then prey starts to decrease, and therefore they follow each other in this manner. Moreover, it can be noted that in time 2, the prey population do not extinct, it just reaches very close to the extinction. That is, it drops to a very small value.



FIGURE 3.33: Increasing the predators in the interaction from $\gamma = 2$ and $\gamma = 4$

Increasing the interaction number of the predator will cause oscillations in time steps. After 5 time steps, it has been observed that isolated regime has occurred in both stations. Moreover, these oscillations stop in almost 30-time steps (see Fig. 3.33).



FIGURE 3.34: Increasing the predators in the interaction from $\gamma = 4$ and $\gamma = 6$

In this situation, Fig. 3.34, the isolation will start at time step 9 in these both stations. As usual at time steps when oscillations occur, these populations will behave on the contrary; where predator increases, then prey drops. These oscillations continue until 30 time steps, then populations' behaviour will be more smooth. Therefore, predators will have a linear increase and preys will have just an insignificant drop. At time step 20, it is interesting to state that the predator population has too many oscillations.

3.8 Discussion

We suggested a model of purposeful kinesis with the diffusion coefficient directly dependent on the reproduction coefficient. This model is a straightforward formalisation of the rule: "Let well enough alone". The well-being is measured by local and instant values of the reproduction coefficient. Gorban et al. [83] discussed the problems of definition of instant individual fitness in the context of physiological adaptation. Let us follow here this analysis in brief. The proper Darwinian fitness is defined by the long-time asymptotic of kinetics. It is non-local in time because it is the average reproduction coefficient in a series of generations and does not characterize an instant state of an individual organism [75, 91, 134, 142]. The synthetic evolutionary approach starts with the analysis of genetic variation and studies the phenotype effects of that variation on physiology. Then it goes to the performance of organisms in the sequence of generations (with adequate analysis of the environment) and, finally, it has to return to Darwinian fitness.

The ecologists and physiologists are focused, first of all, on the observation of variation in individual performance [174]. In this approach we have to measure the individual performance and then link it to the Darwinian fitness. This link is not obvious. Moreover, the dependence between the individual performance and the Darwinian fitness is not necessarily monotone. (This observation was partially formalized in the theory of r- and K- selection [128, 173].) The notion 'performance' in ecology is 'task-dependent' [226] and refers to an organism's ability to carry out specific behaviours and tasks: to capture prey, escape predation, obtain mates, etc. Direct instant measurement of Darwinian fitness is impossible but it is possible to measure various instant performances several times and treat them as the components of fitness in the chain of generations. The relations between performance and lifetime fitness are sketched on flow-chart (Fig. 2.1) following [226] with minor changes. Darwinian fitness can be defined as the lifetime fitness averaged in a sequence of generations.

The instant individual fitness is the most local in time level in the multiscale hierarchy of measures of fitness:

Instant individual fitness \rightarrow Individual life fitness \rightarrow Darwinian fitness in the chain of generations. The quantitative definition of the instant and local fitness is given by its place in the equations as the reproduction coefficient. The change of the basic equation will cause the alter of the quantitative definition.

We have used the instant and local reproduction coefficient r for defining of purposeful kinesis. The analysis of several benchmark situations demonstrates that, indeed, sometimes this formalisation works well (see also Appendix B for different types of purposeful kinesis models). Assume that this coefficient r(u, s) is a monotonically decreasing function of u for every given s and monotonically increasing function of s for any given u. Then our benchmarks give us the following hints:

- If the food exists in low-level uniform background concentration and in rare (both in space and time) sporadic patches then purposeful kinesis defined by the instant and local reproduction coefficient (3.1) is evolutionarily beneficial and allows animals to utilise the food patches more intensively (see Figs. 3.3 and 3.4).
- If there are periodic (or almost periodic) fluctuations in space and time of the food density *s* then purposeful kinesis defined by the instant and local reproduction coefficient (3.1) is evolutionarily beneficial and allows animals to utilize these fluctuations more efficiently (see Figs. 3.5 and 3.6).
- If the reproduction coefficient r(u, s) is not a monotonically decreasing function of u for every given s (the Allee effect) then the "Let well enough alone" strategy may delay the spreading of population (see Figs. 3.8, 3.9, 3.11, and 3.12). This strategy can lead to the failure in the evolutionary game when the colonization of new territories is an important part of evolutionary success. This manifestation of the difference between the local optimisation and the long-time evolutionary optimality is important for the understanding of the evolution of dispersal behaviour. At the same time, the "Let well enough alone" strategy can prevent the effects of extinction caused by too fast diffusion (see Figs. 3.13 and 3.14) and, thus, decrease the effect of harmful diffusion described in [42].

These results of exploratory numerical experiments should be reformulated and transformed into rigorous theorems in the near future.

Purposeful kinesis is possible even for very simple organisms: it requires the only perception of local and instant information. For more complex organisms perception of non-local information, memory and prediction ability are possible and the kinesis should be combined with taxis. The idea of evolutionary optimality can also be applied to taxis. This approach immediately produces an advection flux, which is proportional to the gradient of the reproduction coefficient. Cantrell et al. [27] introduced and studied such models. Moreover, the evolutionarily stable flux in these models should be proportional to $u\nabla \ln r$ [9, 72]. Here, ∇r could be considered as a 'driving force'. It would be a very interesting task to combine models of purposeful kinesis with these models of taxis and analyse the evolutionarily stable dispersal strategies, which are not necessarily unique even for one species [24]. Of course, the *cost of mobility* should be subtracted from the reproduction coefficient for more detailed analysis.

If we go up the stair of organism complexity, more advanced effects should be taken into account like collective behaviour and interaction of groups in structured populations [169]. Moreover, the evolutionary dynamics in more complex systems should not necessarily lead to an evolutionarily stable strategy and cycles are possible [75, 209]. Even relatively simple examples demonstrate that evolutionary dynamics can follow trajectories of an arbitrary dynamical system on the space of strategies [74]. Human behaviour can be modelled by differential equations with use of statistical physics and evolutionary games [170], but special care in model verifications and healthy scepticism in the interpretation of the results are needed to avoid oversimplification.

Chapter 4

Mobility Cost and Degenerated Diffusion in Kinesis Models

4.1 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 locomotion is called kinesis. These 'innocent' definitions cause many problems and intensive conceptual discussion [52]. 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 unambiguously then in the PDE (partial differential equations) approach to modelling taxis corresponds to change of *advection* terms, whereas kinesis is modelled by the changes of the *mobility coefficient*.

Einstein introduced the theory of the diffusion coefficient for liquids which includes diluted particles. In addition, he discussed the motion of particles in liquids under a constant extrinsic force and diffusion in [57]. Einstein's kinetic theory connected the diffusion coefficient and mobility

$$D = \mu k_B T$$

where D is the diffusion constant; μ is the mobility; k_B is the Boltzmann constant; T is the absolute temperature. In 1935, Teorell [210] studied the mobility-based approach. He developed the diffusion of ions through a membrane. The notion of mobility was developed by Einstein. It is summarised by the Teorell formula [82, 210]

$Flux = mobility \times concentration \times force.$

Teorell studied electrochemical transport and measured specific force as force per 'gram-ion', in physics various 'gram-particle' definitions are also used to deal with moles that contain the Avogadro number of particles rather than with individual particles. Of course, for ecological models [124] so large numbers are not needed the concentration of animals u (not of moles of animals) are 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 the dispersal of animals this means that the intensity of kinesis and taxis should be connected: for example, the decrease of mobility means that both taxis and kinesis decrease proportionally.

The kinesis strategy controlled by the locally and instantly evaluated wellbeing can be described in simple words: Animals stay longer in good conditions and leave quicker bad conditions. If the well-being is measured by the instant and local reproduction coefficient then the minimal diffusion model of kinesis gives for mobility μ_i of *i*th species [79]:

$$\mu_i = D_{0i} e^{-\alpha_i r_i (u_1, \dots, u_k, s)} \tag{4.1}$$

The correspondent diffusion equation is

$$\partial_t u_i(x,t) = \nabla \cdot \left[\mu_i(u_1, \dots, u_k, s) \nabla u_i \right] + r_i(u_1, \dots, u_k, s) u_i, \tag{4.2}$$

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 *i*th species,

- *s* represents the a-biotic characteristics of the living conditions (can be multidimensional),
- r_i is the reproduction coefficient of *i*th species, which depends on all u_i and on s,
- $D_{0i} > 0$ is the equilibrium mobility of *i*th species ('equilibrium' means here that it is defined for $r_i = 0$),
- The coefficient α_i > 0 characterises dependence of the mobility coefficient of ith species on the corresponding reproduction coefficient.

This model aimed to describe the 'purposeful' kinesis [79] that helps animals to increase their 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.

We demonstrated on a series of benchmarks for models (4.2) with mobilities (4.1) that [79]:

- If the food exists in low-level uniform background concentration and in rare (both in space and time) sporadic patches then purposeful kinesis (4.2) 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 (4.2) allows animals to utilize these fluctuations more efficiently.
- If the presence of the Allee effect the kinesis strategy formalised by (4.2) may delay the spreading of the population
- The "Let well enough alone" strategy (4.1), (4.2) can prevent the effects of extinction caused by too fast diffusion and decrease the effect of harmful diffusion described in [42].

In that study, Cosner described the ecological effects of the reaction-advectiondiffusion models. Moreover, he explained the mathematical methods to analyse the system of equations, and the population dispersal on this model. Cosner studied single species population, the population interaction between species and their dispersal strategies from the harmful conditions. This model can explain the dispersal behaviour of individuals; how this behaviour can affect the ecological interactions and how this interaction affects the evolutionary selection.

The "Let well enough alone" assumption (4.1), (4.2) provides the mechanism to stay in a good location because mobility decreases exponentially with the reproduction coefficient. High mobility for unfavourable conditions allows animals to find new places with better conditions and seems to be beneficial. Nevertheless, it is plausible that the 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.

4.2 Cost of mobility

The 'cost of mobility' had been introduced and analysed for several research purposes. It is a well-known notion in applied economic theory [212]. In that study, it has been presented that changes in the cost will affect the change in the quantity produced and the change of community cost should be determined. We can give an example of that economic theory.

The 'psychic cost of mobility' and its influence the human choice of occupations was also discussed in [193]. Schwartz presented the economic determinants of the adverse effect of distance on migration. Negative distance elasticity of migration demonstrated to show this effect. These determinants are represented into two groups: the first psychic cost can be increased and second decreasing the information with distance. He also discussed that how the individual age and education will influence these two groups. As a result, getting older does not affect the distance elasticity. However, on the other hand, education decreases this distance elasticity. Analysis 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 [119]. 'Staying and helping' behaviour of organisms is a common behaviour among organisms. In 2004, Le Galliard et al. analysed the joint evolution of altruism and mobility. It also explained that how can the network depend on physiological costs, ecoevolutionary feedbacks, and a complex interaction between the evolving traits. Habitat saturation can be accepted as the key of altruism and mobility evolution. When altruism and mobility are together, then first the cost of mobility influences the cause of altruism. Second, the cost of altruism determines that the decrease of mobility will be either preceded or the adaptive altruism will rise. Third, the evolutionary stable levels can increase for altruism and mobility.

Different costs of mobility on land and in the sea are considered as an important reason for higher diversity on land that in the sea [221]. It was mentioned that the cost of mobility may lead to surprising evolutionary dynamics. Vermej and Grosberg suggested in this study that surviving the population in low density can be possible with the low cost of mobility of consumers on land. In the mid-Cretaceous period, 110 million years ago led to increasing the population density at the low rate and to a selection intensity increase for high mobility and habitat specialization.

The optimality paradigm of movement is the key part of the modern movement ecology paradigm [145]. Movement can help animals to find better conditions for foraging, thermoregulation, predator escape, shelter seeking, and reproduction. That is, movement can result in the 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 were measured in the field experiment (in non-migratory, wing-monomorphic grasshopper, *Stenobothrus lineatus*) [189]. For some other insects (the Glanville fritillary butterfly *Melitaea cinxia*) the fecundity cost of mobility was not found [94]. 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 increase 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 the trade-off between the direct loss of fitness due to mobility and probable increase of fitness due to condition change.

In our previous model (4.1), (4.2) the trade-off between the cost of mobility and the possible benefits from mobility was not accounted [79]. Let us introduce here the cost of mobility as a negative linear feedback of the mobility μ on the reproduction coefficient r:

$$r = r_0 - C\mu, \tag{4.3}$$

where r_0 depends on the population densities and abiotic environment, C is the cost coefficient and $C\mu$ is the cost of mobility. We selected the linear dependence at reproduction coefficient r on mobility, since basically the difference between initial and current reproduction coefficient defines the mobility. Linear dependence of r on μ is a standard decomposition of r into the sum of inputs from different factors (in continuous time). Haldane and Fisher used such decomposition first. We selected this hypothesis as the first one and most common choose (for discrete time this will be factorisation in the product).

According to "Let well enough alone" assumptions (4.1), $\mu = D_0 \exp(-\alpha r)$. Let us introduce $\mu_0 = D_0 \exp(-\alpha r_0)$, that is the mobility (4.1) for the system with the reproduction coefficient r_0 instead of the coefficient r (4.3) with the cost of diffusion. Obviously, $\mu_0 \ge \mu$ and $\mu/\mu_0 = \exp(-C\alpha\mu)$.

Simple algebra gives:

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

Therefore,

$$\mu = -\frac{W(-\alpha C\mu_0)}{\alpha C},\tag{4.4}$$

where W is the Lambert W-function [41]. The Lambert W-function is the inverse function to $x \exp(x)$, Fig. 4.1.

In 1758, Lambert solved the equation $x = q + x^m$. He gives many solutions for x in powers of q. Euler later has recreated this equation to a symmetrical form

$$x^{\alpha} - x^{\beta} = (\alpha - \beta) v x^{\alpha + \beta}. \tag{4.5}$$

Euler's Lambert series solution is

$$x^{n} = 1 + nv + \frac{1}{2}n(n + \alpha + \beta)v^{2} + \frac{1}{6}n(n + \alpha + 2\beta)(n + 2\alpha + \beta)v^{3} + \frac{1}{24}n(n + \alpha + 3\beta)(n + 2\alpha + \beta)(n + 3\alpha + \beta)v^{4} + etc.$$
(4.6)

Euler later checked special cases with $\alpha = \beta$. When we divide Eq. (4.5) by $\alpha - \beta$ and then $\beta \to \alpha$ to get

$$log x = v x^{\alpha}.$$

If we multiply this equation by α , then we get left side as $log x^{\alpha}$, put $z = x^{\alpha}$ and $u = \alpha v$. We get log z = uz, which is the same equation as $\alpha = 1$.

Euler first analysed $\alpha = \beta = 1$ for Eq. (4.6) as a series for $\frac{x^n-1}{n}$. Then, when we set n = 0, it follows as

$$log x = v + \frac{2^1}{2!}v^2 + \frac{3^2}{3!}v^3 + etc.$$
(4.7)

This series converges for |v| < 1/e, defines a function which equals -W(-v), where W(z) is the function satisfying as follows

$$W(z) e^{W(z)} = z.$$
 (4.8)


FIGURE 4.1: The Lambert function y = W(x) is defined for $x \ge -1/e$. For negative x, the upper branch of W is used, the so-called W_0 , which is realanalytic on $(-1/e, \infty)$.

Function W(x) is defined for x > -1/e. Therefore, the mobility μ (4.4) exists for

$$\alpha C\mu_0 \le \frac{1}{\mathrm{e}}.\tag{4.9}$$

The argument of the function W in (4.4) belongs to the interval [-1/e, 0). The dependence of the dimensionless variable $\alpha C \mu$ on the dimensionless variable $\alpha C \mu_0$ (Fig. 4.2) is universal for all models of the form (4.1), (4.2) with the cost of mobility (4.3).

The universal limit (4.9) can be represented in terms of the reproduction coefficient: the mobility formula (4.4) is valid for

$$r_0 > \frac{1}{\alpha} (1 + \ln(\alpha C D_0)).$$

For r_0 below this critical solution, the equation for mobility loses solution. This is a *critical transition* [191]: a 'critical thresholds' is found, where the behaviour of the systems is changing abruptly.

Definition of mobility for $\alpha C\mu_0 > \frac{1}{e}$ requires additional assumptions beyond (4.1), (4.2), and (4.3). We have no sufficient reasons now for the definite choice.



FIGURE 4.2: The universal dependence of the dimensionless variable $\alpha C\mu$ on the dimensionless variable $\alpha C\mu_0$ for all models of the form (4.1), (4.2) with the cost of mobility (4.3).



FIGURE 4.3: The population size on space at time 10. $\alpha = 0.1, C = 0.3, D = 0.1.$

The simplest assumption is:

$$\mu = 0 \text{ for } \alpha C \mu_0 > \frac{1}{e}.$$
 (4.10)

This extension by zero has some biological reasons: if the further increase of mobility leads to the catastrophic decrease of the reproduction coefficient (because the cost of mobility) then the reasonable strategy is to stop the dispersal at all.

4.3 Equations of population dynamics with kinesis and mobility cost

Consider an ODE model for space-uniform populations in uniform conditions:

$$\frac{du_i}{dt} = r_{0i}(u_1, \dots, u_k, s)u_i$$
 (4.11)

(it should be supplemented by dynamic equation for abiotic components s). The correspondent reaction-diffusion equations with kinesis and the mobility cost have the following form. Three additional positive coefficients are needed for each species: α_i , D_{0i} , and C_i . The equations are:

$$\partial_t u_i(x,t) = \nabla \cdot (\mu_i \nabla u_i) + r_i u_i,$$

$$r_i = r_{0i} - C\mu_i,$$

$$\mu_i = \begin{cases} -\frac{W(-\alpha_i C_i \mu_{0i})}{\alpha C_i} & \text{if } \alpha C\mu_0 \leq \frac{1}{e}; \\ 0 & \text{if } \alpha C\mu_0 > \frac{1}{e}, \end{cases}$$

$$\mu_{0i} = D_{0i} \exp(-\alpha r_{0i}).$$

$$(4.12)$$



FIGURE 4.4: Typical dependences of the mobility μ (a) and the modified reproduction coefficient r (b) on the unmodified reproduction coefficient r_0 .

Dependence of the mobility μ on the initial reproduction coefficient r_0 is schematically represented in Fig. 4.4. If r_0 decreases below the critical value then the mobility nullifies. This means that diffusion degenerates. Nullifying of mobility leads to the increase of the reproduction coefficient r because the mobility cost vanishes (see Fig. 4.4). Degenerating diffusion attracted much attention in the theory of porous media [220]. The 'porous media equation' is

$$u_t = \Delta u^m,$$

where Δ is the Laplace operator, m > 1.

Diffusion coefficient vanishes smoothly when u tends to zero. Barenblatt [11] found his famous now analytic auto-model solutions for equations of diffusion in porous media, and these solutions were used for modelling of the nuclear bomb explosion.

Existence and regularity properties were studied in a series of works in the 1960s-1970s [6]. In the 1970s, the equation of diffusion in porous media was introduced in ecological modelling [89]. This equation predicts a finite speed of spreading of a population, which is initially confined to a bounded region. This property is in strong contrast with the well-known properties of the classical diffusion equation, the infinite speed of propagation.

The divergent form of the porous media equation with power diffusion coefficient is

$$u_t = \nabla \cdot (u^{\delta} \nabla u), \quad \delta = m - 1 > 0.$$

Exact solutions for propagation of fronts for equation

$$u_t = \nabla \cdot (u^{\delta} \nabla u) + u^p - u^k,$$

were analysed in [172] for k > p.

Equations with non-linear diffusion coefficient, which degenerates when $u \to 0$ and goes to ∞ when $u \to 1$ was proposed for modelling of the formation and growth of bacterial biofilms [54]:

$$u_t = \nabla \cdot (D(u)\nabla u) + ku,$$

where $D(u) = \delta \frac{u^a}{(1-u)^b}$, $a, b \ge 1 \gg \delta > 0$. A finite difference scheme for this equation was developed and numerical experiments were provided in [55].

Discontinuity independence $\mu(r_0)$ (Fig. 4.4) causes an important property of

sufficiently regular solutions: the normal derivative of u nullifies on the boundary of the areas of degenerations. Equations (4.12) with non-linear mobility coefficient μ form a new family of degenerate reaction-diffusion equations. The degenerate diffusion equations appear in many physical applications and in geometry (Ricci flow on surfaces, for example). The typical questions are:

- Short and long time existence and regularity;
- Dynamics of boundaries of degenerated areas;
- Formation of singularities;
- Existence through the singularities.

We believe that the detailed analysis of these equations will produce many interesting questions and unexpected answers.

Consider a system with the Allee effect to demonstrate an example of nontrivial problem and interesting effect. For such a system the reproduction coefficient $r_0(u)$ grows with u on some interval. Let the critical effect appear on this interval, at point $u = u_0$ and, in addition, $r(u_0 + 0) < 0$ and $r(u_0 - 0) > 0$ (Fig. 4.5). Under these conditions, the population dynamics $\dot{u} = r(u)u$ stabilises u at the critical value $u = u_0$.

The solution of nonlinear equation $u_t = \nabla \cdot (\mu(u)\nabla u) + r(u)u$ should be rigorously defined near the singularities. Instead of general definitions we apply the regularisation and transform the equation in a vicinity of the singularity into a singular perturbed system with fast relaxation. Consider an ε vicinity of u_0 and the equation for $v = u - u_0$ (assume that $0 < v < \varepsilon$):

$$v_t = \nabla \cdot \left(\mu(u_0+0)\frac{v}{\varepsilon}\nabla v \right) + \left(r(u_0-0) + \frac{v}{\varepsilon}(r(u_0+0) - r(u_0-0)) \right) (v+u_0).$$

Here, $\mu = v\mu(u_0 + 0)/\varepsilon$, $r = r(u_0 - 0) - v(r(u_0 - 0) - r(u_0 + 0))/\varepsilon$.

Solution of this equation stabilises at $v = \varepsilon r(u_0 - 0)/(r(u_0 - 0) - r(u_0 + 0))$. At this state, r = 0 and

$$\mu = \frac{\mu(u_0 + 0)r(u_0 - 0)}{r(u_0 - 0) - r(u_0 + 0)}$$



FIGURE 4.5: Dependence of the reproduction coefficient r on the population density for a system with the Alley effect. A special case is presented when $r(u_0 + 0) < 0$ and $r(u_0 - 0) > 0$. In this situation, the population dynamics $\dot{u} = r(u)u$ stabilises u at the critical value (red arrows indicate the directions of changes).

Therefore, there appear areas with (almost) critical value of the population density $u \approx u_0$ and effective reproduction coefficient $r \approx 0$. This appearance of areas with constant critical density and equilibrium (zero) reproduction coefficient resembles the growth of biofilm [54].

4.4 Generalizations

The observed effect is not a special property of the Lambert function and is robust. Consider equations (4.2) with mobility function

$$\mu_i = D_{0i}h(-\alpha_i r_i(u_1, \dots, u_k, s)), \tag{4.13}$$

where h(z) > 0 is a monotonically growing, convex, and twice differentiable function on real axis, h''(z) > 0 and $h'(z) \to \infty$ when $z \to \infty$ (this h(x) substitutes exponent in (4.1)). Using the same linear cost of mobility $C\mu$ (4.3) we get

$$r = r_0 - CD_0h(-\alpha r) \tag{4.14}$$

or

$$h(y) = \frac{y}{CD_0\alpha} + \frac{r_0}{CD_0},$$
(4.15)

where $y = -\alpha r$. There exists a unique solution y_c of the equation

$$h'(y) = \frac{1}{CD_0\alpha}$$

Therefore, for solutions of equation (4.15) we get:

- If $r_0 > CD_0h(y_c) (y_c/\alpha)$ then (4.15) has two solutions;
- If $r_0 = CD_0h(y_c) (y_c/\alpha)$ then (4.15) has one solution $y = y_c$;
- If $r_0 < CD_0h(y_c) (y_c/\alpha)$ then (4.15) has no solutions.

Qualitatively, the situation is the same as for the exponent: there exists a critical value of the reproduction coefficient r_0 and when it decreases below this critical value, then the equation for mobility has no solution. The explicit solution with Lambert function allowed us a bit more: we found the universal explicit dependence between dimensionless quantities $y = C\alpha\mu$ and $v = C\alpha\mu_0$, y = -W(-v) (Fig. 4.2), which does not change with parameters.

For simple algebraic functions h (proposed by an anonymous MDPI reviewer) the universal explicit solutions are also possible. Consider

$$h(z) = \frac{1}{1-z}$$

This function is defined for z < 1, is convex on this semi-axis, h''(z) > 0, and $h'(z) \to \infty$ when $z \to 1$. Let us use this h in (4.13). Solution of equation (4.14) is

$$g = \frac{q}{2} + \sqrt{\frac{q^2}{4} - 1}, \quad \sqrt{\frac{\alpha C}{D_0}}\mu = \frac{q}{2} - \sqrt{\frac{q^2}{4} - 1}$$

where the dimensionless variables g and q are:

•
$$g = (\alpha r + 1)/\sqrt{CD_0},$$



FIGURE 4.6: The universal dependence of the dimensionless variables $g = (\alpha r + 1)/\sqrt{CD_0}$ (upper branch, dashed line) and $\mu\sqrt{\alpha C/D_0}$ (bottom branch, solid line) on the dimensionless variable $q = (\alpha r_0 + 1)/\sqrt{CD_0}$ for models of the form (4.1), (4.13) with the cost of mobility (4.14) and h(z) = 1/(1-z). The equation for mobility has no solution (suggested $\mu = 0$) when q < 2.

• $q = (\alpha r_0 + 1)/\sqrt{CD_0}$.

Solution exists if $q \ge 2$ and does not exist if q < 2 (i.e. $r_0 < (2\sqrt{CD_0} - 1)/\alpha$) (see Fig. 4.6).

4.5 Mobility and relation between spatial and temporal correlations

Kinesis could be beneficial for animals because it allows them to find better conditions. The probability distribution of such benefits depends on conditions in space and time. Qualitatively, if the relation with the conditions in space is low for bad conditions then it is possible to find better place with random movement. If correlation in time is high then the strategy 'to wait' can be worse than the strategy 'to move' because the probability that the situation will become better at the same place is smaller than the probability to find better conditions in a random walk. In the opposite case, when the correlations in space are high, and the correlation in time is small, then it may be more beneficial to wait at the same place than to move. The benefits from motion should be compared to the mobility cost. Both these quantities should be measured in the reproduction coefficient. The interplay between these quantities determines the optimal kinesis strategy.

Detailed analysis of the optimal mobility by the methods of the evolutionary optimality (see [75, 99]), requires more detailed models and much more data. Dynamics of the adaptation resource of animals spent for mobility [83] and the typical spatial and temporal correlations of conditions should be taken into account.

Nevertheless, qualitative analysis of benefits from kinesis for various space and time correlations is very desirable. Let us simplify the problem and discuss discrete space (two locations) and time. The following simple example demonstrates how the 'stop mobility' effect depends on the relations between the spatial correlations, the temporal correlations and the cost of mobility.

Let us start with the simple model used in [79] to illustrate the idea of purposeful kinesis. An animal can use one of two locations for reproduction. The environment in these locations can be in one of two states during the reproduction period, A or B. The number of surviving descendants is r_A in-state A and r_B in state B. Their further survival does not depend on this area. Let us take $r_A > r_B$ (just for concreteness).

The animal can just evaluate the previous state of the locations 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. It can either select the current (somehow chosen) location or to move to another one. It can do no more than one change of locations. The change of location decreases the reproduction coefficient by multiplication on e^{-C} (cost of mobility).

Let $S_1(t)$ and $S_2(t)$ be the states of the locations 1 and 2, correspondingly. Assume also that changes of the pairs (S_1, S_2) can be descried by an ergodic Markov chain with four states (A, A), (A, B), (B, A), and (B, B). Let all the transition probabilities be symmetric with respect to the change of locations $1 \leftrightarrow 2$. Four conditional probabilities are needed for analysis of mobility effects in this model:

$$\mathbf{P}(S_1(t+1) = A | S_1(t) = A), \ \mathbf{P}(S_1(t+1) = B | S_1(t) = A),$$

$$\mathbf{P}(S_2(t+1) = A | S_1(t) = B)$$
, and $\mathbf{P}(S_2(t+1) = B | S_1(t) = B)$.

Assume that an animal is at time t in the location with state A, then:

• if the the animal remains in the initial location then the expected number of surviving descendants is

$$\mathbf{P}(S_1(t+1) = A | S_1(t) = A) r_A + \mathbf{P}(S_1(t+1) = B | S_1(t) = A) r_B,$$

• if the animal jumps to another location then the expected number of surviving descendants is

$$e^{-C}[\mathbf{P}(S_2(t+1) = A | S_1(t) = A)r_A + \mathbf{P}(S_2(t+1) = B | S_1(t) = A)r_B].$$

If an animal is at time t in the location with state B, then:

• if the the animal remains in the initial location then the expected number of surviving descendants is

$$\mathbf{P}(S_1(t+1) = A | S_1(t) = B) r_A + \mathbf{P}(S_1(t+1) = B | S_1(t) = B) r_B,$$

• if the animal jumps to another location then the expected number of surviving descendants is

$$e^{-C}[\mathbf{P}(S_2(t+1) = A | S_1(t) = B)r_A + \mathbf{P}(S_2(t+1) = B | S_1(t) = B)r_B].$$

The choice 'to stay in the current location or to jump' is determined by the selection of behaviour with the highest number of expected offspring. In the evaluation of this number the temporal correlations between $S_1(t)$ and $S_1(t+1)$, the spatio-temporal correlations between $S_1(t)$ and $S_2(t+1)$, and the cost of mobility coefficient e^{-C} are used.

4.6 Discussion

The super-linear increase of the mobility for the decrease of the reproduction coefficient in combination with the linear cost of mobility leads to the critical effect: for the sufficiently bad condition the solution of the equation for mobility does not exist. For some dependencies of mobility on the reproduction coefficient this critical effect can be found explicitly (for example, for the exponential dependence (4.1) proposed and analysed in [79]).

The existence of the critical effect is proven. The question arises: how to find mobility after the critical transition? There is no formal tool to find the answer. We suggest that after the critical threshold, the mobility nullifies. Qualitatively this means that with worsening of conditions mobility increases up to some maximal value. If the conditions deteriorate further, another mobility strategy is activated: do not waste resources for mobility, just wait for conditions to change.

The exact values of the critical thresholds and the optimal dependence of mobility on the reproduction coefficient depend on the relation of the conditions in space and time. Typical relations during the evolution time should be used. These dealings are unknown, and instead plausible hypotheses and identification of parameters from the data can be used.

There are several directions for further work:

- We expect that the described critical effect is widespread in nature, but its description required a theoretical basis. Now this basis is proposed, and existing data on animal mobility can be revised to understand the new critical effect.
- The new family of models requires additional theoretical (mathematical) and numerical analysis with the development of existence and uniqueness theorems, the analysis of attractors, and the development of adequate numerical methods.
- It would be great to apply the new models for modelling of dispersal of real population.

Chapter 5

Impact of Purposeful Kinesis on Travelling Waves

5.1 Introduction

In this chapter, we have analysed the diffusion model with kinesis. Kinesis is the non-directional movement according to the change of the local environment. That is, the organism gets the information from the living area, and therefore prefer to stay or move to the other beneficial place. Taxis is also related to mobility. However, taxis requires the non-local information. The organism with taxis has the directed movement towards to the condition or opposite side of the stimulus.

We aim to explore the impact of purposeful kinesis on travelling waves using PDE models. The classical PDE model of population dispersal was proposed in [165] and [108]. It was used to model taxis behaviour [98]. The reaction-diffusion model can be used for kinesis modelling. The diffusion coefficient can depend on the local situation. Cosner [42] studied the reaction-diffusion models on animal dispersal. He presented the study on animal movement: which is the better condition to stay or leave, being slow or random movement, increasing the population size is harmful or not.

In this study, we employ the purposeful kinesis model [79]. Often 'Purposeful' means intentionality that individuals are unable. Rosenblueth and Wiener [181] developed the general concept of purposeful behaviour. 'Purpose' brings the optimization idea and this concept requires the evolutionary optimality [162]. There is a connection between the reproduction rate and diffusion coefficient. Average reproduction coefficient was defined as Darwinian fitness [91, 142, 75]. Migration should increase Darwinian fitness.

In this study, we analysed impact of the purposeful kinesis on travelling waves. In particular, it was presented that the population with the Allee effect can spread late but with a higher diffusion the population will stay alive, and in time will continue the travelling wave behaviour. We did numerical experiments that kinesis model holds spreading invaded area, while the population without kinesis dies.

5.2 Main results

In this section, we will give the main results.

5.2.1 Travelling waves

The kinesis model was selected in the following form [79]:

$$\partial_t u_i(x,t) = D_{0i} \nabla \cdot \left(e^{-\alpha_i r_i(u_1,\dots,u_k,s)} \nabla u_i \right) + r_i(u_1,\dots,u_k,s) u_i,$$
(5.1)

where:

 u_i is the *i*th species-population density,

s is the abiotic characteristics of the living conditions,

 r_i is the reproduction coefficient,

 $D_{0i} > 0$ is the equilibrium diffusion coefficient which is defined when the reproduction coefficient is 0,

 $\alpha_i > 0$ defines the relation between the diffusion coefficient on the reproduction coefficient.

 $D_i = D_{0i}e^{-\alpha r_i}$ characterizes the diffusion depending on reproduction coefficient. According to that model, the diffusion depends on well-being which is measured by the reproduction coefficient. We will present below how the dependence of diffusion on well-being effects the travelling waves of the population density on space.

Let us compare two models:

• The PDE model for population with the constant diffusion coefficient: without kinesis, KPP (Kolmogorov, Petrovsky and Piskunov, 1937):

$$\partial_t u(t,x) = D\nabla^2 u + (1 - u(t,x))u(t,x),$$
(5.2)

• The PDE model for population with kinesis (KPP with modified diffusion coefficient [110]):

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(t,x))} \nabla u \right) + (1-u(t,x))u(t,x), \tag{5.3}$$

We have first used MATLAB pdepe [166] function to solve one dimensional system of PDE. Then, we used the MATHEMATICA NDSOLVE [146] solver which is applied the Hermite method and Newton's divided difference formula to solve two dimensional system.

We selected the space on the interval [-50, 50] with Dirichlet boundary conditions and with the initial conditions:

$$u(0,x) = \frac{1}{1 + e^{\lambda x}}$$

The values of the constants are: D = 1, $\alpha = 1$, $\lambda = 10$.

In the large time the travelling waves converge to a unique front with the velocity v. For example, the logistic growth model r(u) = au (1 - u/K) speed will be $v_0 = 2\sqrt{aD}$ and for the kinesis model the speed will be $v = 2\sqrt{aDe^{-\alpha r(u)}}$.

Fig. 5.1 presents that the proposed 'minimal purposeful kinesis model' has the travelling wave behaviour on space. In these given conditions, the waves in the population model with kinesis is slower which is explained in Fig. 5.2. When we increase the kinesis parameter α , the spreading velocity will decrease monotonically.

We have done numerical experiments on MATLAB to see the relations between the wave velocity and the kinesis parameter α (see Fig. 5.2). While α is



FIGURE 5.1: Travelling waves of Population density: a) for animals without kinesis for model (5.2) and b) for animals with kinesis for model (5.3). The values of the constants are: D = 1, $\alpha = 1$, $\lambda = 10$.



FIGURE 5.2: Wave velocity as function of the kinesis parameter α for model (5.3).

increasing, the velocity starts to decrease monotonically. After $\alpha = 6$, the velocity is almost stabilizing. That is, the population spreading on space can be almost the same in the different time lines.

5.2.2 Travelling waves with the Allee effect

The Allee effect was introduced as nonmonotonic behaviour of the reproduction coefficient as a function of population density. At the beginning, the reproduction rate is minimum and then reaches to the peak. After the maximum reproduction rate, it starts to decrease monotonically while the population size is increasing [2]. There are a lot of reasons why populations show the Allee effect such as low rate feeding [228, 229], and for some reasons the population reduces the predator defence [109, 111], give up the breeding for psychological reasons [177, 206], and a wide variety of reasons [28, 63, 64, 216].

Lewis and Kareiva [122] explored the population spread of asymptotic rates with the Allee effect. In two dimensional analysis, they investigated that the patterns of spread have been influenced by this population model. We have used the coefficients in that study to analyse how the population with kinesis affects the two-dimensional patterns of spread.

The basic form of the reproduction coefficient with the Allee effect is

$$r(u) = r_0(K - u)(u - \beta).$$

The models with purposeful kinesis on the Allee effect were studied in [79] previously.

Gorban [81] introduced the study that when the average population size is less than the optimum density, the evolutionary optimal strategy for populations with the Allee effect collapses with optimal density. There are some other consequences of the Allee effect with diffusion: the population spreads in a massive way through the formation, the interaction between species and the movement of separate patches even if the population is inhomogeneous external condition [143, 171].

We may present the reaction-diffusion equations for a single population with the Allee effect for a system without kinesis (5.4) and for a system with kinesis (5.5).

$$\partial_t u(t,x) = D\nabla \cdot (\nabla u) + k(1-u)(u-\beta)u(t,x), \tag{5.4}$$

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha k(1-u)(u-\beta)}\nabla u\right) + k(1-u)(u-\beta)u(t,x).$$
(5.5)

The values of constants are: D = 1, $\alpha = 1$, $\beta = 0.7$.

Eqs. (5.4) and (5.5) are solved for one space variable $x \in [-50, 50]$ with Dirichlet boundary conditions and with the initial conditions:



FIGURE 5.3: The travelling waves of population densities with the Allee effect: (a) for animals without kinesis (5.4), (b) for animals with kinesis in time 0 to 100 (5.5). The values of constants are: D = 1, $\alpha = 1$, $\beta = 0.7$.

$$u(0,x) = \frac{1}{1+e^{\lambda x}}; \lambda = 10.$$
(5.6)

We choose $k = k(\beta)$ as the normalization constant which was given in [122] as determined by the maximum growth rate. k has been determined as

$$k = 1; \tag{5.7}$$

$$k = 4/(1-\beta)^2; (5.8)$$

$$k = 27/\left(2\left(\left((1+\beta)^2 - 9\beta/2\right)(1+\beta) + \left((1+\beta)^2 - 3\beta\right)^{3/2}\right)\right).$$
 (5.9)

It is considered that travelling wave solutions to Eqs. (5.4) and (5.5) are in the form of u = U(z) with z = x - vt, where v is the velocity.

It was shown that there is a unique solution to these Eqs. (5.4) and (5.5) with a unique v velocity with the condition $0 < \beta < 1$ in [58]. When the Allee effect parameter is negative, there is a minimum value of velocity such that there exists a corresponding travelling wave solution [8, 58, 90]. After a long time period $t \to \infty$, the solution of the system 5.4 may converge to a travelling wave solution.

The numerical results (Fig. 5.3) show that the population with the Allee effect has the travelling wave behaviour both with kinesis and without kinesis. Population with kinesis demonstrates faster travelling waves on space. Fast-spreading effect of the population could also end up to extinction for the population with the Allee effect. When the Allee effect is higher than the population density, the



reproduction coefficient becomes negative. Therefore, this leads the population to extinction.

FIGURE 5.4: The Allee effect parameter and speed $\alpha = 1$ and D = 1. The population with kinesis and without kinesis a) the normalization constant is k = 1 for models (5.4) and (5.4), b) k is given for model (5.8). c) k is given for model (5.9). The system has been solved with the numerical method for the travelling wave front u = 0.5

Wave velocity for different models has been displayed as the Fig. 5.4 with the Allee effect parameter $-1 \leq \beta \leq 0.5$. The Allee effect decreases the rate of spread of an invading population. We can see from the Fig. 5.4 that with these conditions the spreading of the population with the Allee effect is decreasing when β is getting higher value. Moreover, the spreading velocity of the population without kinesis is faster than the population with kinesis.

5.2.3 Two-Dimensional spread

Analytical representation of two-dimensional system may be too complex to solve. [8] presented that the planar travelling waves exist and this form can be used by an invading population. They studied the two-dimensional population model with Allee dynamics to see the invaded area of the population. The population, with the Allee effect, may end up with extinction. This can happen even if the population density exceeds the threshold. The reason is that reproduction, the population growth, cannot be sufficient to prevent the population dispersal. There are some critical factors to determine the invading success: shape and size of the environment. It has been already shown that how the population stay alive between invaded areas and unoccupied places [122].

Now, in this section, we present the two-dimensional model that we want to see the invaded and unoccupied areas of the population with kinesis and without kinesis. In addition to that model, we discuss the population with the Allee effect.



FIGURE 5.5: Initial distribution (t = 0): $u(0, x) = \frac{1}{1+e^{\frac{x^2+y^2}{2}}}$. The invaded area by the population with kinesis and without kinesis.

Fig. 5.5 shows the initial distribution that the invaded area is the same for the population with kinesis and without kinesis.

5.3 Predator-Prey travelling waves

In this section, we consider competing species in the same environment. These two species interact with the model without kinesis and the new model with kinesis. Volpert and Petrovskii analysed the travelling waves of predator-prey interaction model in their study [222]. Now, we compare the population with kinesis and without kinesis as travelling wave behaviour.



FIGURE 5.6: 2D Population without kinesis $\alpha = 1$ and D = 1.



FIGURE 5.7: 2D Population with kinesis $\alpha = 1$ and D = 1.



FIGURE 5.8: The 2D Allee effect without kinesis $\alpha = 1, D = 1, \beta = 0.05$.



FIGURE 5.9: The 2D Allee effect with kinesis $\alpha = 1, D = 1, \beta = 0.05$.



FIGURE 5.10: Invaded areas at center by the population without kinesis and the Allee effect. The parameters are: $\alpha = 1, D = 1, \beta = 0.05$.



FIGURE 5.11: Invaded areas at center by the population with kinesis and the Allee effect. At time t = 16, the population dies out and there is no waves. The parameters are: $\alpha = 1$, D = 1, $\beta = 0.05$.



FIGURE 5.12: The 2D Allee effect without kinesis $\alpha = 5$, D = 0.5, $\beta = 0.05$ with Neumann boundary conditions.

• The PDE model for population with the constant diffusion coefficient (i.e. without kinesis):

$$\partial_t u(t,x) = D\nabla \cdot (\nabla u) + r_u u(t,x), \qquad (5.10)$$

$$\partial_t v(t,x) = D\nabla \cdot (\nabla v) + r_v v(t,x), \qquad (5.11)$$

• The PDE model for population with kinesis:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\sigma_u r_u} \nabla u\right) + r_u u(t,x), \qquad (5.12)$$

$$\partial_t v(t,x) = D\nabla \cdot \left(e^{-\sigma_v r_v} \nabla v\right) + r_v v(t,x).$$
(5.13)



FIGURE 5.13: The 2D Allee effect with kinesis $\alpha = 5$, D = 0.5, $\beta = 0.05$ with Neumann boundary conditions.



FIGURE 5.14: Invaded areas at center by the population without kinesis and the Allee effect. At time t = 16, there will be no waves since the population dies. The parameters are: $\alpha = 5$, D = 0.5, $\beta = 0.05$.



FIGURE 5.15: Invaded areas at center by the population with kinesis and the Allee effect. The parameters are: $\alpha = 5$, D = 0.5, $\beta = 0.05$.

We consider the simplest predator-prey model in the classical Lotka-Volterra form in dimensionless variables $r_u = k - v$ and $r_v = u - m$; u and v are the population densities of prey and predator.

Eqs. (5.10), (5.11), (5.12) and (5.13) are solved for one space variable $x \in [-100, 100]$ with Dirichlet boundary conditions and with the initial conditions:

$$u(0,x) = v(0,x) = \frac{1}{1+e^{\lambda x}}; \lambda = 10.$$
(5.14)

The numerical simulations with the 1D case show that depending on the values the systems (5.10), (5.11), (5.12) and (5.13) show a variety of travelling fronts.



FIGURE 5.16: Travelling waves of predator-prey diffusion (a) for animals without kinesis, (5.10, 5.11) $\sigma_1 = \sigma_2 = 1$ (b) for animals with kinesis (5.12, 5.13) $\sigma_1 = \sigma_2 = 1$. The values of constants are: D = 1, k = 1, m = 1.



FIGURE 5.17: Travelling waves of predator-prey diffusion (a) for predators with kinesis and preys without kinesis $\sigma_1 = 0$, $\sigma_2 = 1$. (b) for predators without kinesis and preys with kinesis $\sigma_1 = 1$, $\sigma_2 = 0$. The values of constants are: D = 1, k = 1, m = 1.

We compare four cases with Figs. 5.16 and 5.17:

- both predator and prey without kinesis,
- both predator and prey with kinesis,
- predator without kinesis and prey with kinesis,
- predator with kinesis and prey without kinesis.

All of them have the travelling wave behaviour. We demonstrate with Fig. 5.16b that the predator and prey populations with kinesis have the travelling wave behaviour and the peaks between predator and prey increase. For the predator without kinesis and prey with kinesis (Fig. 5.17a), the amplitude decreases. On the other hand, the predator with kinesis and prey without kinesis (Fig. 5.17b) travelling wave peaks of the population density become sharper.

5.4 Discussion

It has been suggested a purposeful kinesis model that the diffusion coefficient depends on well-being which is measured by the reproduction coefficient in [79]. The system formalizes the simple rule: "Let well enough alone". Volpert and Petrovskii presented the study on travelling waves of the reaction-diffusion model [222].

In this chapter, we analysed the travelling wave behaviour of the reactiondiffusion model with kinesis. The travelling wave theory begins with [60] and Kolmogorov, Petrovskii and Piskunov [110]. They defined the travelling wave solutions of the scalar reaction-diffusion equation and analysed their existence, stability and the speed of these waves. Lewis and Kareiva explored the relevance between the Allee effect parameter β and the relative wave speed. They also studied on the two-dimensional spread of invading populations with the Allee effect.

In this study, we have demonstrated the speed of the travelling waves of the population with kinesis. These following have been observed:

- While the relation between the diffusion coefficient and reproduction coefficient α is increasing the travelling wave speed monotonically decreases, and at some point stabilizes (see Fig. 5.2).
- The Allee effect parameter β and velocity v have been displayed by Fig. 5.4 for the values of normalization coefficient k on the travelling wave front u = 0.5. While the Allee effect parameter is increasing, the populations' travelling speed decreases. When $\beta = 0.5$, the velocity is 0. After that value of β , the waves of the population model show the travelling wave behaviour through the left hand side. The individuals with kinesis run slower than the population without kinesis. This may lead up an extinction in the invaded area.
- The initial distributions of the invaded area are the same for both populations (see Fig. 5.5). System stabilization is observed by r = 0. Therefore, Kinesis does not change the stability of homogeneous positive steady-states.

- The invasion of the population with kinesis occupies the larger area than without kinesis. That is, they stay alive in the habitat.
- Allee dynamics can affect the population extinction (see Fig. 5.14). On the other hand, with the higher diffusion, the population with kinesis do not extinct and can invade a large area (see Fig. 5.15).
- We have also presented the travelling wave behaviour of the predator-prey model with kinesis. The constant diffusion model waves were recently analysed in [222] for the predator-prey model. We have observed also that this model can have travelling wave behaviour. Kinesis of prey decreases amplitude of the wave smaller, whereas kinesis of the predators can significantly increase the peak value (Fig. 5.17b).

These population models with kinesis can be adapted to several models. It can be seen that individuals may have the travelling wave behaviour in the invaded areas.

Chapter 6

Conclusion

Modelling of biological populations assume that organisms move randomly and aimlessly. This assumption causes appearing of unexplained phenomena. In population dynamics, when we want to discuss the population density, the diffusion term describes the random movement of individuals and reaction term describes the population reproduction. The population dynamics is widely used as a tool for biological community. Volterra's studies [223, 224] of reaction-diffusion systems are the fundamental work for mathematical ecology and modelling of population dynamics (see also [127, 215]). He explained biological processes as mathematical expressions. Later, because of the limitations of this methodology, the reactiondiffusion models were presented by [3, 15, 16, 17, 35, 50, 56, 73, 127, 144, 164, 183, 202, 211, 215].

The aim of this dissertation is to develop the reaction-diffusion model which can be more realistic to explain individual migration and surviving through migration. This model presents the new idea "Let well enough alone". Animal migration depends on the natural selection (Darwinian fitness). This models assume that organisms move randomly and aimlessly. Our new model includes kinesis parameter which depends environmental conditions. Animals will leave the dangerous place and run away randomly. We presented this reaction-diffusion equation with diffusion coefficient depending on well-being. This coefficient depends the reproduction coefficient.

In the first Chapter, we give the review to animal movement, previous studies, the general aim of the study and the mathematical basis of the model. Organisms move randomly or with a purpose in the real environment and this brings us to discuss the behaviour 'purposeful' and 'non-purposeful'. Darwin, Wallace and Weismann [46, 227, 230] presented evolution theory by the explanation of the natural selection. Darwinian fitness natural choice to define the capacity for reproduction and survival. Fisher presented Darwin's ideas in a mathematical way. In this chapter, we give an example of insect movement: how they survive and what the survival strategies are. Abiotic factors can affect insect migration (Chapter 1.1.4.1). In the higher temperature, the population size of insects may decrease. On the other hand, the lower temperature can cause the same mortality conditions. In the next subsection, we give the methodological and theoretical basis of the model. Einstein introduced the diffusion of liquids. His theory connected the diffusion coefficient and mobility. Later, Teorell presented the diffusion of ions and flux. In Section 1.4, we give the main model where the diffusion coefficient depends on reproduction coefficient. One of the example of such models, the wave equation, firstly was introduced by Jean-Baptiste le Rond d'Alembert [44]. We aim to present the basic form of the reaction-diffusion model. In that model, we choose diffusion coefficient as $D = D_0 e^{-\alpha r}$ to realistically describe animal migration.

In Chapter 2, we presented the biological systems under consideration, especially fitness and kinesis. Our main result is on purposeful kinesis. Therefore, we present the differences between these terms 'purposeful' and 'non-purposeful' behaviour. Animals move on purpose rather than randomly. Purposeful behaviour shows that the animal aims to leave the area with bad condition. Later, we give the definition of evolutionary optimality and Darwinian fitness. Evolutionary optimality brings the adaptation idea. We include Darwinian fitness to present the new model and this idea covers the capacity to survive and reproduce. Darwin expressed his ideas on the struggle for existence. Gause did experiments in the laboratory using bacteria to answer the question 'Why have one species been victorious over another in the great battle of life?'. We studied kinesis model, however, there is a relation between taxis and kinesis movement. Taxis is directed movement; on the other hand, kinesis is undirected. In this chapter, we formulated and answered three crucial questions:

- Which information is available and usable?
- What is the set of the available behaviour strategies?

• What are the statistical characteristics of the environment, in particular, and what are the laws and correlations in the changing of the environment in space and time?

Therefore, we present our new "Let well enough alone" model with described biological backgrounds.

In Chapter 3, we proposed the main model of the reaction-diffusion with kinesis. The new idea is that the diffusion coefficient depends on reproduction coefficient, that is the measure of well-being. Organism mobility is related of the necessity to run anywhere to find a better life. Therefore, while reproduction coefficient is increasing, the diffusion coefficient will decrease. In this chapter, we described our main results.

- The purposeful kinesis model (3.1) is evolutionarily beneficial, if the food exists in low-level uniform background concentration and in rare (both in space and time) sporadic patches. This allows animals to utilise the food patches more intensively (see Figs. 3.3 and 3.4).
- If there is periodic fluctuation environment then purposeful kinesis defined by the instant and local reproduction coefficient (3.1) is evolutionarily beneficial. This allows animals to utilize these fluctuations more efficiently (see Figs. 3.5 and 3.6).
- If the reproduction coefficient r(u, s) is not a monotonically decreasing function (the Allee effect) then the "Let well enough alone" strategy may delay the spreading of population (see Figs. 3.8, 3.9, 3.11, and 3.12). This strategy can cause the failure in the evolutionary game. On the other hand, in the condition of too fast diffusion, the "Let well enough alone" strategy can prevent the effects of extinction (see Figs. 3.13 and 3.14) and, thus, this strategy may decrease the effect of harmful diffusion described in [42].

Chapter 4 proposed that the "Let well enough alone" idea has the mobility cost. In this model, mobility declines for higher reproduction coefficient. Therefore, animals 'prefer' to stay in the good conditions and leave the fatal area. Mobility cost can be measured by the change of reproduction coefficient. Mobility equation can be solved analytically using Lambert W-function. Proposed model has a simple linear cost of mobility. When conditions are getting worse, the mobility increases up to some critical value. For worse conditions, we do not have the mobility. That is, after increasing to the critical point, mobility vanishes.

In Chapter 5, we again used our main model from Chapter 3. In that chapter, we analysed the model impact on travelling waves. The travelling wave behaviour was studied by Fisher [60] and Kolmogorov, Petrovskii, Piskunov [110]. They presented studies on the travelling wave solutions of the scalar reactiondiffusion equation and analysed their existence, stability and the speed of waves. The relation between the Allee effect parameter β and the relative wave speed vwas explored by Lewis and Kareiva. In this chapter, we introduced the speed of travelling waves of our model. We observed that while α (the diffusion and reproduction coefficient relation) is increasing, the speed of travelling wave declines monotonically. Moreover, while the Allee effect parameter is increasing the travelling wave speed decreases and after $\beta = 0.5$, waves stabilize (see Fig. 5.4. The population with kinesis invades larger area than without kinesis. With the Allee effect and higher diffusion, the population without kinesis can have extinction; on the other hand, with kinesis it can survive.

The main result of our work is the introduction, motivation and analysis of a new model of purposeful kinesis. This model formalises the idea "Let well enough alone", which is new for population modelling. We believe that this model with dependence of the mobility on the reproduction coefficient will find more applications in Population Dynamics. As a future study, we plan to combine the purposeful kinesis with taxis and study the corresponding reaction-diffusion models. Such a system of models will allow us to understand animal movement in a more realistic way.

Appendix A

Two Stations Model

In this chapter, we present computational methods for partial differential equations, in particular, the finite difference method for diffusion equations with initialboundary value problem.

Let's consider a two-station model. Suppose that we have two stations which one presents a worse life than another station for animals. Therefore, animals have started to move to the second station to have a better life.

The reproduction coefficients are logistic

$$r_1 = k_1 \left(1 - \frac{u}{u_1} \right),\tag{A.1}$$

$$r_2 = k_2 \left(1 - \frac{u}{u_1} \right),\tag{A.2}$$

where k_1, k_2 are intrinsic growth rate and u_1, u_2 are carrying capacities of these stations. In continuous approximation, we take with a smooth interface

$$\hat{k} = k_0 + \frac{q}{1 + e^{-\beta x}},$$
(A.3)

$$\hat{u} = u_0 + \frac{v}{1 + e^{-\beta x}},$$
(A.4)

$$r = \hat{k}(x) \left(1 - \frac{u(x)}{\hat{u}(x)} \right). \tag{A.5}$$

When r is constant, mobility is the same. That is, we may not have real diffusion. In addition to that, when reproduction coefficient is constant, the animals will not run away from their place. Therefore, the equation is

$$\frac{du}{dt} = r(x)u(x) + d_0\nabla \cdot \left(e^{-\alpha r(x)}\nabla u\right), \qquad (A.6)$$

$$\frac{du}{dt} = \hat{k}\left(x\right) \left(1 - \frac{u\left(x\right)}{\hat{u}\left(x\right)}\right) u\left(x\right) + d_0 \nabla \cdot \left(e^{-\alpha \hat{k}\left(x\right)\left(1 - \frac{u\left(x\right)}{\hat{u}\left(x\right)}\right)} \nabla u\right), \qquad (A.7)$$

$$\frac{du}{dt} = \left(k_0 + \frac{q}{1+e^{-\beta x}}\right) \left(1 - \frac{u\left(x\right)}{u_0 + \frac{v}{1+e^{-\beta x}}}\right) u\left(x\right) + d_0 \nabla \cdot \left(e^{-\alpha \left(k_0 + \frac{q}{1+e^{-\beta x}}\right) \left(1 - \frac{u\left(x\right)}{u_0 + \frac{v}{1+e^{-\beta x}}}\right)} \nabla u\right).$$
(A.8)

From the first station, the diffusion will start, and the population will diffuse to the second station. Therefore, diffusion is going to be slower.

The initial condition, at time 0 the population size is 20

$$u(0,x) = 20, -50 \le x \le 50 \tag{A.9}$$

We can see that Fig. A.1 shows the population will increase in time and space. First station (left hand side) shows well-being is low, and it represents an uncomfortable station. Second station (right hand side) represents a more beneficial area for animals. In the first station, the reproduction coefficient is negative. That is, the death rate starts to increase, and therefore animals want to move to the second station. Firstly, the mobility will be fast; but then it will be slower and reach steady-state.

We can also rescale α ; that is $k_0 = 1$ and α , $d_0 = 5$, q = 2 and v = 5. We can see the result of rescaling α and $d_0 = 5$ with Fig. A.2. That means we increase the diffusion coefficient. Therefore, the mobility to the second station will be more quickly at the beginning, and then it will reach steady-state.



FIGURE A.1: First plot shows population dynamics in time when we take these conditions $k_0 = 1$ and $d_0 = 1$, $\alpha = 5$, q = 2, v = 5, $u_0 = 25$. Second plot shows its 2D view, and third plot changing population every 10 time.

Rescaling all these parameters k_0 , α and d_0 makes the population size decrease. Another possibility affecting population size is to change q, v parameters $k_0 = 1, d_0 = 1, \alpha = 1, q = 5, v = 2$ (see Fig. A.3). Changing q and v constants, the mobility will be stable with strictly increasing. In addition to that, the population size reaches 30.

Suppose that q, v parameters: $k_0 = 1$, $d_0 = 1$, $\alpha = 1$, q = 2, v = 2. If we rescale all the parameters k_0 , d_0 , α and q = v = 2, then the population size will decrease clearly, since we are decreasing the population size. Therefore, the population will want to change its area and the diffusion be more smooth.

Or we can take $k_0 = 1, d_0 = 1, \alpha = 1, q = 5, v = 2$. When we decrease q, then the population size will be 27.

When we increase k_0 the population size will increase and the population want to stay in station 1. Therefore, the diffusion to the second station will be slower.

Suppose that $k_0 \neq 1, k_0 = 5, d_0 = 1, q = 1, v = 1$ and $\alpha \neq 1, \alpha = 2$. When



FIGURE A.2: First plot shows population dynamics in time when we take these conditions $k_0 = 1$ and $\alpha = 1$, $d_0 = 5$, q = 2, v = 5 and $u_0 = 25$. Second plot shows its 2D view, and third plot changing population every 10 time.

we change also α and when we rescale d_0 , the population size will reach to steady state. Changing the capacity will affect the diffusion from station 1 to station 2. Increasing the capacity in space and time will bring the population diffusion from 35 to almost 40.

It is observed that increasing the diffusion coefficient makes the population diffusion smoother from station 1 to station 2. In terms of population behaviour, increasing the diffusion coefficient means that the population wants to transform to the second station because of the maybe unsatisfying conditions of the environment. Therefore, the population size will increase mostly in the second station and then reach steady-state.

As a conclusion, increasing the reproduction coefficient will make the diffusion slower. Since the population wants to increase inside the station 1, the diffusion to the second station will be slow. That is, the population will not want to transport to the second station. To increase the population growth rate can be


FIGURE A.3: First plot shows population dynamics in time when we take these conditions $k_0 = 1$ and $\alpha = 1$, $d_0 = 1$, q = 5, v = 2 and $u_0 = 25$. Second plot shows its 2D view, and third plot changing population every 10 time.

observed when the growth rate is increasing. Hence, the population growth rate and capacity have been changed to show how it affects the diffusion. Moreover, it was introduced that the capacity of the population affects the increasing of the population, and therefore the diffusion to the second station. If the diffusion coefficient is increasing, the population prefers to stay in the second station.

In this chapter, we presented a new model that the diffusion depends on well-being, which is measured by the reproduction coefficient. Therefore, it has been introduced that animals will transport to the second station if it is more beneficial than the first station. The mobility of the population depends on the reproduction coefficient. It was shown that while reproduction coefficient is increasing, the diffusion coefficient starts to decrease. The animals prefer to stay in a good place in station 1. In this logistic growth model, when the growth rate is increasing, the mobility will decrease. Moreover, the carrying capacity is an effect



FIGURE A.4: First plot shows population dynamics in time when we take these conditions $k_0 = 1$ and $\alpha = 1$, $d_0 = 1$, q = 2, v = 5 and $u_0 = 25$. Second plot shows its 2D view, and third plot changing population every 10 time.

of increasing of the population size. Therefore, it was observed that when carrying capacity is increasing, the diffusion coefficient will decrease. Otherwise, when the population size starts to decrease (the reproduction coefficient decreases), the population will start to run to the other place.



FIGURE A.5: First plot shows population dynamics in time when we take these conditions $k_0 = 1$ and $\alpha = 1$, $d_0 = 1$, q = 2, v = 2 and $u_0 = 25$. Second plot shows its 2D view, and third plot changing population every 10 time.

Appendix B

Some Purposeful Kinesis Systems

In this chapter, we introduce a new class of kinesis models for the modelling of the evolutionary migration. The diffusion coefficient is a function of the local quality of life conditions measured by the reproduction coefficient. This modification of diffusion does not affect the stability of uniform positive steady-states, but affects relaxation and non-uniform states. These models formalise a simple wisdom: "Let well enough alone". For large r, mobility should decrease. We analyse how the dynamics of spatially distributed reaction-diffusion systems depends on the kinesis effects modelled. In particular, we study the modification of waves and patch formations caused by these effects.

The reaction-diffusion equations are the main tools for modelling of spatially distributed populations. The standard assumption behind the diffusion models is the randomness of individual migration. Karl Pearson [168] proposed in 1905 a simple model for mosquito infestation in a forest: at each time step, a single mosquito moves a fixed length at a randomly chosen angle. Einstein published his random walk model of Brownian motion in the same year. George Gamow [68] described this motion as the wanderings of a "drunk sailor". For particles, the random walk models have the solid background and work quite well.

The strategy of spatial distribution should increase the average reproduction coefficient. A simple formalisation of this idea is the notion of the ESS-Evolutionary Stable Strategy of spatial distribution. ESS is the optimal strategy among the available strategies. Description of the space of available strategies is a challenging task and includes evaluation of information about the future living conditions, which can be used by a migrating animal. For the first example, we studied relaxation of two simple systems: u is the population density, s is the concentration of substrate and reproduction coefficient is as - b, for system 1 diffusion depends on reproduction coefficient, for system 2 it is constant.

• The population without kinesis System 0:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(t,x))u(t,x),$$

 $u(0,x) = 0.4.$
(B.1)

• The population with kinesis System 1:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(x,t))} \nabla u \right) + (1-u(x,t))u(t,x),$$

(B.2)
 $u(0,x) = 0.4.$



FIGURE B.1: d = 1 and $\alpha = 0.1$; a) for animals without kinesis b) for animals with kinesis.

• The population with the Allee effect and without kinesis System 2:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(x,t))(u(t,x) - \beta)u(t,x),$$

$$u(0,x) = 0.4.$$
(B.3)

• The population with Allee effect and kinesis System 3:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(x,t))(u(t,x)-\beta)} \nabla u \right) + (1-u(x,t))(u(t,x)-\beta)u(t,x),$$

$$u(0,x) = 0.4.$$



FIGURE B.2: $d = 1, \alpha = 0.1, a = 2, \beta = 0.2$; a) for animals with kinesis and b) for animals without kinesis.

(B.4)

• Relaxation to uniform equilibrium for Predator-Prey System 4:

$$\partial_t u(t, x) = \nabla^2 + r_u u(t, x),$$

$$\partial_t v(t, x) = \epsilon \nabla^2 + r_v v(t, x),$$

$$r_u = \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u},$$

$$r_v = \frac{u}{1 + \alpha u} - \delta,$$

$$u(0, x) = 1.2,$$

$$v(0, x) = 0.2.$$

(B.5)

• Relaxation to uniform equilibrium for Predator-Prey System with kinesis System 5:

$$\partial_t u(t,x) = \nabla \cdot \left(e^{-\alpha_u r_u} \nabla u\right) + r_u u(t,x),$$

$$\partial_t v(t,x) = \epsilon \nabla \cdot \left(e^{-\alpha_v r_v} \nabla v\right) + r_v v(t,x),$$

$$r_u = \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u},$$

$$r_v = \frac{u}{1 + \alpha u} - \delta,$$

$$u(0,x) = 1.2,$$

$$v(0,x) = 0.2.$$

(B.6)



FIGURE B.3: $\alpha_u = 1, \alpha_v = 7, \gamma = 3.9, \beta = 0.2, \alpha = 0.1, \epsilon = 1, \delta = 0.5; a)$ prey population with kinesis b) predator population with kinesis.

• The population without kinesis System 0:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(t,x))u(t,x),$$

$$u(0,x) = Ae^{\frac{-x^2}{2}},$$
(B.7)

• The population with kinesis System 1:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(x,t))} \nabla u \right) + (1-u(x,t))u(t,x),$$

$$u(0,x) = A e^{\frac{-x^2}{2}},$$
 (B.8)



FIGURE B.4: d = 1; $\alpha = 0.1$; A = 0.4; a) for animals without kinesis and b) for animals with kinesis c) with kinesis and without kinesis difference d)reproduction coefficient

• The population with the Allee effect and without kinesis System 2:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(x,t))(u(t,x) - \beta)u(t,x),$$

$$u(0,x) = Ae^{\frac{-x^2}{2}},$$
(B.9)

• The population with the Allee effect with kinesis System 3:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(x,t))(u(t,x)-\beta)} \nabla u \right) + (1-u(x,t))(u(t,x)-\beta)u(t,x),$$

$$u(0,x) = Ae^{\frac{-x^2}{2}},$$



FIGURE B.5: The population with kinesis and without kinesis in time a)d = 1, $\alpha = 10, \ \beta = 0.0002, \ A = 1$ b) $d = 5, \ \alpha = 10, \ \beta = 0.0002, \ A = 1$ c) $d = 10, \ \alpha = 10, \ \beta = 0.0002, \ A = 1$ d) $d = 10, \ \alpha = 10, \ \beta = 0.0002, \ A = 5$

• Relaxation to uniform equilibrium for Predator-Prey System 4:

$$\partial_t u(t,x) = \nabla^2 + r_u u(t,x),$$

$$\partial_t v(t,x) = \epsilon \nabla^2 + r_v v(t,x),$$

$$r_u = \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u},$$

$$r_v = \frac{u}{1 + \alpha u} - \delta,$$

$$u(0,x) = A e^{\frac{-x^2}{2}},$$

$$v(0,x) = A e^{\frac{-x^2}{2}},$$

(B.11)

(B.10)

• Predator-Prey with kinesis System 5:

$$\partial_t u(t,x) = \nabla \cdot \left(e^{-\alpha_u r_u} \nabla u\right) + r_u u(t,x),$$

$$\partial_t v(t,x) = \epsilon \nabla \cdot \left(e^{-\alpha_v r_v} \nabla v\right) + r_v v(t,x),$$

$$r_u = \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u},$$

$$r_v = \frac{u}{1 + \alpha u} - \delta,$$

$$u(0,x) = A e^{\frac{-x^2}{2}},$$

$$v(0,x) = A e^{\frac{-x^2}{2}},$$

(B.12)



FIGURE B.6: $\alpha_u = 1; \alpha_v = 7; \gamma = 3.9; \beta = 0.2; \alpha = 0.1; \epsilon = 1; \delta = 0.5; A = 0.8;$ a) prey population with kinesis b) predator population with kinesis.

When we change the initial condition:

• System 0:

$$\partial_t u(t, x) = D\nabla^2 + (1 - u(t, x)),$$

$$u(0, x) = 0.4(-50 < x < 0),$$

$$u(0, x) = 0(otherwise),$$

(B.13)

• System 1:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(x,t))} \nabla u \right) + (1-u(x,t))u(t,x),$$

$$u(0,x) = 0.4(-50 < x < 0),$$

$$u(0,x) = 0(otherwise),$$

(B.14)

• System 2:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(x,t))(u(t,x) - \beta)u(t,x),$$

$$u(0,x) = 0.4(-50 < x < 0),$$

$$u(0,x) = 0(otherwise),$$

(B.15)

• System 3:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha (1-u(x,t))(u(t,x)-\beta)} \nabla u \right) + (1-u(x,t))(u(t,x)-\beta)u(t,x),$$

$$u(0,x) = 0.4(-50 < x < 0),$$

$$u(0,x) = 0(otherwise),$$

(B.16)

• System 4:

$$\begin{aligned} \partial_t u(t,x) &= \nabla^2 + r_u u(t,x), \\ \partial_t v(t,x) &= \epsilon \nabla^2 + r_v v(t,x), \\ r_u &= \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u}, \\ r_v &= \frac{u}{1 + \alpha u} - \delta, \\ (u(0,x), v(0,x)) &= (0.4, 0.8)(-50 < x < 0), \\ (u(0,x), v(0,x)) &= (0, 0)(otherwise), \end{aligned}$$
(B.17)

• System 5:

$$\partial_t u(t,x) = \nabla \cdot \left(e^{-\alpha_u r_u} \nabla u\right) + r_u u(t,x),$$

$$\partial_t v(t,x) = \epsilon \nabla \cdot \left(e^{-\alpha_v r_v} \nabla v\right) + r_v v(t,x),$$

$$r_u = \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u},$$

$$r_v = \frac{u}{1 + \alpha u} - \delta,$$

$$(u(0,x), v(0,x)) = (0.4, 0.8)(-50 < x < 0),$$

$$(u(0,x), v(0,x)) = (0, 0)(otherwise),$$

(B.18)

• $\beta = 0$:

$$\partial_t u(t, x) = D\nabla^2 + (1 - u(x, t))(u(t, x) - \beta)u(t, x),$$

$$u(0, x) = 0.4(-50 < x < 0),$$

$$u(0, x) = 0(otherwise),$$

(B.19)

• System 3:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(1-u(x,t))(u(t,x)-\beta)} \nabla u \right) + (1-u(x,t))(u(t,x)-\beta)u(t,x),$$

$$u(0,x) = 0.4(-50 < x < 0),$$

$$u(0,x) = 0(otherwise),$$

(B.20)

• System 4:

$$\begin{aligned} \partial_t u(t,x) &= \nabla^2 + r_u u(t,x), \\ \partial_t v(t,x) &= \epsilon \nabla^2 + r_v v(t,x), \\ r_u &= \gamma (u - \beta)(1 - u) - \frac{v}{1 + \alpha u}, \\ r_v &= \frac{u}{1 + \alpha u} - \delta, \\ (u(0,x), v(0,x)) &= (0.4, 0.8)(-50 < x < 0), \\ (u(0,x), v(0,x)) &= (0, 0)(otherwise), \end{aligned}$$
(B.21)



FIGURE B.7: $d = 1, \alpha = 0.1, \beta = 0$, a) for animals without kinesis and b)in time c) for animals with kinesis e) the difference f) reproduction coefficient

• System 2:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(x,t))(u(t,x) - \beta)u(t,x),$$

$$u(0,x) = 0.4(-50 < x < 0),$$

$$u(0,x) = 0.2001(otherwise),$$

(B.22)

• System 3:

$$\begin{aligned} \partial_t u(t,x) &= D\nabla \cdot \left(e^{-\alpha (1-u(x,t))(u(t,x)-\beta)} \nabla u \right) + (1-u(x,t))(u(t,x)-\beta)u(t,x), \\ u(0,x) &= 0.4(-50 < x < 0), \\ u(0,x) &= 0.2001(otherwise), \end{aligned}$$

Let's change diffusion coefficient with d = 10: Let's change the initial condition as 0.8:

$$\partial_t u(t,x) = D\nabla^2 + (1 - u(x,t))(u(t,x) - \beta)u(t,x),$$

$$u(0,x) = 0.8(-50 < x < 0),$$

$$u(0,x) = 0.2001(otherwise),$$

(B.24)

• System 3:

$$\begin{aligned} \partial_t u(t,x) &= D\nabla \cdot \left(e^{-\alpha (1-u(x,t))(u(t,x)-\beta)} \nabla u \right) + (1-u(x,t))(u(t,x)-\beta)u(t,x), \\ u(0,x) &= 0.8(-50 < x < 0), \\ u(0,x) &= 0.2001(otherwise), \end{aligned}$$

$$\partial_{t}u(t,x) = \nabla^{2} + r_{u}u(t,x),$$

$$\partial_{t}v(t,x) = \epsilon \nabla^{2} + r_{v}v(t,x),$$

$$r_{u} = \gamma(u - \beta)(1 - u) - \frac{v}{1 + \alpha u},$$

$$r_{v} = \frac{u}{1 + \alpha u} - \delta,$$

$$(u(0,x), v(0,x)) = (0.4, 0.8)(-50 < x < 0),$$

$$(u(0,x), v(0,x)) = (0.2001, 0.2001)(otherwise),$$

(B.26)

(B.23)

(B.25)



FIGURE B.8: $d = 1, \alpha = 0.1, \beta = 0.2, a$)b) for animals without kinesis and c)d) for animals with kinesis e)the difference

• System 5:

$$\begin{aligned} \partial_t u(t,x) &= \nabla \cdot \left(e^{-\alpha_u r_u} \nabla u \right) + r_u u(t,x), \\ \partial_t v(t,x) &= \epsilon \nabla \cdot \left(e^{-\alpha_v r_v} \nabla v \right) + r_v v(t,x), \\ r_u &= \gamma (u - \beta) (1 - u) - \frac{v}{1 + \alpha u}, \\ r_v &= \frac{u}{1 + \alpha u} - \delta, \\ (u(0,x), v(0,x)) &= (0.4, 0.8) (-50 < x < 0), \\ (u(0,x), v(0,x)) &= (0.2001, 0.2001) (otherwise), \end{aligned}$$
(B.27)



FIGURE B.9: $\alpha_u = 1; \alpha_v = 7; \gamma = 3.9; \beta = 0.2; \alpha = 0.1; \epsilon = 1; \delta = 0.5; a)$ prey population without kinesis b) predator population without kinesis, c) prey population with kinesis d) predator population with kinesis.



Figure B.10: $\alpha_u = 1, \alpha_v = 7, \gamma = 3.9, \beta = 0.2, \alpha = 0.1, \epsilon = 1, \delta = 0.5,$

• The population without kinesis coupled system with *s* concentration, System 0:

$$\partial_t u(t,x) = D\nabla^2 + (as(t,x) - b)u(t,x),$$

$$\partial_t s(t,x) = -gu(t,x)s(t,x) + d,$$

$$s(0,x) = Ae^{\frac{-x^2}{2}},$$

$$u(0,x) = 1.$$

(B.28)



FIGURE B.11: $\alpha_u = 1, \alpha_v = 7, \gamma = 3.9, \beta = 0.2, \alpha = 0.1, \epsilon = 1, \delta = 0.5$. a) prey population without kinesis b) predator population without kinesis, c) prey population with kinesis d) predator population with kinesis.

• System 1:

$$\partial_t u(t,x) = D\nabla \cdot \left(e^{-\alpha(as(t,x)-b)}\nabla u\right) + (as(t,x)-b)u(t,x),$$

$$\partial_t s(t,x) = -gu(t,x)s(t,x) + d,$$

$$s(0,x) = Ae^{\frac{-x^2}{2}},$$

$$u(0,x) = 1.$$

(B.29)

• System 2:

$$\partial_{t}u(t,x) = D\nabla^{2} + (as(t,x) - b)(u(t,x) - \beta)u(t,x),$$

$$\partial_{t}s(t,x) = -gu(t,x)s(t,x) + d,$$

$$s(0,x) = Ae^{\frac{-x^{2}}{2}},$$

$$u(0,x) = 1.$$

(B.30)



FIGURE B.12: $d = 10, \alpha = 5, a = 2, b = 1, g = 1, d = 1, A = 4, a$ for animals with kinesis and b) for animals without kinesis.



FIGURE B.13: The phase portrait of the population with the Allee effect: the same the population with kinesis and without kinesis.

• System 3:

$$\begin{aligned} \partial_t u(t,x) &= D\nabla \cdot \left(e^{-\alpha(as(t,x)-b)(u(t,x)-\beta)} \nabla u \right) + (as(t,x)-b)(u(t,x)-\beta)u(t,x), \\ \partial_t s(t,x) &= -gu(t,x)s(t,x) + d, \\ s(0,x) &= Ae^{\frac{-x^2}{2}}, \\ u(0,x) &= 1. \end{aligned}$$

(B.31)



Figure B.14: $d = 10, \alpha = 5, a = 2, b = 1, g = 1, d = 1, \beta = 0.5, A = 4,$



FIGURE B.15: System 2 and 3 stability.

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