Chapter 1
A Cross-Disciplinary Way Forward in the Study of Movement

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1.1 Newton's Legacy

Newton's legacy has inspired generations of mathematicians and physicists who have dedicated their lives to the study of motion in all its shapes and forms. His accomplishments, together with those of other giants of yore that came after, have provided the foundation to advance the study of movement in classical mechanics, kinetic theory, partial differential equations, probability theory and stochastic calculus, to name but a few. As movement processes are ubiquitous, these areas of mathematics and theoretical physics have advanced due to an influx of problems from across the entire scientific spectrum creating a set of concepts, tools and techniques that may be collectively termed the mathematics of movement. While the external influx of problems has been instrumental in realising a high level of formal sophistication, it has created cultural and technical barriers between movement modellers working in different disciplines. Following the revolution in sensor technologies during the last few decades [1], these barriers have grown even further as the unprecedented resolution and amount of movement data [2, 3] have often pushed researchers to focus their efforts on tackling questions that are system or species specific.

To make technological advances valuable beyond the scientific areas from where they originated, we advocate for a more holistic framework with a common language that helps address general questions and contributes to new insights across the different types of movement processes. A fruitful first step to do this is to classify or

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categorise the modelling choices available to study movement. These classifications, even if broad, may help investigators understand the limits of their findings or realise when it is more profitable to change the type of modelling approach than to collect more data [4]. An essential classification is the scale of description, which customarily reduces to a binary choice between ‘microscopic’, i.e. at the level of the individual, and ‘macroscopic’ or coarse-grained, i.e. at the level of a group or an entire population, although multi-scale approaches to model biological systems are becoming increasingly important [5, 6]. The choice of the formalism being stochastic or deterministic is another important decision in the modelling paradigm to follow [7], even if it is often constrained by the numbers of moving agents involved, with random effects being negligible when population densities are high. These and other more detailed modelling choices, e.g. whether predictions are on transient dynamics or long-term dependencies and whether space is represented via continuous or discrete variables, i.e. a lattice or a network, bring about a set of concepts and techniques that are universal, whose regime of validity is well known, and can be applied independently of the species or environment where movement and interactions occur.

While many would agree on statements about the universality of mathematical tools, the specificity of the observations and the hard-to-measure interactions between biological organisms may cause some to hesitate considering of practical value the existence of underlying quantitative commonalities to describe movement. But this is precisely the reason why the applied disciplines historically have taken centre stage, not only in inspiring and motivating novel modelling approaches but also in influencing the development of new mathematics to quantify movement. Ascribing to a long-held philosophical belief in science [8], we consider that progress is best achieved by a dynamic dialogue between the unearthing of new concepts and the development of novel tools or refinement of old ones. In our context, a vehicle to ensure that such a dialogue occurs is via knowledge exchange, systematisation and integration of the ideas and techniques employed to analyse movement and interactions in animal ecology and cell biology. It was this strong belief that first inspired us, and our co-organisers, to conceive and run the Mathematics of Movement programme at the Isaac Newton Institute for Mathematical Sciences held in Cambridge during the second half of 2023 (see ref. [9] for a popular article on the Mathematics of Movement and interviews from three of the six programme co-organisers).

1.2 The Value of a Shared Approach

In highlighting the importance of bridging gaps and sharing knowledge between animal ecology and cell biology, we are drawn first to the common trajectory that the two fields have witnessed recently, namely, a leap forward in quality, types and number of movement data. In the last decades, as a result of empirical advances in animal tracking technologies [10, 11] and tissue imaging tools [12–14], the analysis and quantification of movement of organisms, and their environments, has undergone a significance upsurge.

In terms of data quality in animal studies, the ratio between the average speed of an organism and its size is now often larger than the sampling frequency of tracking data, making movement observations highly resolved in space and time. Across research areas experimental apparatuses have steadily improved. While laboratory experiments are linking movement decisions to neurological circuitry with the help of immersive volumetric virtual reality techniques [15], the increasing miniaturisation of tracking devices continues to expand the species whose movement can be recorded in the field, lowering the intrinsic limits dictated by the device body weight relative to that of the animal. In addition, the plethora of sensors [16, 17] measuring an animal's state, from its heart rate and body temperature to its locomotion and energetics, as well as the environmental information ranging from vegetation to chemical contents and climatic conditions [18], is creating new ways of thinking, analysis and modelling.

A recent milestone in ecological field studies to boost the number and accuracy of movement data has been the deployment of the ATLAS system [19–21], a high-throughput wildlife tracking system based on reverse-GPS (time-of-arrival) principles, which is capable of tracking multiple free-ranging wild individuals automatically and simultaneously, at high temporal frequency and spatial accuracy and low costs yielding up to 2.5 million data points (localisations) per day. This type of system plays a key role in uncovering how animals interact, not only with the environment but also with other conspecific or heterospecific individuals. While highly resolved GPS localisations have been instrumental in enabling us to infer interaction rules in various species of mammals [22, 23], the low cost, high resolution and high throughput of the ATLAS system is poised to provide the field counterpart of video tracking data in laboratory experiments, the latter traditionally employed to study the behaviour of insects [24, 25] and fish [26].

In cell biology, given the relative higher population density when compared to animal groups, the need to employ low frame rate image sequence to capture time-lapses with high resolution on multi-points requires appropriate software to ensure the proper identification of cells between consecutive images [27]. Improvement in optical microscopy has thus always been linked to the refinement of algorithms for track segmentation. Testament of this fundamental link between hardware and software is the ongoing Cell Tracking Challenge (http://celltrackingchallenge.net), an initiative in existence for more than 10 years, whose goal is to promote the development and evaluation of automated cell tracking algorithms (see ref. [28] for its most recent publication).

The nature and sophistication of data type have also been expanding, with spatio-temporal trajectories now routinely accompanied by a plethora of auxiliary information, e.g. real-time changes in cell shape, cell cycle, phenotypes and molecular transcriptional activities when imaging cell displacements. Of late, the analysis of fine-scale cellular imaging data via high-resolution confocal laser scanning microscopy (see, e.g. [29]) and the use of AI tools such as deep learning software (see, e.g. [30]) have allowed rapid progress in detecting differences in functional, molecular and anatomical properties of cells. These experimental approaches, and the associated analyses of the data, provide parameter information for mathematical models that marry descriptive details with the underlying mechanisms.

While the higher resolution of empirical observations has been beneficial to tackle many unsolved problems, the finer nuances required to analyse these novel datasets have created a series of conceptual and semantic barriers between the two disciplines, making modellers in animal ecology and cell biology move along parallel paths, with minimal exchange of ideas, tools and techniques. Given the vast methodological knowledge to model movement and resolve the data analysis challenges that the tracking revolution has brought, it behooves any researcher in one of the two disciplines to seek to profit from insights gained in the other. Although animals and cells move and interact in very different ways, many spatio-temporal movement patterns are common to both. Looking at them through the mathematics of movement language would bring a quantitative understanding that may not be available within the constraints of disciplinary thinking. We make these assertions more precise by presenting a couple of examples.

During some processes in morphogenesis and cancer development, cells move collectively through what appear to be velocity alignment processes and the establishment of heterogeneities with so-called leaders and followers (see, e.g. [31, 32]). During collective migration of epithelial cells, identifying the mechanical forces [33, 34] and chemical gradients [35] that drive this alignment over long distances has been key to understanding how polarity and movement occurs in a cell cluster. These studies have revealed that the leaders are able to pull the remaining individuals through a sustained propagation of extracellular signal-regulated kinase activation and contractile force generation, although the latest findings also indicate that collective cell migration requires a global mechanical organisation within the cell cluster [36].

Similar examples of group movement through alignment exist in schools of fish, herds of mammals and flocks of birds [37]. In these higher organisms, there are also examples where individuals respond not only to who is in front but also to individuals behind [38]. Addressing who is "paying attention" to whom, or who is mechanically or chemically connected to whom, appears key for interpreting and explaining collective movement data both in cell populations and in higher organisms. An interplay between multiple scales of alignment, attraction and avoidance is at the heart of the patterns that emerge from collective movement, but identifying the role that each type of interaction plays is the challenge. Techniques to do that are well-developed in the animal ecology literature (see, e.g. [39]) and could be exploited in analysing cell tracking data.

The spatial spread of an infectious disease in an animal population depends locally on individual interactions, namely, the encounter and transmission probabilities (or rates) between infectious and susceptible animals, which in turn are influenced by the animal movement statistics [40]. Globally the number of individuals depends on the environmental conditions in the habitat, as the latter determines the average population density that a region of space is able to sustain, the so-called carrying capacity. This direct relation between number of individuals and the availability of resources creates, in certain instances, natural hotspots or reservoirs of the disease, also called infection refugia [41], where the infected population never dies out. A classical example where infection waves emerge from refugia is the Hantavirus epidemic in mice populations in the Southwest USA. The emerging waves have been predicted by modelling the spatio-temporal dynamics of infected and susceptible populations in a spatially heterogeneous environment comprising optimal and sub-optimal habitats of the animal host, *Peromyscus maniculatus* [42]. The predictions of advancing and retracting waves of infection, in the form of pushed-type travelling fronts following vegetation gradients [43], have been recently verified and measured to reach the average speed of the order of tens of meters per day [44].

Wave-like propagation resulting from changes in the surrounding environment is also present in cell biology, the prototypical example occurring during durotaxis [45, 46], when cells move by latching and pulling onto the extracellular matrix, the fibre-like proteins in human and animal tissues. Recent modelling approaches via the Cellular Potts model [47] are providing mechanistic explanations of the measurements observed in live-cell cultures of local strain stiffening in biopolymer networks [48]. These types of mechanical waves provide a long-range guidance that allows cells to navigate at relatively lower speed, of the order of microns per minute or per hour [49], when compared to the Hantavirus example.

While the latter two examples above arise due to the interaction between organisms and their environment, the vastly different magnitudes of their speed may lead one to conclude that the movement of certain cells in the extracellular matrix and that of mice moving through different vegetation types is fundamentally different. And yet, while cells degrade and reshape the underlying fibre network leaving guidance signals for the ones that follow, mice consume the resources in the landscape and leave cues by depositing scent marks over the terrain. These marks contain a great deal of information and may direct others away or towards other conspecifics, thus generating a form of animal-animal interaction mediated by the environment. This form of indirect interaction, named stigmergy [50], is well-known to exist in eusocial insects [51] and has also been shown to be present in scent-marking mammals [52]. This deeper connection may be further exploited to encourage the use of Cellular Potts models to study how mice, while tracking vegetation gradients to forage, also influence the spatial spread of other individuals.

Quantitative similarities are not only present at the microscopic scale. They may also appear when coarse-graining the individual agent dynamics to describe the emerging pattern. This is precisely the context of the mathematical models of territorial scent-marking animals. The mesoscale mobility of the scented territories as a function of the time for which scent marks remain active displays spatial characteristics akin to those of two-dimensional colloids that possess a liquid-hexatic-solid melting scenario [53, 54]. While this so far remains a theoretical link, it may be another fertile ground to share tools and study how cells arrange spatially within tissues.

1.3 Some Common Research Challenges

Up to now we have presented examples of where movement modelling in one specific area may help in the study of movement processes in another, but there exist other challenges that go beyond the use of ad-hoc techniques in a specific scenario or a system and that could be addressed from the collaboration of movement modellers across disciplines. One such example is the development of a general theory of organism interaction. Being able to characterise from observations the type of mechanisms by which animals interact among themselves and with the environment is a big open question and it is at the core of pressing scientific and societal problems. At the ecosystem scale, to tackle the loss of biodiversity there is an urgent need for more rigorous predictions of how animals respond to changes in the environment [55, 56]. At the cellular level, quantifying how a tumour cell responds to the presence of nearby cells or the adjacent structures is critical to help determine disease initiation, maintenance and progression [57]. While mathematical techniques to estimate interaction events between moving organisms [58] and between an organism and its physical surroundings [59, 60] are starting to become available, they are often based on basic forms of interaction, e.g. spatial exclusion [61], attraction [62] or exchange of a binary form of information, e.g. infection status [63]. While more complex types of interactions, such as alignment processes, can be modelled explicitly [64], there is a need to develop a general mathematical theory where the motion parameters are coupled with the internal variables of the individuals (see, e.g. ref. [65] for an example of a model of collective sociogenesis). Such general development would be extremely valuable to animal ecologists and cell biologists and it will undoubtedly require a concerted effort from both communities. Recent theoretical developments of data-driven approaches to disentangle information about deterministic forces from stochastic effects [66–68] will play an important role in this respect and more generally in tackling the inverse problem of inferring from movement data the equations that govern the interaction dynamics.

Another fundamental open problem, rather ubiquitous in the context of phenomenological models, is the robustness of the behaviour of population-level descriptions to different hypotheses and assumptions employed for individual-level interactions, often refereed to as the micro-to-macro connection. In ecology, to tackle this issue one approach is to find the critical spatial, temporal and organisational scales of the system [69] and build a model that describes the basic interactions between a small number of individuals so that insights gained from the study of such simplified systems can be translated to complex population-level phenomena. Some of these methodologies have already influenced interdisciplinary approaches to study, for example, allometric scaling [70, 71], animal foraging patterns [72] and collective animal movement [37, 73, 74]. Connecting different levels of description has also taken centre stage in cell biology [75, 76]. A prototypical example is the historical development of the modelling approach to gliomas, a type of primary brain tumour arising from the glial cells of the nervous system. The early proliferation-infiltration glioma models [77] and 'go versus grow' hypothesis [78], proposing the switching between proliferative and migratory phenotypes, were superseded by anisotropic diffusion models [79] to account for the different movement spread occurring in the grey matter compared to the one occurring in the bundles of nerve fibres that make up the white matter tracts in the brain. But following the observations that glioma cells employ microtubes as a means for invasion and proliferation in the brain [80], more recently focus has shifted to mathematical representations of invading tumours that incorporate contact guidance and chemotaxis [81, 82].

Accumulating evidence from the high resolution of tracking data is pushing movement modellers to abandon the Markov assumption, that is, the condition for which the dynamics of a stochastic system depends only on its current state and not on its history. Although the Markov property has been used as a workhorse in theoretical investigations across disciplines, many biological examples do not fulfil that requirement. While animals are known to exploit their cognitive memory for foraging and navigation purposes [83], recently also cells have been shown to utilise a molecular mechanism in receptor signalling akin to a working memory in order to migrate (chemotaxis) within irregular and locally varying gradient cues [84]. Despite the ubiquity of non-Markovian dynamics across the life sciences and the existence of a wide variety of computational approaches to represent history-dependent movement processes, we still lack general null models that may help identify signatures of memory dependence from movement data. While recently some first-principled non-Markov movement models have appeared [85, 86], understanding mathematically how simple modifications, e.g. the introduction of an absorbing, permeable or reflecting boundary, affect the dynamics of a history-dependent movement process remains a challenge [87]. Given the high degree of spatial heterogeneities that animals perceive in the landscape or that cells detect in the surrounding tissue, it is imperative to quantify rigorously the interplay between spatial disorder and non-Markovian movement statistics.

Movement ecology [88–90] has been influential in bringing mathematical and physical approaches to improve methodologies to cluster movement data into distinct movement modes, importing from statistical physics techniques that allow for the analysis of individual trajectories and extraction of anomalous diffusion exponents [91–93], and ageing behaviour (loss of ergodicity) [94, 95]. At the conceptual level, movement ecology has given rise to a general framework to identify the components that shape animal movement, between the external ones and the internal ones, namely, the motivating factors, the motion capacity and the navigation capacity. As such a framework has demonstrably helped bridge knowledge gaps across ecological communities, an analogous framework that spans animal ecology and cell biology would also be valuable. One may look for various parallels, for example, the level of satiation of an animal may be related to the level of saturation in cell receptors, certain environmental triggers for animals may be compared to those present in the extracellular matrix, and an animal behavioural plasticity may be similar to a cell phenotypic plasticity. Initial efforts along this line of thinking are underway and appear promising [96].

While we have discussed here only a handful of common open problems, the abstraction that underpins mathematics allows us to compare many other quantitative approaches across disciplines. In exploiting the vast knowledge accumulated across different areas, it is imperative to establish a platform where scientists can learn about commonalities and where mathematical and modelling ideas can be easily translated from one setting to another in distinct scientific fields. This book aims to help build such a platform and to initiate a closer dialogue between animal ecology and cell biology by presenting studies at different organisational levels, across spatio-temporal scales and with distinct organisms.

1.4 Topics Covered in This Book

As the chapters straddle multiple areas, it has not been possible to group them around distinct themes—they have been ordered alphabetically based on the last name of the first author. Some of the topics introduce methods of analysis of data, while others present abstract/theoretical work, with the latter in some instances developed to interpret empirical observations. The chapters that include data analysis present specific techniques to extract movement characteristics either from laboratory observations, e.g. ant, bumblebee, fish and white blood cells, or from field recordings, namely, African buffalo, grey seal, jaguar, loggerhead sea turtle, raven and sheep, but also general procedures to quantify spatial patterns, such as self-organisation, across disciplines. Some of the theoretically focussed chapters analyse individual stochastic movement processes, e.g. epidemic propagation, resetting dynamics and resource-limited exploration, but also population-level movement models, e.g. dynamics of pattern formation with competition and exclusion, prospection and dispersal in meta-populations. Other chapters are more formal and tackle general methodological questions, e.g. deterministic versus stochastic descriptions in reaction-diffusion processes, information theoretic path segmentation techniques and the number of distinct and common visited locations by a random walk. A brief summary of each chapter within their respective literature context is provided below.

A major challenge in the simulation of stochastic spatially extended systems is that the number of individuals, be they molecules, cells or animals, can vary from large to small across the spatio-temporal domain of interest (see, e.g. [97]). In the regions of large numbers, modelling each individual is computationally expensive, and, typically, a partial differential equation (PDE) formulation is used, as random effects are negligible. However, for small numbers, deterministic PDEs are no longer viable and a stochastic description becomes necessary. This leads to what are called hybrid approaches for the regimes of intermediate numbers, and these are the focus of Chap. 2 by Alarcón et al. This chapter starts with a review of different hybrid formulations before moving on to the authors' recent work in addressing and overcoming a number of limitations of previous schemes. One of the recent advances in this context is when more than one species is being modelled, as the dynamics of such multi-species systems is much richer than that of a single species.

The comparative analysis of movement data of closely related species in the wild provides a valuable resource to study the consequences and future threat of global change. This is the philosophy underpinning the work in Chap. 3 by Ashkenazi et al. The authors compare the movement dynamics of two species of ravens living across the Dead Sea valley and the Judean Desert plateau in Israel, of which one, the fan-tailed raven, has been declining in numbers compared to the other one, the brown-necked raven. The study showcases the importance of employing multiple metrics [98]—in this case maximum displacement, start to end distance, linearity index, mean speed and home range size—over different temporal scales to identify disparity in foraging behaviour as animals may display divergent spatio-temporal responses to resource variability. As location, abundance and nutritional content of food sources may vary, among other factors, due to human-induced environmental changes, competition and landscape composition, similar sympatric species may exhibit different searching strategies, as is the case for the two raven species explored here.

Searching for targets, be they food items, mate or invaders, is a fundamental task that most organisms need to execute to reproduce and survive [99], and has been a central focus in the analysis of movement of biological organisms. The literature on search strategies of biological organisms has a long history (see, e.g. [100] in the ecological context and [101] for cell biology) and not without controversy in regard to animal foraging strategies [102–105]. Among random search strategies stochastic resetting has recently generated a large body of work [106]. Introduced as a movement model more than 20 years ago for continuous variables (Brownian walks) [107] and lately formalised for discrete variables (lattice random walks) [108], it entails a searcher returning at random times to its initial position so as to minimise the time spent searching unsuccessfully in the same region of space. For this reason it has been proposed as a potential mechanism for reducing the time to find targets in an unbounded domain. In the cellular transport context the searcher may be regarded as a motor complex carrying vesicles to synaptic targets in the axon of a neuron or the tip of a filament that delivers a morphogen to a cell during development, as explained by Bressloff in Chap. 4. This chapter is dedicated to the continuous variable formalisms that describe stochastic resetting for a diffusive walker, both at the probabilistic and stochastic level. For a one-dimensional system it explores the first-passage time problem when resetting is instantaneous, and the effects of finite return times and refractory periods when resetting is non-instantaneous.

A great number of movement models have traditionally assumed, for simplicity, Markovian dynamics [109, 110]. Among them, hidden Markov models (see, e.g. [111]), represent a versatile framework with which to identify behavioural switching between movement modes or states from animal movement paths, e.g. resting, running, soaring, etc. Chapter 5, by Campioni et al., extends the application of these models to when the statistics of sojourn times in each behavioural state are gamma distributed, the so-called semi-Markov case, rather than exponentially distributed. By using a continuous time Ornstein-Uhlenbeck process for the velocity vector and allowing for irregular sampling of the movement, a Monte Carlo expectationmaximisation algorithm allows for the extraction of information about directional persistence, mean speed and its variability, and sojourn statistics. The usefulness of the proposed framework is tested with synthetic data as well as data on grey seal and Merino sheep as case studies.

Since its inception from the early theoretical work in the 1980s [112, 113], the study of collective movement has fostered a culture of interdisciplinarity spanning a large number of disciplines, from biology, neuroscience and physics to engineering, computer science and mathematics (see, e.g. [114–119]). The imaging and tracking revolution, in conjunction with the theoretical development of movement models, share part of the recent successes in advancing the understanding of how animals move cohesively in groups. Chapter 6, by Escobedo et al., gives a detailed account of one of the latest advances in methodology to reconstruct social interactions from highly resolved animal trajectories and is applied to laboratory experiments with schooling fish, namely, *Hemigrammus rhodostomus*. Without making assumptions about the form or the intensity of the interactions, the procedure accounts for each individual animal interacting with its environment, e.g. physical obstacles or other conspecifics, through variables such as the instantaneous distance and orientation with respect to the physical boundaries of the experimental set-up and with respect to other individuals. By measuring fluctuations in speed and heading angles, the extracted pairwise attraction and alignment interactions are made up of the product of three components, namely, a probability governed by the relative distance, a probability dependent on the relative angle and a probability as a function of the viewing angle. Two of the methodological advantages, compared to other approaches, are the minimal computational power required and the ability to generate analytical expressions for the interaction probabilities.

The manner in which animals occupy space, the so-called animal space use, is a complex and highly integrated characteristic of the underlying movement processes [120]. It depends on multiple factors, including intra- and inter-specific interactions, environmental features, spatial memory effects and energy considerations. The spatial distributions that emerge may vary from migratory [121, 122] and nomadic patterns [123] to the formation of home ranges [124] and territories [61] or features displaying site fidelity [125]. How to quantify and extract information on these and other types of spatial patterns from movement observations is one of the important challenges in movement ecology. Chapter 7, by Fleming et al., explores the mathematical properties and biological meaning of various spatial distributions, namely, occurrence, individual and population range, corridor, encounter and revisitation. With the help of African buffalo GPS collar data, as well as a GPS jaguar dataset, the differences between interpolative predictions, e.g. occurrence distribution, and extrapolative predictions, e.g. range distribution, are made clear. As a result of the high resolution of movement data available, these topics are destined to attract further attention from the statistical physics community, which has a long tradition of devising theoretical approaches to access multi-target first-passage statistics, e.g. that of an individual revisiting certain locations or of a pair of individuals being in close proximity framed, respectively, as first-return or first-encounter events [126].

With movement tracks now reaching temporal resolution of seconds, there is growing interest in developing a general framework that allows track segmentation to be placed on a firm theoretical ground. Part of the motivation comes from the increase in the computational burden for the traditional approaches such as hidden Markov models and behavioural change point analysis (see, e.g. [127, 128]) and their limitations in identifying rare events such as parturition, migration initiation, etc., when the behavioural shift is not known a priori to have occurred [129]. Chapter 8, by Getz, makes advances in this direction by relying on concepts from Shannon's information theory [130]. Building on a recent multi-modal step-selection kernel framework [131], it proposes to cluster relocation data into segments characterised by different symbols and these, in turn, into words to build a behavioural classifier that automatically assigns a classification error rate. While the proposed approach requires a fixed length to avoid ambiguity in the number of elements to build any track segment, it is relatively flexible. It does not limit the type of AI clustering methods that can be applied to extract statistical movement elements and can accommodate for data obtained from inertial sensors such as accelerometers and gyroscopes, to help compensate for the intrinsic positional errors.

Chapter 9, by Kenkre, showcases the theoretical application of various statistical mechanics methods to ecological phenomena. The first method involves the determination of the probability of transmission of an infectious pathogen as a function of time from an infected animal to a susceptible one when living in separate but neighbouring burrows or dens. By employing techniques developed in solid state physics, namely, the problem of excitons mutually annihilating when close to one another [132], this work uncovers an interesting non-monotonicity in the temporal dependence of the overall infection probability. By modelling animals as Brownian walkers tethered to a focal point—the burrow or den—the overall infection rate exhibits a non-monotonic dependence as a function of the tendency of the animals to return to their respective home range centre. The second application is related to the dynamics of an entire animal population subject to the constraints imposed by the resources in the environment, the so-called carrying capacity. The growth of the population is described by a set of coupled Fisher-Kolmogorov-Petrovsky-Piskunov PDE equations [133, 134] with a spatially dependent carrying capacity. When the environment separates regions of high carrying capacity from regions where population survival is not possible, there exists a critical length below which the population disappears. While the existence of such a transition for a single region was known in the past [135, 136], it is the case of multiple neighbouring regions of high carrying capacity and their critical size dependence that is discussed in detail in this chapter. A further extension of the problem of a critical size domain is the case when an animal population may spread an infectious disease, which is used here to analyse the formation of the so-called refugia of infection in the environment. The final application concerns the so-called effective medium theory, which enables the study of movement in spatially disordered space providing analytical prescriptions that link features of the spatial heterogeneities to time non-locality in the equations of motion.

Chapter 10, by Klages et al., is a historical journey covering the main mathematical formalisms that model the movement of individual organisms. The journey is across the theoretical literature in active matter, anomalous diffusion and movement ecology, as the theory of active particles has often been applied to study the movement of organisms at the microscale [137], while the theory of diffusing or anomalously diffusing particles has formed the basis of many models of animals moving at the macroscale [7, 138, 139]. Two important modelling frameworks, namely, the correlated random walk [140, 141] and active Brownian particle models [142], are shown to be generally different as the former entails a description in a co-moving reference frame, whereas the latter is in a laboratory or Cartesian reference frame. While the special case of an overdamped Brownian particle with the velocity driven by Gaussian changes in the orientation angle is equivalent to a correlated random walk model, the two formulations lead, in general, to different dynamics. By taking an egocentric perspective [143], generalised overdamped coupled Langevin equations for the turning angle and the modulus of the velocity are proposed. The added value of the modelling framework is that the specific choice of the noise terms and non-linearities of the Langevin equations are reconstructed directly from movement data. Application of the model to data is illustrated for observations of bumblebees foraging in a laboratory arena, while other active particle models are applied to the movement data of neutrophil cells and the off-shore foraging of loggerhead sea turtles.

The study of spatial patterning as an emergent property of a system dates back to the classical work of Turing [144], which showed that diffusion could drive patterning in a two species system that had certain interaction dynamics, the most common being the combination of short-range activation and long-range inhibition [145]. While this mechanism is quite general, other patterning mechanisms are known to exist in cells [146] and animals [147], and identifying which underlying mechanism is responsible for the emerging population-level structure can be arduous. In Chap. 11 López et al. study theoretically the patterns for two such mechanisms, involving competitive-only or repelling interactions. The theoretical framework is the Dean-Kawasaki prescription (see, e.g. [148]), which describes density fluctuations in a system of a large number of indistinguishable particles undergoing diffusion. The mathematical object of interest, when the noise intensity in the system is small, is the so-called influence function, that is, the kernel of the PDE that approximately describes the entire population, whose shape controls the spatially non-local non-linear terms. With certain types of interactions, knowledge of the shape of this function, more precisely its Fourier transform, is sufficient to determine whether spatial patterns will emerge and whether they are of Turing type or not (see, e.g. [149]). In the context of a birth-death system this chapter also analyses the link between the influence function and the movement statistics, e.g. when individuals move following a Lévy process rather than diffusing. This link is explored by modifying phenomenologically the transport operator from a diffusive to a fractional one [150].

Fundamental concepts, such as the union and the intersection of a given number of sets, take centre stage in Chap. 12, authored by Majumdar and Schehr. For moving organisms the union may represent an entire habitat covered by multiple animals of the same species [151], while the intersection may refer to a resource-rich area for animals in the environment such as a water body [152] or a region of inflammation in the body to which neutrophils, that is, phagocytic white blood cells, are drawn [153]. Formally, these two statistical quantities can be represented, respectively, by the number of distinct [154] and commonly visited sites [155], by independent random walkers. This chapter explores the dependence of the dynamics of the probability distribution of the two quantities and their averages as a function of the number of individuals. By employing a link to extreme value statistics [156], the temporal scaling of the entire distribution in one dimension is obtained, while for arbitrary dimensions the temporal scaling of the averages is calculated. By relating the sought-after quantities to the probability that a site on a lattice is visited by a walker within a certain time, all findings are derived analytically. The key insight allowing for this analysis is to realise that for estimating scaling relations it suffices to replace the lattice random walker dynamics by the dynamics of a Brownian motion in continuous space and continuous time. The regimes of growth of the average number of commonly visited sites display an interesting transition in the exponent as a function of the spatial dimensions and the number of walkers.

Individual behavioural heterogeneity, also referred to as animal personality, is a burgeoning area of research in animal ecology and has been documented across many taxa [157–159]. With regard to movement, different traits in the exploratory behaviour of individuals may have evolutionary advantages since they support the ability of a population to adapt to changes or shifts of resources in the environment [160]. This is the premise that underscores the joint empirical/theoretical study on the foraging efficiency of the ant species *Aphaenogaster senilis* in Chap. 13, by Marris et al. In this species of ants within a colony, there exist two types of foragers with distinct movement statistics, the scouts, who tend to explore further from the nest, and the recruits, who tend not to stray too far away from the nest. To explain observations of *A. senilis* search behaviour in a laboratory experiment with multiple food patches on a finite Y-maze arena, a model of diffusive dynamics on honeycomb lattices [161] is extended to account for correlation in the movement steps [162]. The variable of interest is the *first* first-passage time to either of the food items within the patches and is studied by constructing a general analytic theory of the first first-passage probability for multiple random walkers with distinct movement statistics ranging from diffusive to correlated. The model allows for a rigorous quantification of how scouts outperform recruits in both exploring space and finding food items.

Understanding animal decision-making processes is a vast and rich area of investigation at the interface of behavioural ecology, computer science, ethology and neuroscience [163–165]. In recent developments there is a growing interest in employing quantitative approaches from the cognitive sciences to help provide a mechanistic explanation of how animals implement decisions to achieve specific goals, e.g. homeostasis, survival or reproduction [166]. The advances in tracking technology are playing an important part in this development. The ability to track groups of animals for long periods of time makes it possible to test hypotheses that were considered empirically out of reach just a decade ago. One example is prospection, i.e. an animal's ability to envisage future scenarios and organise current actions accordingly [167]. As empirical evidence is accumulating [168–170], general theoretical frameworks on prospection are starting to be proposed [171]. Chapter 14, by Molas and Campos, is part of this theoretical push and proposes an extension to the classical Voter model (see, e.g. [172]) in which information gathered from other individuals does not result in instantaneous decision-making but, instead, is accumulated before being acted upon. The new model explores the role that individual personal preferences and this accumulated "crowd" information play in making decisions. The main interest of the model is to determine the time to reach consensus, i.e. the time for all individuals within the system to reach the same decision among multiple options, and the so-called extinction time, which is the time required for one of the options to disappear.

In Chap. 15, Régnier et al. are concerned with the so-called starving random walk problem, a simple model representation of a diffusing organism performing a resource-limited exploration [173], a challenge that any living entity faces in order to uptake energy to move. The quantity of interest that helps to quantify the organism's success is the time elapsed between the finding of one food item and the next. It is represented through the so-called k-th inter-visit time, i.e. the time it takes for a random walker to find a site which has never been visited before, given that k sites have already been visited [174, 175]. The statistical distribution of the inter-visit times is analysed and shown to differ in its extreme values from the classical type, e.g. the Gumbel distribution [176]. Two important variables are studied: the lifetime of the walker and the total amount of food collected at starvation. Analytic scaling expressions for these variables are derived for arbitrary spatial dimensions in terms of a single parameter characterising the recurrence or transience of the walk [177]. As a null model of movement in an environment with depleting resources, the findings in this chapter offer various insights to guide explorations of resource-limited motion in more realistic scenarios.

One of the most striking features of the natural world is that individuals, be they cells, birds, fish, etc., self-organise to form spatial patterns [178, 179], and a significant part of the field of mathematical biology has been, and continues to be, devoted to developing a mechanistic understanding of this phenomenon. As a result, there are now a very large number of models that can produce an astonishing range of spatial patterns. To take these models to the next level requires validation against experimental data, and a major frustration in the field over the past decades has been the lack of suitable spatio-temporal data that is fit for this purpose. However, this situation has changed thanks to technologies that are now making it possible to harvest data at many scales across disciplines. In light of these developments one of the major challenges is how to extract suitable metrics, and this is the key question reviewed in Chap. 16 by Volkening. This chapter surveys a number of the methods that are being used to transform qualitative spatial data into quantitative information that can then be used to parametrise models, validate and test predictions or make comparative analyses. These methods include the identification of order parameters, the generation of pair correlation functions as well as techniques from the field of topological data analysis that are well suited to investigate both cells moving through a developing embryo and animals moving collectively.

We conclude by reminding the reader that, despite the impressive progress over the last decades chronicled in part in the abovementioned chapters, many open questions and unsolved problems remain. We are optimistic that this book will stimulate further developments to tackle these challenges, building new bridges and collaborations across animal ecology and cell biology. We hope that the state-of-the-art techniques and methods explored, the large variety of topics presented, the cited literature and the clarity of exposition of all contributions will make this book a go-to reference to learn about the mathematics of movement and its practical value in tackling challenges in the life sciences.

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