Modelling paradigms in movement ecology

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Abstract

Organisms can move in a wide variety of ways and for many different reasons. The processes leading to and affected by movement have become the subject of the field of movement ecology. The introduction of the 'movement ecology framework' by Nathan et al. and the recent technological advancements of the methods for the collection of movement data have lead to an increase in the use of models to study movement. The type of model employed is dependent on the research questions and the system being studied. This review focuses on two modelling paradigms in movement ecology and their applications in research. The first I call parameterisation, because stochastic models are used here in order to determine the importance of potential factors in influencing the movement path of an individual. By comparing summary statistics of various simulations of these models with summary statistics of observed movement paths, the models can be parameterised to most closely resemble the processes at play in nature. The second paradigm focuses on the observation of evolutionary patterns in individual based models. In these models, traits affecting movement decisions are evolvable and can lead to interesting spatial and temporal dynamics, which can give insights into the evolutionary causes and consequences of movement. With the use of case studies, potential applications of the two paradigms are demonstrated and ways in which these methods have advanced our knowledge of movement are explained.

Introduction

There is a lot of variation in the movement of organisms in nature. Not just in the way an organism moves (e.g. walking, flying), but also in the processes behind movement (i.e. the reasons for moving to a certain location). Movement can be achieved actively or passively and it may occur locally or over greater distances. As a result of this large amount of diversity in the scale and means of movement, the effects of this process are widespread. The fates of individuals, populations and even ecosystems can be affected by the patterns that result from the way movement takes place. Community compositions change due to migration events of organisms for instance (Schlägel et al., 2020). On the other hand, the state of the environment can also play a major role in the

manner individuals move around. For example, several migratory bird species have changed the timing of migration from their overwintering areas to their breeding grounds in response to climatic changes (Zaifman et al., 2017). Due to the impacts movement processes can have on several temporal and spatial scales, they have become a popular subject of research over recent years.

Because it is difficult to study such a wide variety of behaviours, Nathan et al. (2008) proposed the movement ecology paradigm - a general framework for studying all aspects of movement (figure 1). They suggest that a focal individual is characterised by three components: an internal state, a motion capacity and a navigation capacity. The internal state represents the individual's physiological and cognitive state, which drive the individual to move for a certain reason. Such reasons could be the need to look for food or to move away from predators. The motion capacity describes the organism's ability to move in different ways. These differ between species, but also between different manners within an organism (e.g. pinnipeds are better at swimming than at moving on land). An individual's navigation capacity explains how well an organism can use information to determine where and when to move. These three components interact with one another, as well as with a fourth component: the external factors. Such factors can be any aspect of the environment that has an effect on the movement process. All of these components, and their interactions, result in a movement path, which in turn can affect some of these components. This movement path can be observed, and understanding the underlying processes leading to this path as well as the effects of this path on the organism and the environment are the main goals of movement ecology.

In recent years, technological advancements have improved the ability of movement ecologists to gather and record more data (Katzner & Arlettaz, 2020; Kays et al., 2015). This has lead to a surge in the use of models in order to analyse these large data sets more effectively (Joo et al., 2022). Since it is difficult to accurately measure an individual's motion and navigation capacities, models can also provide a way to study the role these components play in the individual's decisions that lead to a certain movement path (Joo et al., 2022). Currently, models are in widespread use in this field and several paradigms have been developed to answer questions related to the movement of individuals. In this literature study, I will review two modelling paradigms in the field of movement ecology. The frameworks of these techniques will be explained and the applications will be discussed on the basis of a number of case studies. Finally, I will give an overview of the advantages of and the potential issues for the different paradigms.

Parameterisation

A first way in which models can be used in movement ecology is as a tool to unveil potential factors affecting the movement paths of individuals. This is usually done by trying to relate a stochastic model to an observed movement path. The stochastic model includes several factors which could play a role in
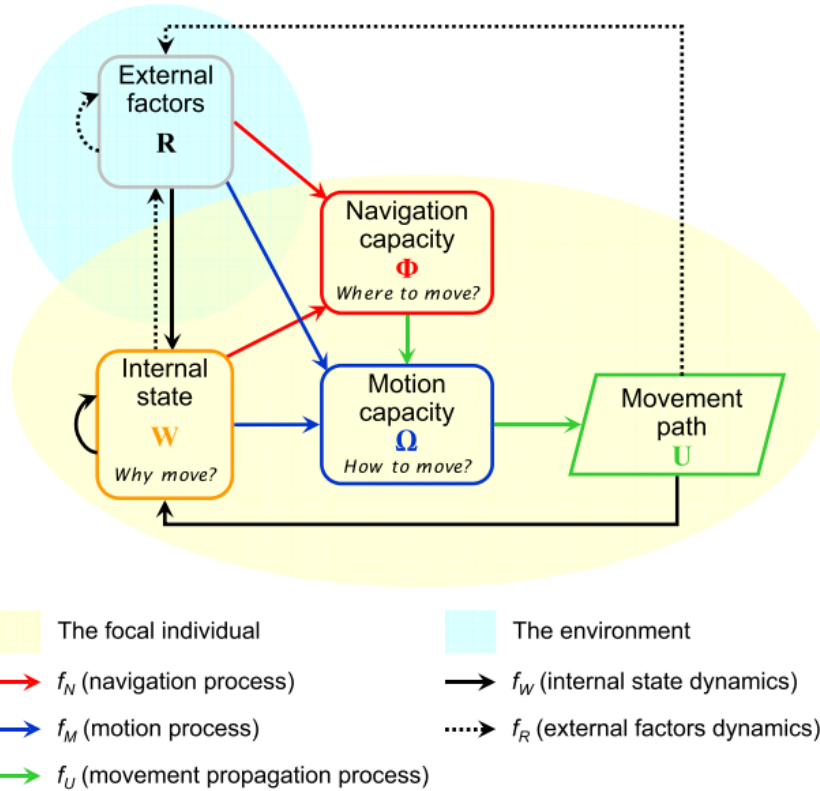
Figure 1: The movement ecology paradigm as proposed by Nathan et al. (2008). It shows how three components (yellow background) relating to a focal individual (internal state, motion capacity and navigation capacity) and a fourth external factor (light blue background) affect the movement path of this individual. Arrows indicate the direction of the relationships between these different components. The resulting movement path can also affect the internal and external factors.

the individual's decisions regarding its movement and the importance of these factors is determined by some statistical analysis. This is done by calculating summary statistics based upon which a comparison can be made between the movement path generated by the stochastic model and the observed movement path. Such a comparison results in an approximation of the likelihood of obtaining the observed data with the parameter values used in the model, i.e. the importance of certain factors for the shape of the movement path. Based on the likelihoods of different parameter values, an interpretation of the data can be made.

There are several different methods for determining the likelihood of parameter values. One can use a simple calculation of how close the summary statistics are to the observed value or use a rejection filter approach, to name a few (methods reviewed in Hartig et al., 2011). However, in order to learn how this likelihood varies over larger parameter space, the posterior distribution of the parameters is needed. This is usually achieved through Bayesian inference methods. One such method that has become widely used, is Approximate Bayesian Computation, which in essence bypasses the need to calculate the likelihoods and immediately produces the posterior density. These parameterisation techniques have been utilised by many movement ecology studies.
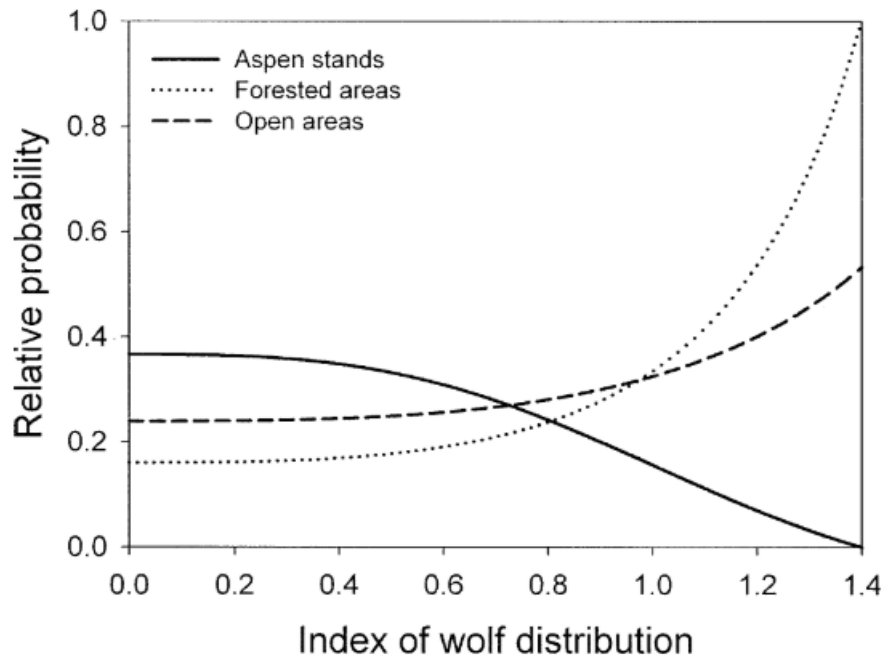

Figure 2: The relative probability of elk selecting steps that end in either aspen stands, conifer forests or open areas depending on the probability of the presence of wolves. Taken from Fortin et al., 2005.

A study on the movement of elk (*Cervus canadensis*) used parameterisation to uncover a potential explanation for a trophic cascade in Yellowstone National Park (Fortin et al., 2005). The authors had collected movement path data of 13 female elk, the locations of which were identified every five hours. They paired each step (the distance between two consecutive locations) with 200 random steps with the same starting point but with different distances and directions. The observed and simulated steps were combined with landscape variables, such as the probability of a wolf being present, the distance to the nearest road and the type of habitat cover, and were used by a step selection function model to estimate the importance of these landscape variables for the decision making process behind the movement paths. They found that the movement of elk was influenced by many different factors, but the most interesting result was the effect wolves had on the type of habitat elk ended their steps. Steps were most likely to end in aspen stands, followed by open areas, and then conifer forests when the elk were in an area that wasn't used much by wolves, whereas in areas with a higher probability of encountering a wolf, steps were most likely to end in conifer forests, followed by open areas and finally aspen stands (Figure 2).

A more modern approach to understand the processes underlying movement was taken by Zhang et al. (2017). They used a case study on black petrels (*Procellaria parkinsoni*) to highlight the application of Approximate Bayesian Computation (ABC) in deriving information from individual based models. They obtained movement paths from 11 petrels using GPS telemetry, with positions being estimated every 5 minutes. A Hidden Markov model (HMM) was used to determine that the individuals exhibited three distinct behavioural states during their foraging trips. The authors selected nineteen different summary statistics, based on either spatial or temporal variables, which provided enough information for parameterisation and comparison of individual based models. In these models, individuals could be in either a foraging or a searching state (the third behavioural state identified by the HMM was excluded because it was related to commutes, which were not relevant for the authors' research questions), and their movement was influenced in different ways according to which state they were in. For ABC, they used a rejection filter to determine the 100 model simulations which approximated the observed movement patterns the best out of the total of $1 * 10^6$ simulations. The difference between the prior and posterior distributions of the parameters (i.e. a measure which shows whether the accepted models used a specific subset of the explored parameter space) was used to figure out which parameters had the biggest influence on the petrels' foraging trajectories. They found that the distributions of six out of ten of the parameters had become significantly narrower during the ABC process (see figure 3). Energy consumption rate was the one which had been constrained the most out of all parameters. The authors also used ABC to determine how well a simpler model, which did not include the effects of wind speed and site fidelity, performed in comparison to the full model. Out of the 200 accepted simulations (same acceptance rate as during the parameterisation, but double the total simulations since twice as many models were used), 62 came from the simpler model, whereas 138 were from the full model, and so they concluded
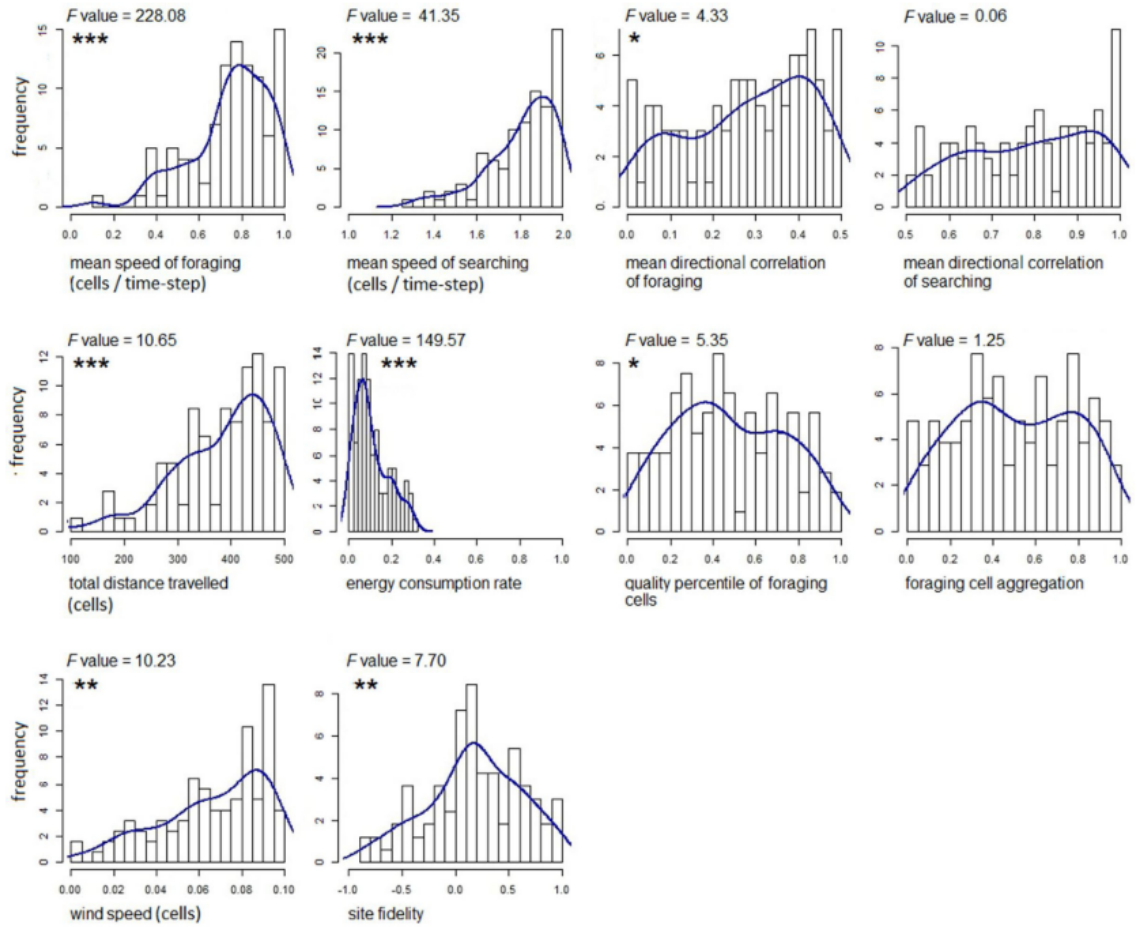
Figure 3: Posterior distributions of parameters used in an individual based model on foraging movement in black petrels. The F-values indicate how much these distributions differ from the prior distributions. Taken from Zhang et al., 2017.

that the performance of the simpler model was reasonable even though it was rejected.

Comparing different versions of the same model is a rather useful application of ABC, since this can help bypass a major obstacle for ecological modelling - the need to create an accurate model of the natural system. A nice demonstration of this is a study on site fidelity and long distance dispersal in Fowler's toads (*Anaxyrus fowleri*) on the north shore of Lake Erie (Marchand et al., 2017). The authors attached radiotransmitters to a number of toads, located their daytime refuges once a day and identified which individual used which refuge. They used a certain multiscaled random walk model which allows an individual to return to a location it has been at before. Three different versions of this model were created, which differed in the way the probability to return to a given location was calculated. The random return model had the same constant probability for each refuge, with multiple visits to a refuge increasing the probability of returning to this one. Individuals in the nearest return model always returned to the nearest refuge. In the distance-based return model, the probability of returning to a refuge decreases exponentially with the distance to this refuge. Approximate Bayesian Computation was used to determine which model resulted in the summary statistics that were closest to those of the observed data. This selection process produced 15% support for the random return model, 0% for the nearest return model and 85% support for the distance-based return model. However, during cross-validation of the models, the authors found that data from the random return model was often thought to have come from the distance-based return model (34.5% of the time) and vice versa (22.6% of the time), and so they also computed the number of distinct refuge sites, which was not used directly during model fitting. This statistic showed the best fit for the random return model. Marchand et al. mentioned that this model, which they developed with the help of ABC, could be used to estimate the connectivity of between certain toad populations for example.

As shown by the case studies discussed before, models can be a powerful tool to learn which ecological factors affect the movement of individuals. However, models are only as useful as they are capable of accurately simulating natural systems, which means that one does need to gather data about the system first in order to be able to make confident claims about the results of the model. This can be somewhat bypassed by comparing different models with the use of Approximate Bayesian Computation, but these models do need to be based on realistic assumptions to be useful. Moreover, the data used to parameterise the models also needs to be of good quality. As many techniques there are to gather movement data, they all come with their own potential types of error (Patterson et al., 2008). There may be a sampling bias, inaccuracy in estimating the location of individuals or incomplete data, to name a few. In recent years, technological advancements have lead to vast improvements of the ability of these methods to gather more accurate data (Katzner & Arlettaz, 2020; Kays et al., 2015), but error correction is still an important step during the analysis. Another potential issue is the inability to derive behavioural patterns from the data due to a temporal mismatch between observations and movement decisions.

In other words, the resolution of the data is not sufficiently high to capture certain behaviours, which can lead to biases in the interpretation of the data (Patterson et al., 2008). State-space models are able to take such observational errors into account, as they couple the stochastic model of movement with a model of the observation method (Patterson et al., 2008). Such models can allow scientists to create more realistic approximations of observed movement paths (Avgar et al., 2013).
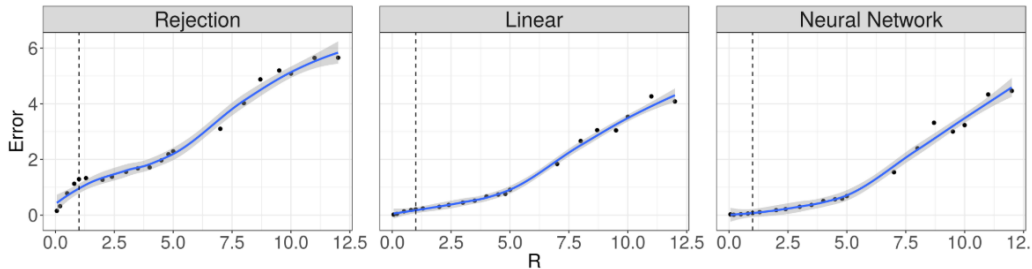

Figure 4: The predicted errors for the estimated time between changes in direction at different temporal mismatches between the movement process and the observations. A higher R indicates that observations were made more frequently relative to the frequency at which movement decisions were made. Different graphs indicate different methods of Approximate Bayesian Computations. Taken from Ruiz-Suarez et al., 2020.

Ruiz-Suarez et al. (2020) used a state-space model to study the effect of a temporal mismatch between the process and the observations on the prediction errors of ABC algorithms. They used a correlated random walk as their movement model, where individuals walk in a certain direction for a time of λ (drawn from an expontential distribution) before making a turn (angle drawn from a von Mises distribution with a mean of 0 and a concentration of κ). Observations of individuals' locations were made at regular time intervals. Based on these locations, four summary statistics were calculated. To obtain posterior parameter distributions, three different ABC algorithms were employed: a simple rejection-based algorithm, and two algorithms which correct the imperfect match between the observed and accepted summary statistics by use of either linear regression or a neural network. Then, the authors evaluated how accurate these algorithms were in estimating the posterior probabilities for λ as a function of the ratio R between the temporal scale of observation and the temporal scale of at which movement decisions are made. They found that the predicted error increases with the ratio R, which indicates that more frequent observations can lead to inaccurate parameter estimations. Because of this, Ruiz-Suarez et al. recommended that the observations are less than five times the average of the times between direction changes (Ruiz-Suarez et al., 2020).

After a state-space model has been estimated, it can be used to infer the true path the individual has taken based on the observed data, to generate addi-

tional observations at times when the individual was not able to be located or to predict future movement (Patterson et al., 2008). The former two applications show this method's true power, whereas the latter is applicable to more general stochastic modelling methods. Parameterisation, as well as model comparison, is able to provide information about the processes underlying movement. This information can then be used to make predictions about which movement decisions an individual may make in a novel environment and knowledge of this can be used for conservation purposes for example (Patterson et al., 2008).

Pattern Observation

Models have not just been used to reveal which potential processes lie at the basis of an observed movement path, but also to study the evolutionary implications of movement (Gupte et al., 2022; Netz et al., 2022). In such models, individuals tend to have a number of heritable traits which determine their preference for certain characteristics of the environment (e.g. the amount of food or the presence of conspecifics). Because individuals produce offspring according to their fitness, preferences which lead to a higher foraging success or better survival will be passed on more frequently. This process leads to the evolution of movement strategies and observing the patterns that arise as a result of this is the core of studies using this method.

The patterns resulting from the evolution of movement strategies can be, for example, an evolutionary response to a selective pressure in the environment or the way certain strategies can outcompete other strategies, potentially leading to cycles in the most common movement strategy. The observation of these patterns can be achieved through recording the heritable traits over time, measuring emergent properties of the system (e.g. distribution of individuals, distance moved) or other means depending on the implementation of the stochastic model. The usage of this method in eco-evolutionary studies has been successful in bringing the evolutionary causes and consequences of movement to light (Gupte et al., 2022; Jager et al., 2011; Netz et al., 2022).

A study on pattern formation in mussel populations used an individual based model to understand how and why mussels (*Mytilus edulis*) are distributed in regularly spaced clumps (Jager et al., 2011). By observing the movement paths of 12 solitary mussels, the authors were able to determine that the distribution of step lengths matched that of a Lévy walk (a power-law distribution) with an exponent of approximately 2. They used this information to develop an individual based model where mussel movement is determined by the density of mussels within 3.3cm (short-range density) and within 22.5cm (long-range density). A higher short-range density and a lower long-range density incentivise the individuals to stay where they are, whereas the individuals move according to a Lévy walk when the short-range density is low and/or the long-range density is high. This minimises competition for resources as well as predation risk and wave stress. The time until the short-range density was on average 1.5 times as large as the long-range density was measured for different exponents of the

Lévy walk employed by the individuals. This showed that the time until pattern formation was shortest for an exponent of approximately 2, meaning that this movement strategy is optimal for pattern formation. De Jager et al. also calculated the fitness for every strategy by multiplying survival (proportional to short-range density) with fecundity (inversely proportional to long-range density and energy investment in movement). With this, they created a pairwise invasibility plot, which showed that the Lévy walk with an exponent of 2 was an evolutionary attractor and therefore an evolutionarily stable strategy.

A system which has been of particular interest of evolutionary ecologists is that of predators and prey. Netz et al. (2022) developed a model to gain insights into the evolution of movement strategies for predators and prey and how these strategies shape various patterns in, for example, the resource landscape and population dynamics. In this spatially explicit model, both predators and herbivores were able to move between cells within the environmental grid based on their evaluation of the suitability of nearby cells. This evaluation was dependent on the weighted sums of the grass, herbivore, and predator densities, where the weighing factors were evolvable traits for each individual. Herbivores could gain fitness by consuming the grass in their cell, while predators had a 50% chance of capturing and killing a herbivore if they were present in the same cell, which allowed them to gain fitness. Because individuals with a higher fitness were able to produce more offspring, the trait values for the weighing factors could evolve and give rise to different movement strategies. The results of one simulation of this model are shown in figure 5. Between generations 35,000 and 60,000, the interactions between predators and prey result in shifts between several states of population dynamics (figure 5A). These different dynamical states result in vastly different spatial distribution patterns (figure 5B). Changes in the dynamical states and spatial patterns were brought about by different movement strategies for the herbivores and predators (figure 5C). The authors were able to relate the observed shifts to specific evolutionary changes in movement strategies in the predator and prey populations and they noted that evolutionary changes occured on a similar timescale as ecological changes, which indicates that ecological and evolutionary processes are strongly linked.

Another way this technique can be applied is to understand how movement patterns change in response to a selective pressure. One example of this is a study on the effect of an introduced pathogen on the evolved movement strategies of a population of social animals (Gupte et al., 2022). They developed a spatially explicit model where individuals could find food, which is distributed in clusters across the environment. The individuals' movement decisions were based on their inherited traits, which represent the preferences of the focal individual for the densities of food, individuals handling food and individuals not handling food. The individuals would move to the location (within their movement range) which was the most suitable according to their preferences. Their traits were passed on more frequently the more food they had consumed, and movement strategies could evolve as a result of this. The authors defined four different social movement classes: agent tracking (positive preference for both handlers and non-handlers), agent avoiding (negative preference for both
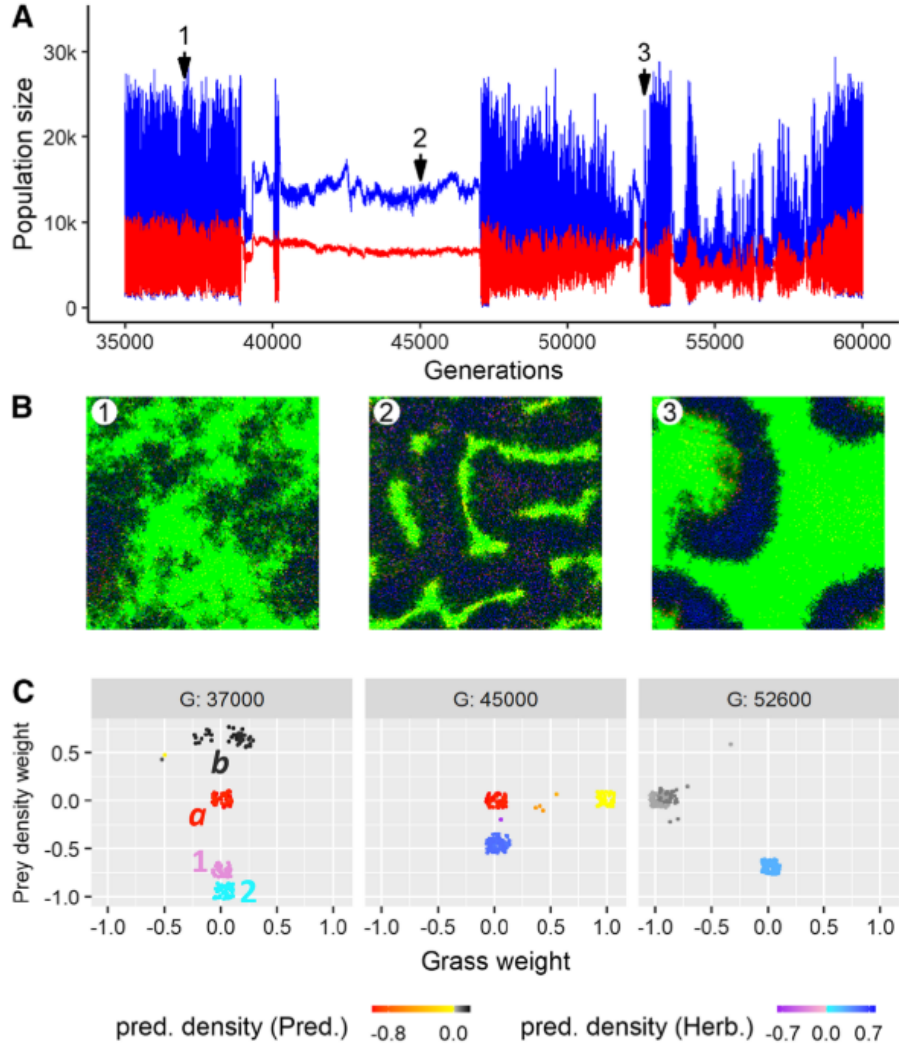
Figure 5: Predator-prey dynamics during one simulation. A) shows the population sizes of predators (red) and prey (blue) over time. B) gives snapshots of the system during 3 different moments in time (as shown in graph A), with grass density in green, herbivore density in blue and predator density in red. Different colours are a result of combinations of grass, herbivores and predators, while black is location of low resources. C) shows the different movement strategies present in the predator (red/yellow/black) and herbivore (purple/cyan/blue) populations at those same moments in time. The x-axes denote the weight of grass density for movement decisions, the y-axis that of prey density and the colours that of predator density. Taken from Netz et al., 2022.
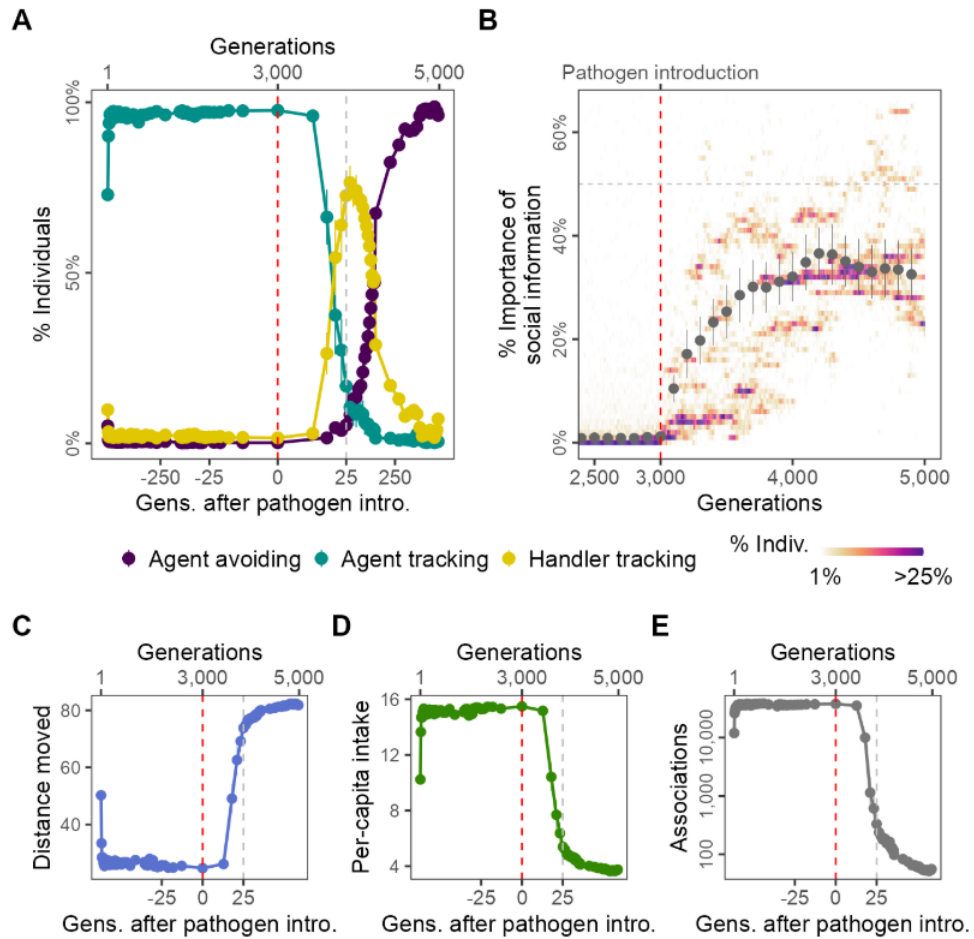
Figure 6: Effects of pathogen introduction on movement strategies and use of social information, resulting in ecological changes. A) depicts a shift in most commonly adapted movement strategy shortly after the introduction of a pathogen. B) shows that social information becomes more important after the pathogen is introduced. C), D), and E) demonstrate an increase in the distance moved and decreases in the resource intake and number of associations respectively. Taken from Gupte et al., 2022.

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handlers and non-handlers), handler tracking (positive preference for handlers and negative preference for non-handlers) and non-handler tracking (negative preference for handlers and positive preference for non-handlers, however this did not occur). For the first 3,000 generations of the simulation, almost all individuals belonged to the agent tracking class, but shortly after the introduction of an infectious pathogen - which made the infected individual incur a fitness cost every time step - after 3,000 generations, the handler tracking class became the most popular, after which the agent avoiding strategy was employed by the vast majority of individuals (figure 6A). Although individuals tracked other individuals for the first 3,000 generations, the importance of this social information was negligible (figure 6B). Only after the pathogen was introduced did the social information become more important, with individuals wanting to avoid coming into contact with other individuals (figure 6B). By trying to avoid other individuals, the average distance individuals moved increased (figure 6C) and resource intake decreased (figure 6D). Individuals did succeed in reducing the number of associations with other individuals (figure 6E). This, in turn, reduced the fraction of the population that was infected and, using an SIR model, Gupte et al. showed that the population post-introduction was more resilient to infections than the pre-introduction population. This study illustrates just how fast movement strategies can evolve in response to selective pressures and can change emergent population wide patterns.

The three case studies show the wide variety of eco-evolutionary systems for which pattern observation can lead to new insights regarding the evolutionary implications of movement. This method is able to expose the potential evolutionary causes and consequences of observed movement patterns, but the interpretation of these results must be done with great care since this technique is best used as an exploratory method. That is the case due to the fact that these models are mainly conceptual by nature, with a lack of data gathered from the lab or field. Therefore, it is difficult to make any strong claims in studies using the technique, but results can reveal interesting dynamics nonetheless. The case studies from Netz et al. (2022) and Gupte et al. (2022), for example, demonstrated that the timescale at which evolutionary changes can take place may be a lot shorter than is typically assumed.

Discussion

With the use of case studies I've shown how the two modelling paradigms can be utilised to answer questions about the processes involved with movement. Firstly, parameterisation can help determine the importance of certain factors for the decision making process behind an individual's movement. Fortin et al. (2005) were able to use this paradigm to uncover the relationship between the external factors (habitat cover) and the movement paths of elk. By using Approximate Bayesian Computation with a rejection filter, Zhang et al. (2017) showed that energy consumption rate was the main driver behind the movement paths of black petrels and that excluding wind speed and site fidelity does make

their model worse at simulating these movement paths. Comparing models with different movement strategies through the use of ABC allowed Marchand et al. (2017) to ascertain that Fowler's toads likely employed a random return strategy for moving to a daytime refuge. These case studies effectively used parameterisation to learn which factors (habitat cover, energy consumption or navigational strategy respectively) influenced movement. The knowledge acquired from these studies can be used as a guide for conservation efforts or as a stepping stone for future studies on these systems.

Secondly, the observation of patterns in evolutionary models of movement can provide insights in the evolutionary causes and effects of movement. De Jager et al. (2011) showed that mussels moved according to a Lévy walk with an exponent of 2 due to the fact that this strategy results in the fastest pattern formation and is also evolutionarily stable. In a predator-prey model, Netz et al. (2022) were able to determine that evolutionary changes could occur as fast as ecological changes by relating observed changes in population dynamical patterns to changes in movement strategies for predators or prey. The potential speed at which movement strategies can evolve was even more evidently demonstrated by Gupte et al. (2022), who found that the introduction of an infectious pathogen can lead to rapid evolution of strategies aimed at avoiding other individuals in order to reduce the probability of becoming infected and suffering a fitness reduction. These insights have improved our understanding of the evolutionary implications of movement and can be used to change the often made assumptions during the development of eco-evolutionary models.

The effectiveness of the parameterisation paradigm is strongly dependent on the accuracy of the stochastic models in terms of realistically simulating the natural system. Excluding an important factor for the movement process from the model may lead to inaccurate parameterisation, as the absence of this factor can cause different behaviour and therefore the importance of other factors (which were included in the model) may be over- or underestimated as a result (Conroy et al., 1995). Identifying the most accurate model can be achieved through model comparison with ABC (Avgar et al., 2013), but omission of an important determinant from each of the models being compared can still occur. For this reason, knowledge of the natural system is necessary for the construction of a realistic model, for which accurate parameterisation is possible. The results one can infer from the parameterisation of an accurate movement model tend to be limited to the relative importance of modelled processes. However, knowledge of these processes can be valuable for improving our understanding of, for example, the population patterns that stem from individuals' movements (Schlägel et al., 2020).

As discussed before, pattern observation in evolutionary models on movement is mainly speculative as these models are often purely conceptual with no direct influence from data gathered from the field. Nevertheless, patterns demonstrated by such studies can be a complementary part to experimental and comparative studies in understanding the evolutionary implications of movement. For example, movement models may be able to help explain how flyway evolution occurs much faster than is predicted by modern synthesis (Piersma,

2011). Certain factors or relationships in such models can still be rooted in empirical data, as shown by De Jager et al. (2011). The inclusion of data in the development of evolutionary movement models will certainly make these models more credible and the patterns produced by them more convincing, but I personally believe that, as long as the conclusions drawn from the patterns observed are done so with caution, even purely conceptual models can further our understanding of the evolutionary causes and effects of movement.

The two paradigms reviewed in this essay are potent methods in elucidating the relationships between the different components from the movement ecology framework (as proposed by Nathan et al. 2008). One does need to appreciate the shortcomings of these paradigms, however, and apply them in the proper context, which the various case studies have demonstrated. The described paradigms are only two of the available methods for studying movement, and other methods can be just as useful for the research of the different factors involved in movement. Path segementation, for example, can be used to describe movement patterns, to detect changes in movement behaviour and to identify the underlying processes (reviewed in Edelhoff et al., 2016). Attempts at expanding the movement ecology framework to include related fields (e.g. animal dispersal, Baguette et al., 2014; biodiversity, Jeltsch et al., 2013) have been made and some of the challenges encountered in these attempts can be negated by modelling methods such as the ones described here. As the field of movement ecology continues to advance with the improvement of methods for gathering movement data, the methods for analysing the vast amounts of data will become ever more important for enhancing our understanding of the processes involved with movement.

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