Memory-driven movement model for periodic migrations

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ABSTRACT

We propose a model for memory-based movement of an individual. The dynamics are modeled by a stochastic differential equation, coupled with an eikonal equation, whose potential depends on the individual's memory and perception. Under a simple periodic environment, we discover that both long and short-term memory with appropriate time scales are essential for producing expected periodic migrations.

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1. Introduction

The interaction between dynamic landscapes and animal movements has been an important research topic in biology, particularly with regard to the process of migration. For instance, insufficient spatio-temporal change in the distribution of resources may 'short-circuit' migration in some seasons (Bartlam-Brooks et al., 2013). In other cases, the age structure of an animal population can create new migratory patterns in response to environmental changes (Teitelbaum et al., 2016). From theoretical work, we know that gathering of nonlocal information is beneficial for resource uptake in dynamic landscapes (Fagan et al., 2017).

Among the long list of factors that one could consider as a variable in this rich topic, the effects of spatial memory on animal movements in dynamic landscapes has attracted considerable recent attention. Many works have demonstrated the essential role of memory in animal migration patterns (Abrahms et al., 2019; Bracis and Mueller, 2017; Fagan, 2019). A variety of models have been proposed to explore this memory effect, some of which have been quite complex (Bennett and Tang, 2006; Schlägel and Lewis, 2014). Memory and environmental persistence are both clearly connected with migratory movement (Berbert and Fagan, 2012). However, even with abundant existing results, the underlying memory mechanism and its relation with animal movement remain unclear.

The goal of this work is to obtain a better understanding of the effects of memory on animal migration patterns. For this purpose, we propose a memory-driven movement model at an individual level. Our model consists of a stochastic transport equation, the evolution equations for memory and fitness, and an eikonal equation with a potential depending on the animal's perception and memory. Our model explicitly describes a wide range of different memory mechanisms, and the corresponding migration patterns can be directly observed by numerical simulations. However, it should be pointed out that the interactions between individuals have not been considered in this work, and hence our model cannot be regarded as a mean-field approximation.

Migration patterns have long been known to follow seasonal changes in the environment and it is natural to expect that such periodic changes in the environment are the main factor contributing to such migrations (Bartlam-Brooks et al., 2013; Fagan et al., 2013). We thus test our model under a simple, idealized time-periodic environment to investigate memory effects on the migration patterns.

The use of the eikonal equation was inspired by the Hughes model for pedestrians (Hughes, 2002, 2003). There are many works in the Hughes model from both analytical (Amadori et al., 2014; Di Francesco et al., 2011) and numerical aspects (Cartee and Vladimirsky, 2018; Twarogowska et al., 2014). The Hughes model contains a conservation law for pedestrian flow, and an eikonal equation with a potential depending on the density of pedestrians. In our case, the potential of the eikonal equation depends on the animal's memory and perception. The article (Xia et al., 2009) combined both the conservation law of pedestrians and an eikonal equation with memory to discuss the memory effect for pedestrian flows.

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One advantage of using the eikonal equation is that it provides a natural interpretation for an animal's decision-making process under the context of optimal control theory. This view of optimal individual-level movement strategies complements mathematical theory on optimal population-level movement that has sought to identify the best movement strategies for different resource landscapes in an evolutionary context using invasibility criteria (e.g., Cantrell et al., 2010; Lam and Lou, 2014). As an optimal control problem at the individual level, an animal's migratory journey consists of a series of movements in which the animal relocates to the region with the best resources by choosing an optimal path that minimizes a certain cost function. The cost function therefore offers an easy way of introducing environmentally based preferences in the individual's movement. A similar concept of utilizing a cost function for memory-based movements can also be seen in Jesmer et al. (2018). Another advantage of the eikonal equation is that efficient algorithms are available; see for example Chacon and Vladimirsky (2012), Sethian (1996) and Zhao (2005). These algorithms help accelerate our computations and make our numerical simulations much less expensive.

This paper is organized as follows. The mathematical model is introduced in Section 2. Its application to the migration behaviors under a periodic environment is in Section 3. After the numerical simulations, we shall discuss the model components and the time scales of memory in Section 4. Several examples of simulations under more complicated environments are provided in Section 5. Finally, we conclude our findings in Section 6.

2. Mathematical model

2.1. Overview of the model

For this section we shall construct a model for an individual's movement, which depends on its health status, the local environment conditions, and its memory for the global environment. The dynamics follow the following assumptions:

- The animal tries to move to, or stay in, the places with the most resources that it remembers.
- An animal's desire to move depends on its fitness and the condition of the animal's current location. We assume one would be less likely to move if it is in good health, or its surrounding is full of resources.
- The movement has a small stochastic effect for the explorations for the local environment.

The dynamics are recorded by the individual's position $X(t)$ for time $t \in \mathbb{R}^+$. The first two important factors that affect our dynamics are the individual's fitness and the environment condition. We consider the fitness $P(t)$, and the environment $E(t, x)$ on $\mathbb{R}^+ \times \mathbb{R}^n$. The value of $E(t, x)$ indicates the condition of environment at time t and location x. The larger the value is, the more resources (or fewer predators) are available for the individual. P is therefore evolving according to the condition of local environment,

$$\frac{dP}{dt} = E(t, X(t))(\overline{P} - P(t)),$$

where $\overline{P} > 0$ is the optimal fitness, which quantifies the maximal strength that the individual possesses and is an intrinsic quality of the individual. The description for P and E in our model are simplified. As our main interest for this model is the effect of memory on movement, we only keep those parts necessary to our focus.

We model the dynamics with the above hypotheses by the following stochastic differential equation:

$$dX = \sigma dW_t + \chi(P(t), E(t, x)) v \, dt,$$

where $\sigma > 0$, W_t is the Brownian motion, and $\chi(P, E) := (\overline{P} - P)e^{-E}$ is called the desire function, which modifies the magnitude of velocity. Consistent with our second assumption of the dynamics, the value of χ is close to 0 when P is close to $\overline{P}$, or when E is large.

The velocity v would be chosen according to the information in memory and perception. We shall introduce our model for memory and perception in Section 2.2, and clarify the choice of velocity in Section 2.2.1.

2.2. Mechanism of memory

While a memory mechanism could be quite complicated (e.g. Bennett and Tang, 2006), here we extract only some basic features that we consider important for our purpose. The assumptions are as follows.

- A memory system consists of multiple channels of memory.
- Each channel of memory fades over time with a rate depending on the intensity of the memory. The stronger the memory intensity is, the slower it would be forgotten. The weaker, the faster.
- Each channel is updated independently over time with new information gathered by the individual within its perception range.

We assume all memory channels operate on the same principle but with different decay and update rates. We first clarify the evolution of each channel, and finish this subsection with a description of a whole memory system.

2.2.1. Evolution of one memory channel

One memory channel is modeled by a memory function $M(t, x)$ on $\mathbb{R}^+ \times \mathbb{R}^n$. The value reflects how the individual remembers the situation of environment at time t and point x.

The evolution of memory contains two terms, one is losing information, another is gaining. Each channel is characterized by two positive indices, the decay rate d and update rate u. We assume the two rates are in the same order, otherwise the channel would fail to capture information correctly over time.

What the second assumption above suggests is a nonlinear term for the fading memory. For the desired behavior we choose the function $-sgn(M)\sqrt{|M|}$. (In fact every function in the form $-sgn(M)|M|^s, 0 < s < 1$ will do.) $-sgn(M)$ guarantees positive memory decays and negative memory increases.

Comparing to the linear function M, which has its slope identically 1, the function $\sqrt{|M|}$ possesses the characteristic that when $|M|$ is large, its slope is smaller than 1, while when $|M|$ is small, it is larger than 1. This matches our description that when the intensity of memory $|M|$ is large, the change of the forgetting rate is slower than when the strength is small. Moreover, another feature of using $-sgn(M)\sqrt{|M|}$, is any memory with finite intensity shall return to zero within finite time.

The memory update is assumed to depend on the individual's perception of the actual environment. To introduce this factor, we define a perceptual kernel $K(x, y) = k(|x - y|)$, where k is a positive function on $\mathbb{R}$, decreases to zero within a finite distance, and with maximum 1. The magnitude of $K(x, y)$ represents the percentage of information for $E(x, t)$ that an animal can gather when standing at location y.

Combining the above discussion, the evolution of M is governed by the following equation:

$$\partial_t M(t, x) = \tau^{-1} \left[-d \cdot sgn(M)\sqrt{|M|} + u \cdot K(X(t), x)(E(t, x) - M(t, x)) \right], \tag{1}$$

where τ is the time scale of this channel. The introduction of τ is for convenience for later discussion when multiple channels are present.

The perception can also be included in our definition as one memory channel, simply by taking its time scale close to zero. Indeed, when τ tends to zero, the memory is forgotten and updated almost immediately. In this case, the corresponding memory function works just like visual perception, which receives instant information for nearby landscapes, but with almost no persistence. As a result, this channel attains almost the same value as the environment function within its perceptual range.

2.2.2. Description of a memory system

We call a collection of independent memory channels a *memory system*. Assume we have m channels, $M_i(t, x)$ where $i = 1, \ldots, m$. Each channel is tagged with a decay rate d_i, an update rate u_i, a time scale τ_i and a perceptual kernel K_i. And each M_i is governed by the following evolution equation:

$$\partial_t M_i(t,x) = \tau_i^{-1}\left[-d_i \cdot sgn(M_i)\sqrt{|M_i|} + u_i \cdot K_i(X(t),x)(E(t,x) - M_i(t,x))\right],$$ (2)

for $i = 1, 2, \ldots, m$.

2.3. Choice of velocity and optimal control

An animals' decision-making is modeled in the context of optimal control theory, with a cost function depending on the memory and perception of its environment. Precisely, we consider the Hamilton–Jacobian-Bellman equation:

$$\partial_t \psi = \frac{|\nabla_x \psi|^2}{2\lambda} - exp(-H(t,x)),$$ (3)

where $\lambda > 0$ is a fixed parameter, and $H(t,x) = \sum_{i=1}^m w_i(t, X(t), x) M_i(t,x)$, with weight functions w_i with $\left(\sum_{i=1}^m w_i\right)(t,y,x) \equiv 1$, for all t, x, y. The value of $H(t,x)$ represents how an individual evaluates the location x at time t, using the information it gathered and stored in its memory system. The protocol for environment assessment is encoded in the weight functions.

A classical argument in optimal control theory (Bardi and Capuzzo-Dolcetta, 2008) shows that the solution ψ in (3) is the value realizing the minimum over of every route $\mathbf{x}(s)$, starting from x at time $s = t$ to $s = T$ by the value function:

$$\psi(t,x) = \inf_{\mathbf{x}(s), \mathbf{x}(t)=x} C(\{\mathbf{x}(s), T\}),$$ (4)

where

$$C(\{\mathbf{x}(s), T\}) = \int_t^T \left[exp(-H(s, \mathbf{x}(s))) + \frac{\lambda}{2}|\mathbf{x}'(s)|^2\right] ds,$$

with a fixed time horizon $T > 0$. The cost functional consists of the evaluation of environment and the kinetic energy, which penalizes high speed. For completeness, the derivation from (4) to (3) assuming $\psi \in C^1$ can be found in Appendix A.

As our setting does not carry a specific finite time horizon, we take time horizon T to infinity. This leads us from (3) to the eikonal equation:

$$\frac{|\nabla_x \psi|^2}{2\lambda} = exp(-H(t,x)).$$ (5)

We assume that the individual would choose to move along the path that minimizes the cost function. The velocity of our choice is therefore the gradient of ψ:

$$v = -\lambda^{-1}\nabla_x \psi,$$

where ψ solves (5).

3. Migration behaviors under periodic environments

We shall now simulate our general model under a simple periodic environment with two types of evaluation functions H. Our goal is to see which settings allow the animal to successfully follow resources and generate a periodic migration pattern.

3.1. Simple time-periodic environment

We assume there are two potential habitats, modeled by two disjoint circular regions A and B; see Fig. 1. The region with positive values of E (*good resources area*) is alternating between A and B with a fixed duration T. E is assumed uniformly negative (*poor resources area*) outside the one region with positive values. For our interest in memory effect, we also assume A and B are far enough from each other so that the individual cannot observe the environmental condition of the other region when it locates inside one. That is, we assume

$$d(A, B) = \inf\{|x - y| : x \in A, y \in B\} > \sup\{|x - y| : x, y \in supp(K)\},$$

where K is the perceptual kernel. Note that there can be multiple points inside A and B, which provides us an option to model environments with finer resolutions. Nevertheless, it is assumed for now that each patch has a uniform environmental condition in this simple setting.

3.2. Two simple memory models

3.2.1. Memory model I: One single memory channel

We first consider a memory system with only one memory channel M, with H in the following form:

$$H = KE + M,$$ (6)

where K is a perceptual kernel. This form means when a place x is close to where the individual stands, the evaluation mainly depends on what it sees. For distant places, it depends mainly on memory.

To encourage the first migration from A to B, we initiated the memory function M with positive values in both A and B, and zero otherwise. We also set the decay rate d small and update rate u large. While memory model I appears reasonable, it cannot produce a periodic migration pattern under the simple periodic environment as one expected, see Fig. 2.

After the individual's first return for A, the value of M was updated negative in both A and B. The individual thus explores the other places that haven't been visited before, instead of returning to A or B.

3.2.2. Memory model II: Long and short-term memory

Because memory model I is too simple to produce a periodic movement in a periodic environment, we increase the complexity and introduce the concept of short-term memory.

Memory model II contains two memory channels, including the long-term memory $M_\ell(t,x)$ and short-term memory $M_s(t,x)$. We assume M_s has larger decay and update rates than M_ℓ, so that it
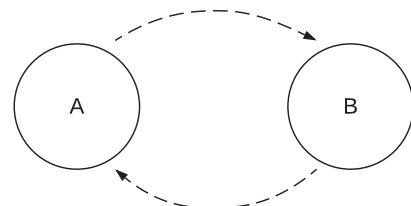

Fig. 1. Time-periodic Setting: The location of the good resources alternates between A and B with duration T.
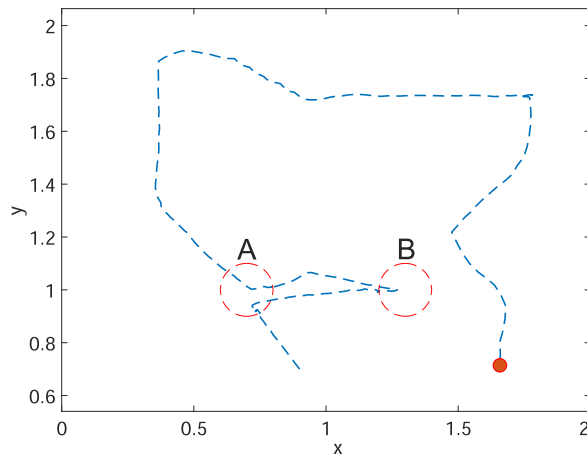
Fig. 2. Trajectory for memory model I. The blue dashed line represents the trajectory and the red dot is the location of the individual at the end of the experiment. In this case, the individual was not able to repeat the migratory process because its memory structure was mismatched to the dynamics of the resource landscape. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
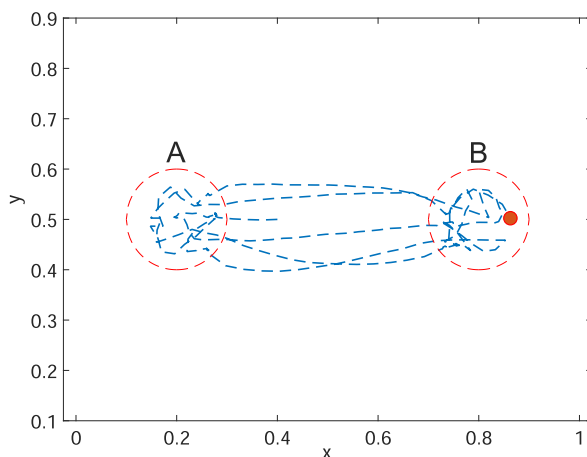

Fig. 3. Trajectory for memory model II. In this case, a periodic migration pattern is successfully produced.

takes longer time to update and forget for information in M_ℓ, while M_s responds to changes quickly, and fades easily.

In this model, we define H as:

$$H(t, x) = M_s + M_\ell. \tag{7}$$

With (7), the individual makes a decision depending more on its local environment when it is in an extreme condition. Otherwise, it tends to rely more on the long-term memory. The following experiment shows a successful result.

Under the same simple periodic environment, memory model II successfully produced the desired migration patterns, see Fig. 3. Observe that the individual will leave an exhausted region after a bit of explorations because of M_s, and return to A or B according to M_ℓ.

4. Discussion

4.1. Remarks on model components

Our main model components include the position, memory, and fitness. The eikonal equation is also important as a policy that utilizes the information in memory to make travel decisions. To inves-

tigate memory effects on animal migrations, the position and memory are indispensable in our model.

The fitness P has two roles in this work. It not only provides a universal measurement for different experiments, but also becomes an index to indicate when an animal would have the desire to move. Recall that we assume an animal would not want to move when the value of P is large.

Note that one could easily increase the complexity of memory and fitness models, by adding more assumptions or even introducing more functions to describe them. Here we intended to keep our model as simple as possible, and only considered essential features.

The eikonal equation, on the other hand, can be replaced by any other reasonable policy. Even though it is not the only option, the existence of efficient algorithms for the eikonal equation accelerates the numerical simulations. This advantage makes the eikonal equation a practical choice for us here.

4.2. Cognitive capacity of our memory model

Our memory model can be utilized to simulate a wide range of cognitive capacity, owing to its flexibility in the number of memory channels. Each channel can be considered as a single cognitive map that stores certain spatial information in the individual's memory. It has been agreed among biologists that cognitive maps are at least parts of the memory mechanism that numerous taxa utilize for different types of movement. For instance, it is employed to record the flower locations for the trapline nectaring of bees (Osborne et al., 1999) and hummingbirds (Gill, 1988). For the case with at least two channels, long and short-term memory can be imitated. From a biological perspective, long and short-term memory are believed to be relied on by diverse species (including invertebrates and vertebrates) for seasonal or long-distance migration (Kitchin et al., 2002). More examples of memory-aided movement and its corresponding mechanism can be found in Fagan et al. (2013).

4.3. Comparison between memory model I and II: Time scales of memory channels

Both memory model I and II have two memory channels but with different time scales. In fact, the perception in memory model I can be seen as a channel with its scale close to zero. This observation combining with the experimental outcomes in Section 3.2, shows that the time scales play a decisive role on whether periodic dynamics can be produced. We shall demonstrate the relation between time scales and dynamic patterns with simulation results.

Consider $0 < \tau_2 < \tau_1$, where τ_1 is the time scale for the long-term memory, and τ_2 for the short-term. We again perform experiments with the same environment introduced in Section 3.1, and initiate M_ℓ with positive value in both A and B. Fig. 4 shows the simulation results for time scales in different orders.

We see from Fig. 4 that there are roughly three different issues that could prevent us from having periodic dynamics:

1. **The individual does not return to habitats if τ_1 is not large enough.**
   The larger τ_1 is, the more enduring the long-term memory would be. With a rather small τ_1, the individual would lose a positive long-term memory of both habitats A and B relatively quickly. Hence the individual ends up wandering around, instead of returning to A or B directly. See Fig. 5 as an example.
2. **The individual does not leave an exhausted habitat, if τ_2 is not small enough.**
   The smaller τ_2 is, the faster the short-term memory is updated. If the short-term memory is not updated fast enough, the indi-
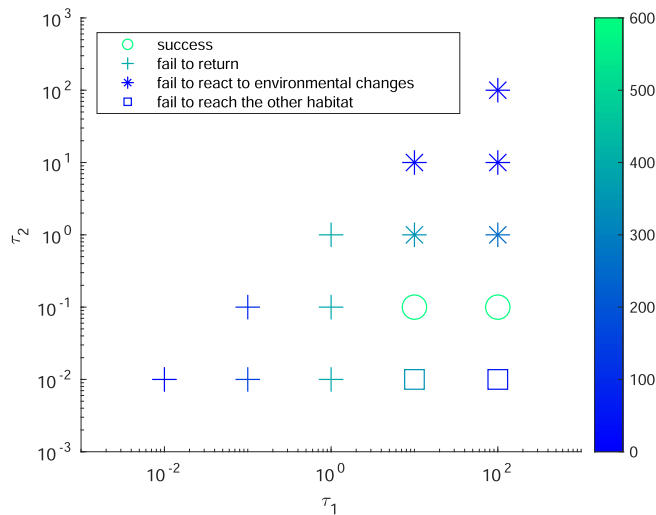
Fig. 4. This graph shows the outcomes for several combinations of time scales. The different symbols correspond to different qualitative outcomes, whereas the color bar on the right hand side indicates the time step at which the periodic dynamic breaks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

vidual cannot respond to the environmental change rapidly. Therefore, in this case the individual never leaves its current habitat; see for example Fig. 6.

3. **The individual could have an early return and never reach the other habitat, when τ_2 is too small while τ_1 is large.**
   We mentioned in the second case that τ_2 needs to be small enough for the fast update of short-term memory, but there is also a lower bound for τ_2. The purpose of this lower bound is to make sure that the short-term memory has a high enough strength, so that the individual remembers the previous habitat is exhausted at least until it moves past the middle point of A and B. Otherwise, an early return could happen and the migration would not be successful.
   See Fig. 7 as an example. The individual starts to leave A when the resources in A become exhausted, but the individual forgets that A lacks of resources before it moves past the middle point of its journey. Because the individual has a positive long-term memory of both habitats and it is closer to A, the individual chooses to return before reaching B.
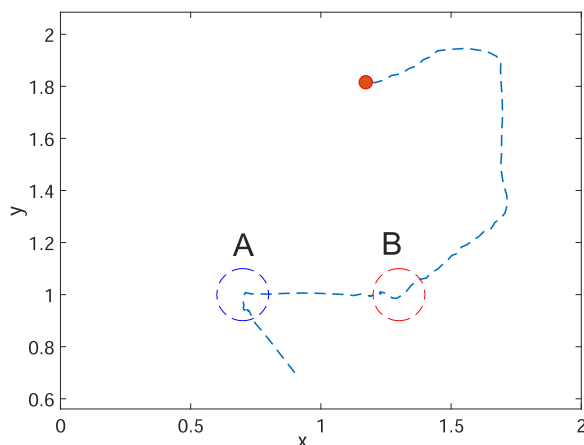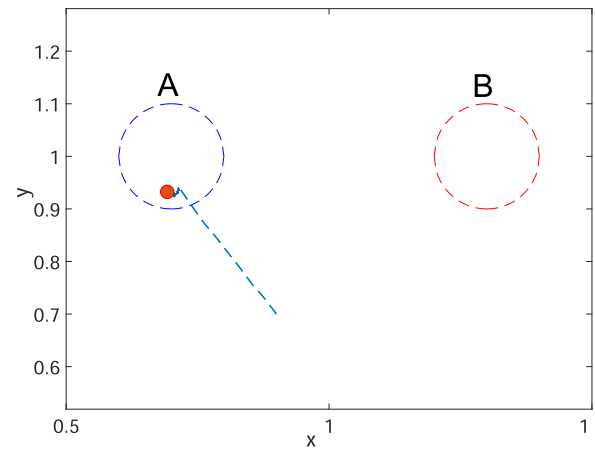

Fig. 6. Trajectory when $\tau_1 \sim \tau_2 \sim 10$. The individual never leaves A because of the large τ_2.

5. Examples of further experiments

Beyond the simple time-periodic environment introduced in Section 3.1, several different environments could also be tested for further experiments. Four examples are given in the following:

- **Three habitats.** Our model was tested under a time-periodic environment with three habitats A, B and C. With the appropriate time scales of long and short-term memory, a periodic dynamic in this environment can also be recovered; see Fig. 8.
- **Changing habitats.** Here we again have two habitats A and B, but with A shrinking and B growing. At the end of the experiment, the region A disappears entirely. See Fig. 9 for an example of resulting trajectory of this experiment.
- **Intermediate habitats/Dangerous locations.** In this example, dangerous areas in the middle of A and B and two intermediate habitats above the dangerous regions were added; see Fig. 10. Our simulation shows that the dangerous regions are always avoided and the intermediate habitats are good enough to retain the migrants. This type of phenomena has been observed in nature; see for example the article (Teitelbaum et al., 2016).
- **Two habitats with random seasonal changes.** In this example, it is again assumed that the good habitat alternates between A and B. But different from before, each duration that resources
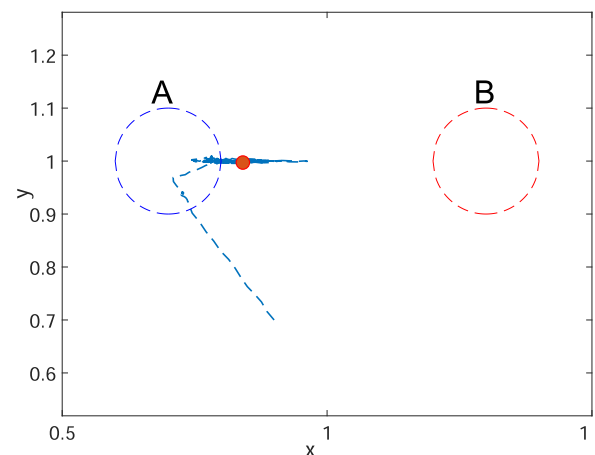

Fig. 5. Trajectory when $\tau_1 \sim \tau_2 \sim 0.1$. In this case the animal does not return to A directly after visiting B.

Fig. 7. Trajectory when $\tau_1 \sim 100, \tau_2 \sim 0.01$. Because of the small τ_2 the information of M_s has been lost before the individual moves past the middle point of A and B. Hence the return to A happens early and the individual never reaches B.
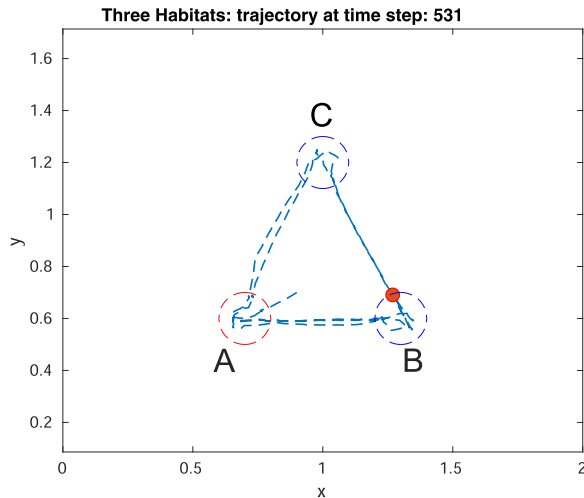
Fig. 8. Here we have periodic dynamics, but the migration dynamics and environmental change do **not** have the same period. This result can be observed from the animation: https://github.com/hsinyilin19/memory_model/blob/master/habi3_movie.gif
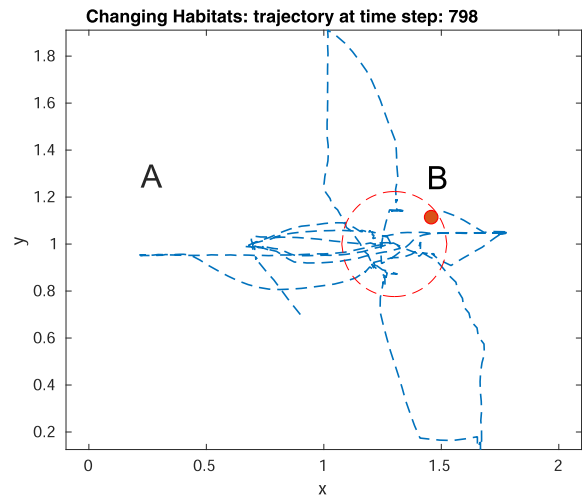

Fig. 10. We see from the trajectory that the individual always avoids the dangerous areas, and sometimes chooses to reside in the intermediate habitats over *A* and *B*. Those intermediate habitats could retain the migrants. An example of simulation can be found in: https://github.com/hsinyilin19/memory_model/blob/master/intermediate_movie.gif

Fig. 9. This is a result with an relatively small τ_1. The trajectory shows that the individual does not return to the area of *A* after the disappearance of that habitat. The animation can be found in: https://github.com/hsinyilin19/memory_model/blob/master/change_movie.gif

stay in *A* or *B* is a random variable. The random variable is positive and uniformly distributed with the mean *T* and variance σ^2.

We say the individual succeeds one journey, if it reaches one habitat from the other before the destination becomes exhausted. If the location of good resources changes *n* times across an experiment, it is considered there are totally *n* possible journeys.

In our experiments the time scales of long and short-term memory are fixed, and *T* is chosen such that the individual can succeed all possible journeys when the environment is time-periodic with *T* as the fixed duration for both habitats.

Recall from Section 4.3, we showed there is only a small region of appropriate time scales that the individual can successfully produce periodic dynamics under a time-periodic environment. When the duration of resources changes, the appropriate time scales change accordingly. The appropriate time scales should be smaller for a shorter duration, while larger when the duration is longer.
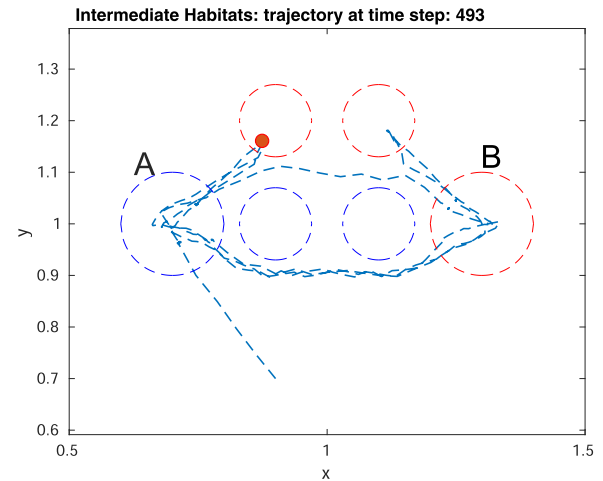
Now the duration of resources staying in one habitat is random each time, the appropriate time scales for each possible journey can be different. Every time our prior fixed time scales locate outside of the appropriate region corresponding to a certain duration in the experiment, the corresponding possible journey fails. For instance, if one of the duration of resources is really short, the individual could miss the corresponding possible journey because the fixed τ_2 is not small enough to respond to the fast environmental change, (which is the second case discussed in Section 4.3).

Therefore, the larger the variance in environmental duration is, the more likely that migratory journeys will fail. To visualize this tendency, we ran a series of experiments. All experiments have a total of 10 possible journeys and the time scales are fixed ($\tau_1 \sim 10, \tau_2 \sim 0.1$). *T* is set at 60 time steps, such that all 10 possible journeys are successful when there is no variance. A small ($\sigma^2 \sim 10$), moderate ($\sigma^2 \sim 100$) and large variance ($\sigma^2 \sim 1000$) case are then considered. We run 10 trials for each case. There are on average 9.5 successful journeys for the small variance case, 7.7 for moderate variance, and only 3.3 for large variance; see Fig. 11. Roughly speaking, it becomes harder for the individual to follow the resources when the variance in the resource duration is increased. From this point of view, **environmental persistence** is very important for a memory-based migration to have a periodic pattern.
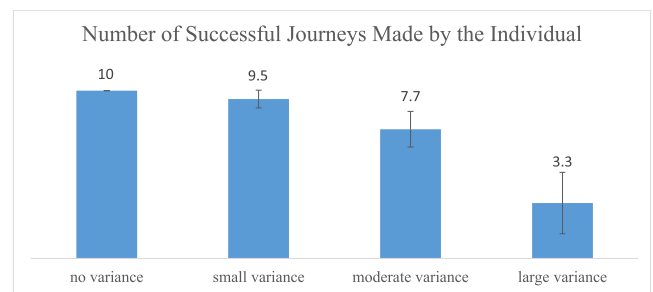

Fig. 11. This chart indicates how many journeys on average the individual succeeds for the entire experiment time. A tendency is shown from this chart that the larger the variance in environmental duration is, the less successful journeys the individual has.

6. Conclusion

In this paper we develop a model for memory-based migrations of one individual over a broad range of memory mechanisms. Through numerical simulations under a simple time-periodic environment, periodic migration patterns are successfully recovered. Furthermore, we discover that in order to produce a periodic movement, the individual must be able to gather and carry enough information from both short and long-term memory, and capable of discriminating which information is more important with appropriate time scales.

While periodic movements can be recovered, the memory systems in our model do not include any intrinsic, a priori periodicity. The resulting periodic migration patterns are developed by the individual as its adaptation to periodic environmental changes.

A memory model with spatio-temporal information that leads to avoidance of recently visited locations can be used to discuss the efficiency of resource detection (Schlägel and Lewis, 2014), and can even give rise to territoriality (Schlägel et al., 2017). Our model can simulate a similar avoidance process by initiating a memory channel to record the last visited region, with the length of avoidance time as its timescale. With the ability to model avoidance from memory, our model renders a general framework for memory effects in applications such as territoriality, foraging, and home residency.

Here we have considered the dynamics of one individual. For future research, it would be interesting to extend this memory-based model to a model for multiple individuals. Information sharing behaviors have been observed in many different species and shown beneficial for foraging efficiency (Martínez-García et al., 2013). For a future extension, the spatial memory of the individual will be regarded as a type of information that can be exchanged among individuals within a population. In this way, memory could be not only updated by perception, but also affected by the memory of another individual. Consequently, the interplay between information exchanges, individual memory, and group dynamics can be further explored.

CRediT authorship contribution statement

Hsin-Yi Lin: Conceptualization, Methodology, Investigation, Software, Visualization, Writing - original draft. **William F. Fagan:** Supervision, Conceptualization, Writing - review & editing. **Pierre-Emmanuel Jabin:** Supervision, Conceptualization, Methodology, Software, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Derivation of Hamilton–Jacobian–Bellman equation

Proposition 1. *Assume the value function ψ is C^1 in (x, t), then ψ solves*

$$\partial_t \psi = \sup_p \left\{ -p \cdot \nabla_x \psi - exp(-H) - \frac{\lambda}{2} |p|^2 \right\}.$$

Moreover, the optimal trajectory is the one starting with velocity $-\lambda^{-1} \nabla_x \psi$, in which case gives the Hamilton–Jacobian–Bellman equation

$$\partial_t \psi = \frac{|\nabla_x \psi|^2}{2\lambda} - exp(-H(t, x)).$$

Proof. For a $h > 0$, for any vector p, we consider the line segment $\ell(s) = x + p(s - t)$ from $s = t$ to $s = t + h$. Connecting ℓ and any path $\mathbf{x}(s)$ from the point $x + ph$ at time $s = t + h$ to $s = T$, we get a path $\tilde{\mathbf{x}}$ starting from x at time $s = t$ and end at time $s = T$. By the definition of ψ,

$$\psi(t, x) \leqslant \inf_{p, \tilde{\mathbf{x}}} C(\tilde{\mathbf{x}})$$

$$= \int_t^{t+h} \left[exp(-H(s, \ell(s))) + \frac{\lambda}{2} |p|^2 \right] ds + \psi(t + h, x + ph)$$

So

$$\frac{\psi(t + h, x + ph) - \psi(t, x)}{h} \geqslant -\frac{1}{h} \int_t^{t+h} \left[exp(-H(s, \ell(s))) + \frac{\lambda}{2} |p|^2 \right]$$

Taking $h \to 0$, we derive

$$\partial_t \psi \geqslant -p \cdot \nabla_x \psi - exp(-H(t, x)) - \frac{\lambda}{2} |p|^2.$$

This inequality holds for every p, hence

$$\inf_p \left\{ \partial_t \psi + p \cdot \nabla_x \psi + exp(-H(t, x)) + \frac{\lambda}{2} |p|^2 \right\} \geqslant 0.$$

In fact the equality holds as zero is realized when p is chosen as the velocity of the optimal trajectory at $s = t$. Let $\mathbf{x}_{op}$ be the optimal trajectory from $s = t$ to $t + h$, then

$$\psi(t, x) = \int_t^{t+h} \left[exp(-H(s, \mathbf{x}_{op}(s))) + \frac{\lambda}{2} |\mathbf{x}'_{op}|^2 \right] ds + \psi(t + h, \mathbf{x}_{op}(t + h)).$$

So

$$\frac{\psi(t + h, \mathbf{x}_{op}(t + h)) - \psi(t, x)}{h} =$$

$$-\frac{1}{h} \int_t^{t+h} \left[exp(-H(s, \mathbf{x}_{op}(s))) + \frac{\lambda}{2} |\mathbf{x}'_{op}|^2 \right] ds$$

Taking $h \to 0$,

$$\partial_t \psi(t, x) = -\mathbf{x}'_{op} \cdot \nabla_x \psi - exp(-H(t, x)) - \frac{\lambda}{2} |\mathbf{x}'_{op}|^2,$$

for some vector $\mathbf{x}'_{op}$.

We rewrite

$$\inf_p \left\{ \partial_t \psi + p \cdot \nabla_x \psi + exp(-H(t, x)) + \frac{\lambda}{2} |p|^2 \right\} = 0$$

as

$$\partial_t \psi = \sup_p \left\{ -p \cdot \nabla_x \psi - exp(-H(t, x)) - \frac{\lambda}{2} |p|^2 \right\}.$$

Notice inside the parentheses is a quadratic form in p,

$$\partial_t \psi = \sup_p \left\{ -p \cdot \nabla_x \psi - exp(-H(t, x)) - \frac{\lambda}{2} |p|^2 \right\}$$

$$= \sup_p \left\{ -\frac{\lambda}{2} \left(p + \frac{\nabla_x \psi}{\lambda} \right)^2 + \frac{|\nabla_x \psi|^2}{2\lambda} - exp(-H(t, x)) \right\}$$

$$= \frac{|\nabla_x \psi|^2}{2\lambda} - exp(-H(t, x)),$$

which is realized when $p = -\lambda^{-1} \nabla_x \psi$. $\square$

Appendix B. Implementation details for memory model II

Consider $\Omega = [0,1] \times [0,1]$ and the final time $T > 0$. We discretize $[0,T] \times \Omega$ uniformly for $N_t \times N^2$ increments.

1. Update the fitness P with the implicit scheme if E is positive and explicit if negative:

$$P(t_{k+1}) = \begin{cases} \dfrac{P(t_k) + E(t_k, X(t_k), Y(t_k))\overline{P}\Delta t}{1 + E(t_k, X(t_k), Y(t_k))\Delta t} \\ P(t_k) + E(t_k, X(t_k), Y(t_k))\big(\overline{P} - P(t_k)\big)\Delta t. \end{cases}$$

Stop if $P(t_k) \leqslant \underline{P}$.

2. Update the memory functions M_ℓ, M_s:

$$M_\ell(t_{k+1}, x_i, y_j) = M_\ell(t_k, x_i, y_j) \\ + \Delta t\, \tau \Big\{ -d\sqrt{|M_\ell(t_k, x_i, y_j)|}|M_\ell(t_k, x_i, y_j)| + \text{Perception} \Big\},$$

where

Perception $= uK(X(t_k), Y(t_k), x_i, y_j)\big[E(t_k, x_i, y_j) - M_\ell(t_k, x_i, y_j)\big]$.

If M_ℓ changes sign, M_ℓ is updated zero. M_s is updated similarly.

3. Update H:

$$H(t_{k+1}, x_i, y_j) = M_s(t_k, x_i, y_j) + M_\ell(t_k, x_i, y_j).$$

4. Solve the eikonal equation $|\nabla_x \psi^b| = \sqrt{2\lambda exp(-H)}$ with boundaries $\{x : H(x) = b\}$ for $\inf_\Omega(H) \leqslant b \leqslant \sup_\Omega(H)$. Then take $\psi = \psi^{b_0}$ where b_0 minimizes the total cost $c\psi^b(X, Y) + exp(-b)$, with the penalty coefficient c for moving around. $exp(-b)$ is the exit cost imposed on the boundary.

5. Update the position (X, Y):

$$\Delta X = \begin{cases} [\psi(t_k, x_{i+1}, y_j) - \psi(t_k, x_{i-1}, y_j)]/(2\Delta x) & \text{if } \frac{1}{N} < X < 1 - \frac{1}{N} \\ -\psi(t_k, x_1, y_j)/(2\Delta x) & \text{if } 0 \leqslant X \leqslant \frac{1}{N} \\ \psi(t_k, x_{N-1}, y_j)/(2\Delta x) & \text{if } \frac{1}{N} \leqslant X \leqslant 1. \end{cases}$$

ΔY is defined similarly. Let (r_x, r_y) be the normal distribution with zero mean and variance σ^2 in $2d$. Then take

$$\begin{cases} X(t_{k+1}) = X(t_k) - \chi(P, (E(t, X(t_k), Y(t_k))))\Delta X \Delta t + r_x\sqrt{\Delta t} \\ Y(t_{k+1}) = Y(t_k) - \chi(P, (E(t, X(t_k), Y(t_k))))\Delta Y \Delta t + r_y\sqrt{\Delta t}. \end{cases}$$

Repeat this procedure until $t = T$.

We conclude this section with two remarks as follows: First, because $sgn(M)\sqrt{|M|}$ is not smooth and the finite difference method is unstable near zero, whenever M changes sign, we put it as zero at the new step.

Second, to contain the experiment inside a bounded domain Ω for all time, we solve the eikonal equation for multiple level sets inside Ω, instead of $\partial\Omega$, and choose the path with the smallest cost. Otherwise the dynamics will eventually escape as the cost of moving around forever will eventually become larger than one fixed exit cost.

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