Incorporating cognition into models of animal movement and predator–prey interaction

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Abstract

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Incorporating cognition, i.e., learning and memory, into models of animal movement is increasingly important as models seek to answer more complex questions where individuals' prior experiences shape their choices. Two example are foraging behavior and predator avoidance. While models of predator–prey dynamics exist, the impact of cognition on movement and predator–prey interactions is largely unexplored. This dissertation presents a flexible, continuous-space, and continuous-time model incorporating an animal using memory to navigate a landscape of heterogeneous resources. The forager balances attraction to food with avoidance of predators in making movement decisions. Two streams make up the resource memory: a repulsive stream that drives the forager away from recently visited areas and an attractive stream that draws the forager back to high quality areas. The predator memory is solely repulsive. The model is used to examine questions related to the advantage of added cognitive complexity for animals in the context of foraging and balancing the food–safety trade-off with predators.

First, foraging without predators is considered and several movement processes are compared: a simple correlated random walk; kinesis, a correlated random walk that switches between searching and feeding behaviors; and memory-informed movement. The model is used to examine for which landscapes the added cognitive complexity of maintaining memory is advantageous and to analyze the behavioral differences between using and not using

memory. In general, a landscape where there is a larger payoff for finding a resource patch, whether in size, value, or difficulty in locating, favors memory. While memory-informed search can be difficult to differentiate from other sensory-driven search behavior, disproportionate spatial use of higher value areas, higher consumption rates, and consumption variability all point to memory influencing the movement direction.

Next, predators are introduced that vary in their temporal predictability and in their correlation with the prey's resources. Memory outperforms simpler movement processes most for patchy landscapes and more predictable predators, which may be more easily avoided once learned. In these cases, memory aids foragers in managing the food–safety trade-off, as particular parameterizations of predator memory reduce predator encounters while maintaining consumption. Non-consumptive effects are highest in landscapes of concentrated, patchy resources and especially when predators are highly correlated with the forager's resources. These non-consumptive effects are also seen with the shift away from the best quality habitat compared to foraging in a predator-free environment.

Finally, learning is examined in more detail with naive foragers introduced to new landscapes as well as predators introduced partway through the simulation. Most non-extreme learning rates provide the forager with sufficient information. In general, foragers that are low to moderately exploratory in new habitats are successful, though performance is habitat-dependent. In the case of introduced predators, predators vary in the area threatened and foragers vary in their memory state. While area threatened plays a key role in determining how much habitat use changes, the forager's knowledge of alternative habitats and exploratory inclinations affects what types of shifts occur.

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DEDICATION

to my family, both given and chosen

INTRODUCTION

Cognition, and in particular learning and memory, gives animals the ability to make use of their previous experiences in the present or future. This can be used to gain an advantage, for example, and improve foraging outcomes (Kamil and Roitblat 1985) or to avoid negative consequences, as with predator avoidance (Kelley and Magurran 2003; Griffin 2004). In predator–prey systems, both predators and prey exhibit a variety of measures and counter-measures in their interactions that allow for their mutual coexistence (Lima and Dill 1990). Some measures are physiological, such as speed, camouflage, and physical defenses. Others are cognitive, such as strategies that result in a change in the behavior of the prey in response to the potential presence of the predator, e.g., refuge use or increased vigilance. Critical to cognitive strategies is the ability of prey (or predator) to learn from interactions either directly or by observation of other interactions (Griffin 2004).

Historically, many models of predator–prey interactions have been at the population level and have ignored spatial complexity and animal movement patterns. In fact, individual movements underlie virtually all important ecological processes, even those frequently considered at the population scale. Survival means both finding food and avoiding predators. Reproduction often involves encountering mates or undertaking migrations. Immigration and emigration are frequently driven by the need to locate suitable habitat. Movement is often the observable result of cognitive antipredator strategies, such as shifts in habitat use in response to learning from predator encounters. However, the implications of prey and predator movement have not been well-considered. Predators should be treated as dynamic components of predator–prey interaction, rather than simply a fixed risk (Lima 2002). Movement is an important phenomenon, as shown by the failure of optimal foraging theory to explain forager diets with mobile prey (Sih and Christensen 2001). Empirical evidence suggests predator avoidance by prey (Hammond et al. 2007), though alternatives exist to shifting habitats, such as increasing vigilance (Brown et al. 1999; Sirot and Pays 2011). Thus, failure to consider the dynamic behaviors of predators (Lima 2002) or their prey (Sih and Christensen 2001) can result in an incomplete and unrealistic model of the system.

Theories of memory, as well as some experimental results, can give insight into how to incorporate memory in predator–prey models. Because I am interested in modeling predator–prey interactions in a spatially-explicit manner, how the brain encodes spatial information is an important component to consider. For example, in a study of birds foraging on baited and unbaited feeders containing either nectar or invertebrates, birds revisited unbaited feeders more frequently when foraging for invertebrates rather than nectar (Sulikowski and Burke 2010). Sulikowski and Burke (2010) interpret this as a difference between foraging for discrete resources (nectar) versus continuously distributed resources (invertebrates), but one may also interpret these results in terms of resource renewal and persistence. Remembering unbaited nectar locations could be useful to avoid them in the short-term (and potentially return to them in the long-term). Invertebrate locations, on the other hand, may be more temporally ephemeral, and thus it may not be worth remembering the unbaited invertebratelocations in order to avoid them. A win-shift bias has been detected in nectivores (Cole et al. 1982), meaning animals both avoid recently rewarded locations and more easily learn to visit new locations rather than return to previously rewarded locations. This agrees with the idea of avoiding recently visited, and thus depleted, patches in the short-term.

Of course there is some degree of uncertainty to spatial information, whether due to environmental change, or imperfect learning or recall. Speed–accuracy trade-offs underlie many decisions (Gold and Shadlen 2007). The same applies to information acquisition on habitat quality, for example, that will impact the degree of uncertainty in the information. Not only is the external abiotic environment stochastic, but evidence suggests that animal behavior is indeterminate rather than determinate as well (Glimcher 2004), adding an additional source of uncertainty for animals gathering information about other animals.

Given all this uncertainty in the world, it would make sense that animals are able to compensate for the uncertainty inherent in their spatial information. For example, ants navigating using path integration will compensate for the uncertainty of their spatial knowledge by starting to use odor as a secondary cue to locate their nest based on their travel distance (Wolf and Wehner 2005). Uncertainty comes into play in non-spatial contexts as well, e.g., how a prey estimates predator risk to make food–safety trade-offs. In contrast with the extensive literature on optimal foraging, less attention has been paid to the other side of the coin: how prey learn and make decisions about predator information, though the cost for mistakes in this case is higher. Experimental work in tadpoles (Ferrari et al. 2010, 2012) shows that the length of time that prey retain predator information increases with risk. However, the more uncertain the information, the shorter the period of time that prey will use it. Possible factors associated with the length of the predator memory window include both extrinsic factors, such as predator turnover rate, frequency of predator diet shifts, and predator predictability, as well as intrinsic factors, such as prey susceptibility, antipredator behavior development, information reliability, and age (Ferrari et al. 2010).

Foraging and defensive behaviors are likely independent, as suggested by the lack of correlation in response thresholds for positive and negative stimuli (sucrose and shock in honeybees) in the same individual (Roussel et al. 2009). The consequences of mistakes with aversive stimuli such as predator encounters are clearly higher than reward stimuli, and animals can learn predator threats after only one encounter (Wiedenmayer 2004; Ferrari et al. 2006). Fear-conditioned responses tend to be long-lasting (Quirk 2002). Stress from a predator cue can impair spatial memory (Zoladz et al. 2012). Additionally, animals exhibit plastic responses in relation to the level of threat (Thaker et al. 2010), which may allow them to mediate predator induced stress (Clinchy et al. 2013). Furthermore, while an area associated with a stressful experience will be avoided, that behavior can be reversed through environmental change if the new alternative is attractive enough, such as a refuge (Nemati et al. 2013).

It is also important to remember that cognitive abilities, such as learning and memory, also carry an associated energetic cost. For example, evolutionary studies of fruit flies show the genetic capacity to improve general learning abilities (for tasks other than the ones under selection) (Kawecki 2010). However, improved learning performance always came with some fitness cost (e.g., competitive ability or lifespan), and such trade-offs run the other direction as well, with selection to improve other traits resulting in decreased learning performance (Kawecki 2010). Thus, any assumed cognitive ability should be able to show improved fitness over simpler abilities.

Despite considerable information on animal learning (Pearce 2008), memory and cognition have frequently been omitted from models of predator–prey interactions. For example, models have assumed predators and prey had perfect information on each other's distributions (e.g., Hugie and Dill 1994) or that animals have perfect or imperfect knowledge of local conditions (e.g., Brown et al. 1999; Persson and De Roos 2003). However, simple models of learning and memory have been incorporated into an agent-based model of foraging (Anderson 2002) as well as a model of home-range formation (Van Moorter et al. 2009), among others. The rise of individual-based models (Grimm and Railsback 2005) provide one framework for the investigation of memory processes in ecology, though alternatives exist as well. I next review some examples of ecological models which explicitly include memory in various formulations.

Multi-scale random walks (MRWs) are one way to incorporate spatial memory and homing into animal movement models (Gautestad and Mysterud 2005). MRWs are a statistical mechanical approach and mix short-term local steps with infrequent large-scale strategic steps. Behaviors such as central place foraging, foraging with resource depletion and renewal, and limited memory can be modeled depending on which previous locations are considered for revisits (Gautestad 2011). If animals are utilizing landscapes using this form of cognitive map, then analyzing an individual's space use in terms of the dispersion of locations can be used to differentiate whether positive feedbacks (i.e., resource facilitation) and negative feedbacks (i.e., resource depletion) predominate, giving insight into habitat quality (Gautestad and Mysterud 2010). These models tend to be used on a homogeneous landscape and ignore heterogeneity. However, habitat quality can also affect revisit probability in addition to familiarity (Boyer et al. 2012). By analyzing visit length and time between visits, Boyer et al. (2012) conclude that monkey movements are non-random due to the use of memory and driven by environmental heterogeneity. Mueller et al. (2011) created a simulation model using evolutionarily-trained artificial neural networks combining three movement behaviors: oriented (using perceptual cues), non-oriented (correlated with previous step), and memory (evolutionary knowledge). Across landscapes varying in patch size and predictability, memory was most important for locating resources in predictable landscapes.

Grove (2013) investigates for which circumstances spatial memory is useful, pointing out that many models assume either complete omniscience or ignorance. Because spatial memory is assumed to be energetically costly, in any case where performance between informed and uninformed individuals is identical, evolution would presumable favor no spatial memory. Generally spatial memory is predicted to be favored by selection when resources are sparsely distributed (lower patch densities or smaller patch sizes) or detection distance is small.

Several models provide different ways to represent spatial memory. Bennett and Tang (2006) modeled elk migration in Yellowstone, including bioenergetics, resource selection, navigation and spatial memory, and spatial learning. Spatial memory is represented as a graph of connected patches and information is acquired within a perceptual range. Migration includes both when to migrate and where to migrate which is probabilistically determined from the values of adjacent patches. Learning, through observation and mimicry, is modeled with an evolutionary algorithm to find the optimal edge weight on the cognitive map.

Boyer and Walsh (2010) modeled monkeys foraging on fruiting trees. Monkeys remember detailed information about visited trees, and at each step take either a random step or a step towards the best tree (based on food availability and distance). Although they assume a fairly sophisticated set of cognitive abilities, the basic concept of combining local optimization using memory-based movement with exploratory behavior using random movement could be applied more generally.

In a movement model showing a mechanistic basis for home range formation, Van Moorter et al. (2009) utilized two memory processes: the reference memory, which controls preferences for previously visited patches, and the working memory, which avoids backtracking to recently visited patches. Depending on the strengths of the respective decay rates, different dynamics can arise. No reference memory leads to diffusion, while no working memory results in movement in and out of a single patch. Intermediate working memory and low reference memory decay rates result in stable home rages with the highest realized utility, thus reference memory can be considered a long-term memory and the working memory a short-term memory.

Avgar et al. (2013) model an animal moving discretely in time and space with a biased random walk informed by a redistribution kernel calculated at each time step for the animal's current location. Movement decisions based on the redistribution kernel can be made deterministically or stochastically, by taking the maximum or probabilistically matching the cell probabilities. The animal senses information from landscape layers (e.g., resource quality, predation risk) based on sensory distance and commits that information to memory, which decays with time. A location's attractiveness combines perception, memory and travel cost, and the product of the multiple layers forms the redistribution kernel. Avgar et al. (2013) argue that the redistribution kernel facilities the exploration of interactions among parameter values and landscape characteristics, such as testing whether the statistical properties of a movement trajectory show evidence for memory use.

These conceptions of memory (Bennett and Tang 2006; Boyer and Walsh 2010; Van Moorter et al. 2009; Avgar et al. 2013) specifically incorporate habitat quality in one form or another, in contrast to other formulations that depend only on location (e.g., Gautestad 2011; Mueller et al. 2011). They thus are able to represent the intentional state of the animal. Furthermore, these models also get at the dynamic nature of memory. Particular memory decay rates are a necessary condition for home range behavior to arise (Van Moorter et al. 2009). Memory capacity should not be limited only by physiological costs, but also that memory capacity should negatively correlate with the rate of environmental change, given the adaptive value of forgetting in a temporally dynamic landscape (Avgar et al. 2013).

As noted by several researchers (e.g., Gautestad and Mysterud 2010; Boyer et al. 2012), animal trajectories frequently contain returns to previously visited locations that violate the assumptions of low Markovian order models of movement processes, necessitating the development of alternative techniques that take cognitive processes such as memory into account. Indeed, incorporating memory into models of animal movement has been suggested as a future direction in movement ecology (Morales et al. 2004; Patterson et al. 2008). The models discussed above provide ideas for how memory can be integrated into predator–prey models. However, they generally treat predators as searching for immobile prey (or mobile prey within a fixed patch but ignoring the details of the predator catching the prey) and so need to be extended to consider predators a dynamic component of predator–prey models (Lima 2002). Regardless of how memory is implemented, using memory must be demonstrably better that ignorance or random behavior (Grove 2013).

While memory models utilized in predator–prey models are necessarily more simplistic than how these cognitive processes actually work (Avgar et al. 2013; Grove 2013), information on memory function can be gained from the studies in psychology and neuroscience. For example, it is important that information be spatially salient when modeling spatially-explicit memory (Sulikowski and Burke 2010). Another important consideration for modeling is how to incorporate uncertainty about spatial information. Finally, there may be asymmetries in learning food location compared to predation risk.

Given the enormous range of cognitive abilities among species, this raises the question of what advantages cognitive complexity brings and in what circumstances is it most effective. Consider an animal foraging in a patchy environment. This could be an aquatic species, like a fish selecting habitat along a stream or the temporary aggregations of plankton in a pelagic environment. Similarly, in the terrestrial environment, resource distribution is also heterogeneous. For nectarivores, like many species of insects and birds, high quality habitat may be groups of flowering plants or the individual plant itself, while for ungulates like moose or elk, it may be open clearings or sections of forest. Depending on what the animal is eating, the different strategies of the forager (or consumer of the resource) can vary in effectiveness. While returning to patches regularly could be advantageous for nectarivores to coincide with the next set of blooms, the same would not necessarily hold for planktivores if the patches have drifted in the meantime. For other herbivores, the location of the patches could be important to remember, but randomly visiting them may be just as an effective strategy. Next consider how the forager's strategy changes in the presence of predators, which could be a larger fish, bird of prey, or pack of wolves. The forager now has two potentially competing objectives: to obtain sufficient food resources and to avoid being eaten by predators. Depending on the predictability and legality of the predators, it could be more or less advantageous to remember predator encounters and seek to avoid them.

These questions—about how movement and cognitive abilities impact foraging choices and predator–prey interactions—are what this project seeks to address. What is the advantage of added cognitive complexity, such as memory, for animals in the context of foraging and balancing the food–safety trade-off with predators? What environmental characteristics, e.g., of the habitat or predators, make memory more advantageous? How does learning affect forager behavior, such as the case of a naive forager introduced into a novel environment or predators introduced to an environment in which they had not previously been present?

Chapter 1. This chapter describes the foraging model. Several movement processes are compared: a simple correlated random walk; kinesis, in which correlated random walk parameters are set based on consumption rate, i.e., searching and feeding behaviors; and memory-informed movement. Two streams make up the memory: a short-term repulsive stream that drives the forager away from recently visited areas and a long-term attractive stream that draws the forager back to high quality areas. These movement processes are evaluated across a range of landscape characteristics.

Chapter 2. This chapter introduces predation into the model. Predators are formulated as a Poisson process and vary in their spatial correlation with habitat quality and their temporal predictability. Foragers have an additional memory stream for predator encounters which they must balance against the resource memory to determine movement direction. Predator environment and resource distribution are varied to examine when memory is particularly useful and how it impacts the food–safety trade-off as well as the non-consumptive effects of predation.

Chapter 3. This chapter considers newly introduced foragers naive to their environment. The movement processes kinesis and memory both switch between feeding and searching behaviors based on the average consumption rate. While in previous chapters foragers knew the average value of the landscape, they now must learn it. Foragers using memory additionally value unexplored habitat differently based on where they fall on the exploratory–avoidant temperament axis. These individual differences, as well as learning rates, are compared to fully informed foragers and those not using memory to examine how they affect learning of unfamiliar habitats.

Chapter 4. This chapter examines the effects on foragers and the resource of introducing predators to a system in which they were previously absent. After a period of foraging without predation, predators appear in the area of highest resource quality. The habitat use of the forager before and after predation is compared under several predator scenarios to examine the effect on the foragers and the underlying resource.

Chapter 1

INVESTIGATING THE EFFECT OF MEMORY ON FORAGING BEHAVIOR

Abstract

Incorporating memory into models of animal movement is increasingly important as models seek to answer more complex questions regarding individuals whose prior experiences shape their choices. Foraging behavior is one example of learning and memory and is observed across a variety of taxa. This chapter presents a flexible, continuous-space, and continuous-time model incorporating memory of an animal moving through a landscape of variable-quality resources. The model is used to examine for which landscapes the added cognitive complexity of maintaining memory is advantageous and to analyze the behavioral differences between using and not using memory. In general, a landscape where there is a larger payoff for finding a resource patch, whether in size, value, or difficulty in locating, favors memory. These landscapes consist of sparse, contiguous patches of high-value resources that regenerate quickly, located on a space that is mostly devoid of resources. While memory-informed search can be difficult to differentiate from other sensory-driven search behavior, disproportionate spatial use of higher value areas, higher consumption rates, and consumption variability all point to memory influencing the movement direction.

1.1 Introduction

It has long been recognized that foraging behavior in the field provides evidence for learning and memory across a variety of taxa, complementing more controlled laboratory studies (reviewed in Kamil and Roitblat 1985). Observed foraging behavior also motivates experiments based on spatial memory. For example, whether spatial learning can be detrimental with temporally unpredictable food even if it is advantageous for spatio-temporally predictable food (Haupt et al. 2010).

Examples of evidence for spatial memory are many and occur in taxa ranging from insects to primates. Bees, for example, learn reward values (Gil and De Marco 2009). When displaced into familiar territory, they can both choose between two goals and navigate (Menzel et al. 2005). They thus demonstrate a map-like memory (Menzel et al. 2005), though path integration and learned landmarks may be sufficient to accomplish these tasks (Cruse and Wehner 2011). Fish on coral reefs use learned landmarks to navigate between food patches, including the possibility of novel routes indicating a cognitive map (Reese 1989). Birds repeatedly return to previously visited sites (Regular et al. 2013). An analysis of visit length and time between visits suggests that monkey movements are non-random due to the use of memory and driven by environmental heterogeneity (Boyer et al. 2012).

Memory-informed search as a foraging behavior can, however, be difficult to differentiate from other sensory-driven search behaviors (Fagan et al. 2013). Much of the literature on animal cognition from psychology focuses on food-rewarded behavior—essentially foraging behavior (Shettleworth 2001). Memory-driven movement behaviors are numerous, encompassing foraging and more (e.g., migration, caching, home ranging, and searching, among others), and the necessary orientation abilities range from the simple movement along a gradient to more complex goal-oriented behaviors using path integration or landmarks (Fagan et al. 2013).

Unlike other physiological attributes such as energy reserves or hormone levels, memory is an internal state of the animal that cannot be measured directly. This is especially true in ecological contexts when the history of the animal's experiences may be unknown. Even in controlled laboratory conditions, issues such as motivation and salience may confound attempts to study memory. In fact, formulating clear behavioral criteria in order to infer cognitive processes is a particular challenge for studying animal learning and memory (Shettleworth 2001). Models thus are a useful tool to investigate hypotheses that involve direct measures or manipulation of memory.

To date, models of animal movement have generally avoided the complexity of modeling memory in favor of simpler formulations such as area-restricted search or those based on random walks (Watkins and Rose 2013). However, incorporating memory has been suggested as a future direction for improving movement models (Morales et al. 2004; Patterson et al. 2008). Investigations into more complex processes, such as how individual movements affect survival and reproduction and in turn population dynamics, make incorporating memory into movement models more important, as individuals' prior experience will shape their choices (e.g., returning to or avoiding specific locations) (Morales et al. 2010). One technique for including memory include reinforced random walks (random walks on a lattice in which previously visited nodes or edges are more likely to be used again), although an important consideration is to also allow for movements towards distant remembered locations (Smouse et al. 2010). Another suggestion is to represent spatial memory as multiple layers, allowing the modeling of the process of memory decay as declining memory intensity and precision with time, which in turn affects the strength and directionality of the movement process (Fagan et al. 2013).

Previous approaches to including memory in movement models have varied from statistical approaches incorporating current or visited locations into random walks to more mechanistic formulations of spatial memory. For example, in a model combining memory, non-oriented random walks, and perceptually oriented movements using evolutionarily trained artificial neural networks (ANNs), memory is most important for locating resources in predictable landscapes (Mueller et al. 2011). In this model, memory can be thought of as evolutionary knowledge, as learning happens through the generations of the evolutionary algorithm. While memory was also used to create systematic circular searches useful even for unpredictable landscapes, this may have been the ANN exploiting the orthogonal xy-coordinate system used to encode position, and there is little reason to think that animals navigate or search using such human space representations (Bennett 1996). Multi-scale random walks (Gautestad and Mysterud 2005) combining truncated Lévy flight (short-term local steps) interspersed with returns to previously visited locations (infrequent large-scale strategic steps), can model the avoidance of recent locations of foraging with resource depletion and renewal (Gautestad and Mysterud 2010; Gautestad 2011). However, these models tend to be used on a homogeneous landscape and ignore heterogeneity as habitat quality can also affect revisit probability in addition to familiarity (Boyer et al. 2012).

Some mechanistic models of memory are targeted to specific systems. For example, spatial memory is represented as a graph of connected patches and information is acquired within a perceptual range in a model of elk migration in Yellowstone (Bennett and Tang 2006). Modeling monkeys foraging on fruiting trees, Boyer and Walsh (2010) showed spatial memory could result in repeated routes. In this case, the route itself was not learned, but only the state of visited trees, and movement was a mixture of random steps and optimal steps without route planning. However, general theoretical questions can also be addressed. Home range behavior has been shown to arise from learning about the environment as an intermediate state between dispersal and movement centered on a single location (Spencer 2012; Van Moorter et al. 2009). In both models, returning to a location is a function of information decay and distance. Van Moorter et al. (2009) focus on the spatial location of patches with two memory streams: a repulsive working memory and an attractive reference memory. The memory streams are weighted by distance and decay at different rates. Home range behavior arises with intermediate working memory and small reference memory decay rates, leading to a balance between diffusion and single patch fidelity. Spencer (2012) emphasizes learning ancillary site-specific information that improves the foraging rate. An expected value of a linear arrangements of patches is calculated based on the decay of information and the time to regeneration. Home range behavior arises when foragers benefit from information after a time delay, such that there is a dynamic equilibrium between resource consumption and regeneration, and information allows foragers to more efficiently exploit those resources.

Another area of research is determining the environments in which memory is most useful or most likely to have evolved. Avgar et al. (2013) use a biased random walk informed by a redistribution kernel in which a location's attractiveness combines perception, memory and travel cost. The model suggests that memory capacity should not be limited only by physiological costs. It should also negatively correlate with the rate of environmental change, given the adaptive value of forgetting in a temporally dynamic landscape. Because spatial memory is assumed to be energetically costly, in any case where performance between informed and uninformed individuals is identical, evolution would presumably favor no spatial memory (Grove 2013). Using derived inter-patch distances for naive and memory-informed foragers, Grove (2013) computes patch encounter rates. Spatial memory is predicted to be favored by selection when resources are sparsely distributed (lower patch densities or smaller patch sizes) or detection distance is small.

My goal is both to create a flexible, continuous model incorporating memory of an animal moving through a landscape of variable quality resources, and to use that model to examine when the added cognitive complexity of maintaining memory is advantageous. A key feature of the model is that it is continuous-space and continuous-time in order to be a versatile, realistic framework for considering animal movements. While collected movement data are generally a discrete set of times and locations, it is important to remember that data are a sample of a continuous movement trajectory across a landscape (Gurarie et al. in review). While this model would be able to be applied to many organisms and systems, the prototypical scenario is an animal foraging on stationary resources that deplete and regenerate, though scales could vary from a nectarivore foraging on flowering plants to a fish feeding in seagrass beds to a cervid browsing forest clearings. In order to illustrate the model, I compare an animal using three different movement processes: (1) a simple correlated random walk, (2) kinesis, in which correlated random walk parameters are set based on consumption rate, i.e., searching and feeding behaviors, and (3) memory-informed movement, across a range of landscape characteristics (patchiness, correlation, and regeneration rate). These nested behaviors allow the evaluation of what landscape characteristics result in memory outperforming other movement processes, and what that may suggest for the evolution of memory. Further, I analyze the behavioral differences in terms of habitat use and time allocation among the movement processes, and what they suggest one is likely to observe in an animal of using memory.

1.2 Methods

1.2.1 Model

In the foraging model, the animal moves across a habitat of variable resource quality, consuming those resources. Depending on the movement process, the animal's movements are random (random walk), informed by its current consumption rate (kinesis), or informed by its memory of the resource quality and current consumption rate (memory). In the framework of Nathan et al. (2008), the animal's movement is motivated by finding food resources and its internal goal is to maximize consumption. The motion capacity in terms of velocity is the same across all three movement processes, but the navigational capacity differs. For random walk, there is no navigation abilities, and no external factors influence the movement trajectory. Kinesis does not navigate towards a goal, but the current resource quality affects the movement process. With memory, on the other hand, navigation towards previously learned habitat areas is possible as spatial memory and current resource quality affect the movement trajectory. Throughout the model description, almost all components are functions of two-dimensional space $z \in R^2$ and time t (e.g., $f(z,t)$), though the dependent variables are omitted in some equations for clarity. Consult Table 1.1 for a complete list of parameters.

Habitat quality and consumption

In the modeled habitat, resource productivity varies heterogeneously across the landscapes, with both the amount of heterogeneity and the regeneration rate being parameterized. The intrinsic habitat quality, $Q_0(z)$, is constant through time, meaning that transient or moving patches are not considered here. The instantaneous habitat quality, $Q(z,t)$ depends on both consumption, $C(z,t)$, by the animal and logistic regeneration, $R(z,t)$,

$$\frac{\partial Q}{\partial t} = (R - C)Q. \tag{1.1}$$

Table 1.1: Parameters used in the foraging model and values for simulations. Because units are arbitrary in the simulations, L is used for generic length units and T is used for generic time units.

	Parameter	Definition	Units	Values
Simulations				
	Δt	model time step	T	1
	T	simulation length (time steps)		1000
Landscapes				
	μ_Q	patch concentration (GRF mean)		-1.5, -1, -0.5, 0, 1
	γ_Q	patch size (GRF scale)		2, 10
Consumption				
	β_R	regeneration rate	1/T	0.005, 0.01, 0.05
	β_C	consumption rate	1/T	1
	γ_C	consumption spatial scale	L	1
Memory[a]				
	ψ_M	short-term memory factor		2, 5, 10
	β_L, β_S	learning rates	1/T	1
	ϕ_L, ϕ_S	decay rates	1/T	0, 1e-5, 1e-4, 0.001, 0.01, 0.1, 0.5
	γ_L, γ_S	learning spatial scale	L	1
Movement[b]				
	τ_S, τ_F	autocorrelation time scale	T	4, 2
	ν_S, ν_F	length of μ	L/T	6, 1
	γ_Z	memory spatial scale	L	1, 5, 10
	λ	mean time to update θ	T	0.5, 1, 2

[a] L = long-term memory, S = short-term memory

[b] S = searching, F = feeding

Table 1.2: Spatial kernels used in the foraging model. $\mathcal{N}_2$ is the bivariate normal distribution and $\boldsymbol{I}$ is the 2 x 2 identity matrix.

Description	Equation	Form
Consumption kernel	f_C	$\mathcal{N}_2(\mathbf{0}, \gamma_C^2 \boldsymbol{I})$
Short-term memory learning kernel	f_S	$\mathcal{N}_2(\mathbf{0}, \gamma_S^2 \boldsymbol{I})$
Long-term memory learning kernel	f_L	$\mathcal{N}_2(\mathbf{0}, \gamma_L^2 \boldsymbol{I})$
Memory distance-weighting kernel	f_Z	$\mathrm{Exp}(\gamma_Z)$

Consumption and regeneration are defined as

$$C = \beta_C \, f_C(|z - Z|), \tag{1.2}$$

$$R = \beta_R \left(1 - \frac{Q}{Q_0}\right), \tag{1.3}$$

where consumption occurs in the vicinity of an animal's position, $z = Z$ and is described by a spatial kernel, $f_C(|z - Z|)$, and consumption rate, β_C, and β_R is the regeneration rate. The spatial kernel is solely a function of distance from the animal's location, $|z - Z|$, i.e., it is isotropic. Here f_C is the bivariate normal distribution centered on the animal's location Z with the variance parameter γ_C^2 (the length scale of the spatial kernel) characterizing how widely the animal consumes about its location (Table 1.2). This conception of resource consumption, high in the animal's immediate vicinity and decaying to zero at greater distances, is a good fit for grazing animals, with the length scale representing how far an animal can reach for food as it moves or fine-scale movements on a smaller scale than the trajectory.

Memory map

As the animal moves across the landscape observing habitat quality, it builds up a memory map, $M(z, t)$ made up of two streams. Two memory streams have been used to detect changes in the environment (Kacelnik et al. 1987), combine short-term tactical and longer-term strategic behaviors in foraging (Anderson 2002), give rise to stable non-territorial home ranges (Van Moorter et al. 2009), and represent neural circuits in conditioning (Anderson et al. 2010). Multiple memory layers have also been suggested for modeling memory decay (Fagan et al. 2013). The memory map includes a long-term stream, $L(z,t)$, which decays slowly and attracts the animal to high quality habitat, and a short-term stream, $S(z,t)$, which decays quickly and repels the animal from depleted habitat it has recently occupied. The two memory streams combine linearly to form the memory map, so that positive values are attractive, zero indicates neutrality, and negative values are repulsive:

$$M = L - \psi_M S. \tag{1.4}$$

Because L and S have the same maximum value (Q_0) and S decays faster than L, the short-term memory factor, ψ_M, ensures that the value at a just-visited location will initially be negative, or repulsive, with $\psi_M > 1$. As L and S decay, the value will eventually turn positive and thus attractive for good quality habitat.

Each memory component (L and S) is a mixture of two parts, learning and forgetting,

$$\frac{\partial L}{\partial t} = \beta_L f_L(|z - Z|)(Q_0 - L) - \phi_L L, \tag{1.5}$$

$$\frac{\partial S}{\partial t} = \beta_S f_S(|z - Z|)(Q_0 - S) - \phi_S S, \tag{1.6}$$

where β_L and β_S are the learning rates of the long- and short-term memory streams, f_L and f_S are spatial kernels describing learning (Table 1.2), and ϕ_L and ϕ_S are the decay rates. As for consumption, a spatial kernel is used to describe how an animal learns about its immediate vicinity, though the length scale could differ. For example, an animal might be able to visually inspect a larger surrounding area than it is able to browse.

Movement model

Movement process. An animal's movements through a landscape are described by a continuous trajectory, $Z(t)$. Taking velocity, $V(t)$, the animal's position is thus $Z(t) = \int_0^t V(t')dt' + Z(0)$, where $Z(0)$ is the animal's initial position. An autocorrelated, directed, continuous movement process is

$$dV = \frac{1}{\tau}(\mu(t) - V)dt. \tag{1.7}$$

Table 1.3: Behavioral states in the model and corresponding movement process parameters.

State	Direction ($\angle\mu$)	Speed ($\|\|\mu\|\|$)	Time scale (τ)
Searching	memory: $\angle\mu \sim g(\theta)$ kinesis: $\angle\mu \sim U(0, 2\pi)$	ν_S (fast)	τ_S (large)
Feeding	$\angle\mu \sim U(0, 2\pi)$	ν_F (slow)	τ_F (small)

This is similar to the Ornstein-Uhlenbeck process, but without the white noise component. Instead, stochasticity is introduced through the bias vector, $\mu(t) = (\nu, \angle\theta)$. The movement process is parameterized by τ, the time scale of autocorrelation, and $\nu = ||\mu(t)||$, the magnitude of the bias vector which controls the average speed of the process. The angle θ is set probabilistically, either from a uniform circular distribution resulting in a random walk or from a probability distribution computed from the memory map. A Poisson process with rate parameter λ is used to update θ, meaning $\mu(t)$ is constant between updates.

Behavior states. Three versions of the movement process are compared: random walk, kinesis, and memory. For the single-state random walk, a single set of speed and time scale parameters determine the movement process with the bias angle set randomly. With kinesis and memory, the animal switches between searching and feeding states (Table 1.3). These three movement processes have the advantage of being nested, facilitating comparisons. Kinesis is a movement model that performed well in a variety of environments and avoids the strong assumptions of perceptual abilities of area-restricted search (Watkins and Rose 2013), which also performs sub-optimally in very patchy environments (Humston et al. 2004). Random walk provides a useful null model to compare against.

For both kinesis and memory, movement in the feeding state is tortuous and slow as the animal seeks to exploit the local high quality habitat. The angle θ of the bias term is drawn from a uniform distribution as movement is undirected. In the searching state, on the other hand, the timescale of autocorrelation is large, leading to more linear movements and directional persistence, and the animal moves with a higher rate of speed. The bias angle is still set randomly for kinesis, but with memory, the animal seeks productive patches with the direction determined from the memory map. The angular probability distribution is computed by integrating transects of the memory map radiating out from the forager's location with the memory value at each point weighted by distance. The integrated transects are then normalized by the integrated value for the whole memory. The angular probability density function is given by

$$g(\theta) = \frac{\int_0^r M(r,\theta) f_Z(r) dr}{\int_0^{2\pi} \int_0^r M(r,\theta') f_Z(r) dr d\theta'}, \tag{1.8}$$

where $r = |z - Z|$ and $f_Z(r)$ is a kernel function (e.g., exponential with length scale parameter γ_Z) that weights according to distance, such that closer resources are preferred all else being equal (Table 1.2).

If the memory map is empty, the probability is undefined. In this case, an angle is chosen at random with uniform probability leading to an exploratory behavior. Thus each state is defined by its directional bias (random or memory-driven) and the correlation and speed of movement.

Behavioral state transitions. The animal begins in the searching state, transitions to the feeding state when consumption increases, and transitions back to searching whenever consumption drops. Turning to optimal foraging theory, the marginal value theorem states that the animal should leave a patch when the foraging rate in the patch drops below the average foraging rate in the environment (Charnov 1976). Thus the switch between states occurs when the current consumption rate, $C(t)$, crosses the average consumption rate, $\bar{C}$. The average consumption rate is based on the intrinsic habitat quality, $\bar{C} = \beta_C\, f_C(|z - Z|)\overline{Q_0}$, where $\overline{Q_0}$ is a uniform landscape of average habitat quality extending outward from Z in all directions. This assumes the animal knows its habitat and the average consumption rate. Instead, the average consumption rate could be learned, such as for novel environments, which is explored in Chapter 3.

1.2.2 Simulations

The simulations compare the following foraging strategies bases on the movement processes described above: memory (complete model), kinesis (no memory, but animal switches between feeding and searching), and a random walk (single state). The same speed and timescale autocorrelation parameters are used for both memory and kinesis. The random walk uses the searching speed and timescale autocorrelation, which outperformed the feeding parameters and intermediate values aligning with encounter theory favoring faster speeds with destructive encounters of dynamic targets (Gurarie and Ovaskainen 2013).

In order to examine a stationary scenario (i.e., after the animal is familiar with its environment), the simulation begins with the long-term attractive memory stream initialized to the habitat quality, Q_0, and the short-term repulsive stream initialzed to zero. Initializing both memory streams to zero allows one to investigate learning of a novel environment. The simulations compare the three strategies according to the parameter values in Table 1.1. All strategies are compared across the landscape parameters of patch concentration, patch size, and regeneration rate. Additional parameters controlling the memory model are also varied for those simulations.

Landscapes

Landscapes are generated with a Gaussian random field (GRF) using the `RandomFields` R package (Schlather et al. 2014) to be 50 x 50 in size using an exponential covariance function with variance = 1, nugget = 0, and a set of mean (patch concentration, μ_Q) and scale (patch size, γ_Q) values (Fig. 1.1, Table 1.1). Differing amounts of patchiness are simulated by truncating all negative values to zero, so landscapes simulated with smaller mean values have more areas of no resources than landscapes simulated with larger mean values. Landscapes are normalized to sum to one so that the total resource amount remains the same across all landscapes even as the resource distribution differs. For each combination of μ_Q and γ_Q, twenty different landscape replicates were generated.

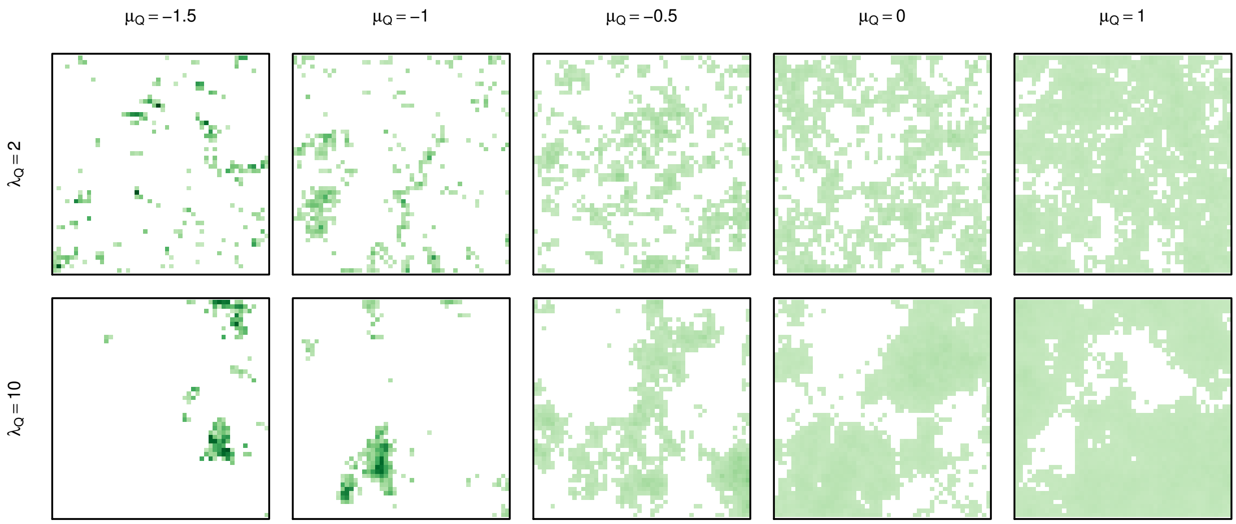

Figure 1.1: Sample generated landscapes for different combinations of patch concentration from patchy to smooth and patch size from small to large. Color indicates resource quality from none (white) to low (light green) to high (dark green). Total resources in each landscape are the same.

The GRF mean parameter, or *patch concentration*, controls how concentrated resources are in space along a gradient from patchy (landscapes of very concentrated, high-value resources amongst mostly no resources) to smooth (landscapes of lower-value resources with few areas of no resources). The GRF scale parameter, or *patch size*, controls the relative size of patches in the generated landscape along a gradient from small discontinuous patches to large continuous patches. The GRF scale parameter controls the scale of the spatial autocorrelation in the generated field. The effect is to vary the patch size since a larger scale value results in spatial autocorrelation at larger distances and thus larger patches once negative values are removed. Note that the parameters are not completely orthogonal. For a given scale value, patch size will still vary with the mean value, i.e. patchier landscapes have smaller patches than smooth landscapes. Similarly, for a given mean value, patch concentration will still vary with the scale value, i.e. more concentrated patches when patches are smaller versus larger.

The boundaries are reflecting boundaries, meaning for any step that would exit the habitat, the velocity is reversed so that the animal travels away from the boundary. In addition, the μ vector is reset on hitting a boundary.

Numerics

For the purpose of simulating the model, the continuous variation in habitat quality is discretized onto a grid. Intrinsic and current habitat quality are tracked for each grid square for each time step Δt. Time is simulated as regular intervals (taking a small Δt to approximate dt, with the requirement $\Delta t < \tau$). If an event from the Poisson process that updates $\mu(t)$ occurs during the interval, then a new angle θ is selected at that interval. The differential equations described above are approximated using the Euler forward method. While this is a relatively simple method with comparatively larger errors, another source of error is the relatively large values of Δt (step size) and Δx (grid size) chosen to meet computational demands. Finally, the reflecting boundaries mean that paths will diverge regardless of time step size once trajectories hit a boundary since the exact time the reflection happens differs. However, using an infinite spatial domain was not computationally feasible nor necessarily ecologically realistic, given natural and artificial barriers to animal movement. This problem is compounded for the kinesis and memory movement processes because the exact moment of switching behaviors is also affected by the time step, and, in the case of memory, feeds back into the memory state.

Because the trajectories will diverge through time because of the issues with boundaries and behavior switching, space use was compared visually using the utilization distribution calculated with `kernelUD` in the `adehabitatHR` package (Calenge 2006) in R (R Core Team 2014). The three movement processes were simulated on a limited number of landscapes representing the four extremes ($\mu_Q = -1.5, \gamma_Q = 2$; $\mu_Q = -1.5, \gamma_Q = 10$; $\mu_Q = 1, \gamma_Q = 2$; $\mu_Q = 1, \gamma_Q = 10$), with one memory parameterization ($\phi_L = 0.001$, $\phi_S = 0.01$, $\psi_M = 2$, $\gamma_Z = 10$). For values of Δt (0.1, 0.5, 1, 2) were compared with three values of λ (0.5, 1, 2). Space use was similar though variable across combinations of Δt and λ for each combination of landscape and movement process (see Appendix A). Slightly more structure in space use was seen with smaller values of Δt and λ, particularly with kinesis and memory. However, the overall areas of intense use were similar. Despite these challenges, simulation modeling can still provide insight into the system dynamics even though the approximations are necessarily coarser than ideal.

Metrics

Analysis of model outputs is done with R (R Core Team 2014). Simulations are evaluated primarily based on total consumption, the sum of the forager's consumption (Eq. 1.2) over the simulation. To track habitat usage differences among movement processes and simulations, the amount of time spent in areas of zero resources and the four quartiles of resource distribution are tracked. Additionally, for kinesis and memory movement processes, time spent in each behavioral state, searching and feeding, is tracked.

To evaluate the contribution of different parameters in the memory model, random forests are used to compute a statistic of relative importance for each parameter (Breiman 2001) using the `party` R package (Strobl et al. 2007). An advantage of random forests is that they are robust to nonlinearity and complex interaction effects (Strobl et al. 2007). The method first permutes one of the predictors (thereby removing the potential association between that predictor and the response), then generates random forests (a set of classification trees fit to bootstrap samples drawn from the original), and compares the prediction accuracy of the permuted and unpermuted predictor. Because the parameters are continuous in the model, but simulations were only run for certain specified values, the random forest analysis is done for treating parameters as continuous and categorical variables.

1.3 Results

1.3.1 Foraging efficiency

Differences in simulation trajectories for each movement process in terms of space use, which translate to differences in consumption, are apparent (Fig. 1.2). Even averaging over all memory parameterizations and landscapes, memory (consumption mean = 0.48, s.e. = 0.32) outperformed kinesis (consumption mean = 0.34, s.e. = 0.13) and random walk (consumption mean = 0.19, s.e. = 0.03). While total consumption was higher for memory, there was also more variability across simulations, even for the same landscape parameters. However, the increased variability with memory was generally towards improved performance: the lower performing memory simulations generally outperformed most kinesis simulations. In fact, every combination of memory parameters outperformed kinesis for consumption averaged across all landscapes. When matching simulations (i.e., comparing a memory parameterization to kinesis or random walk, matching simulations by landscape and regeneration rate), the performance of the 252 parameterizations of memory ranged from outperforming 97–100% of random walk simulations and 64–97% of the kinesis simulations.

However, landscape characteristics affect how much benefit memory provides (Fig. 1.3). In more patchy environments (negative μ_Q), memory (using the best overall parameterization across all landscapes) strongly outperformed kinesis, which in turn out performed random walk, but the effect weakened as the landscapes become smoother (positive μ_Q). Patterns held across regeneration rates, but were strongest for higher regeneration rates. Mean consumption values remained constant across landscape parameterizations for random walk, increased with only increasing patch concentration for kinesis, and increased with both increasing patch concentration and size (γ_Q) for memory. Variability across simulations also increased for all movement processes with increasing patch concentration and size (i.e., landscapes with fewer larger patches). Even with increased variability in landscapes with high-value and/or large patches, the minimum memory consumption was higher than the maximum random walk and generally higher than or close to the mean kinesis value.

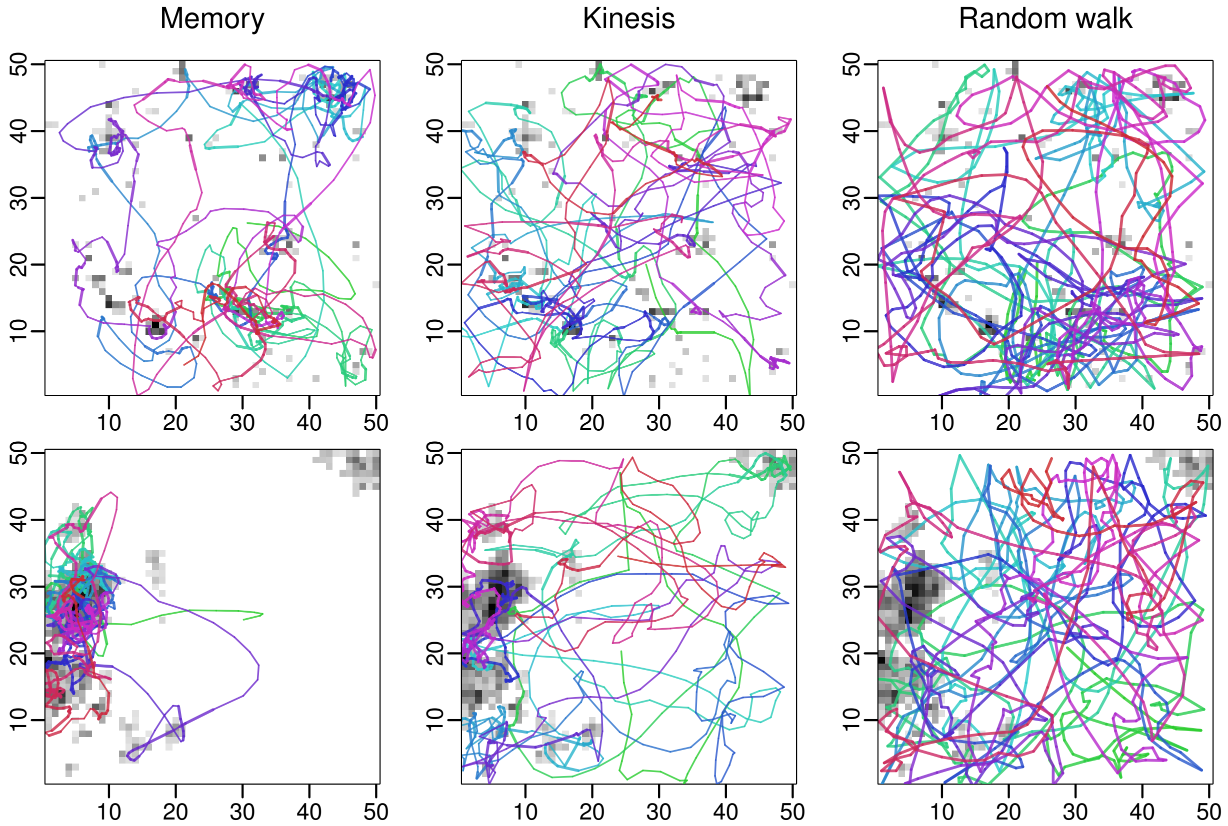

Figure 1.2: Sample trajectories for the memory (left), kinesis (center), and random walk (right) movement processes on a landscape with $\mu_Q = -1.5$ and $\gamma_Q = 2$ (top row) and 10 (bottom row). Trajectories start at the center with color changing through time (green, blue, purple, magenta). For memory and kinesis, thinner lines indicates searching and thicker lines indicates feeding behavior. Resources are shown at their undepleted level at the beginning of the simulation. Memory is parameterized with best overall parameters, $\phi_L = 0.001$, $\phi_S = 0.01$, $\psi_M = 2$, $\gamma_Z = 10$.

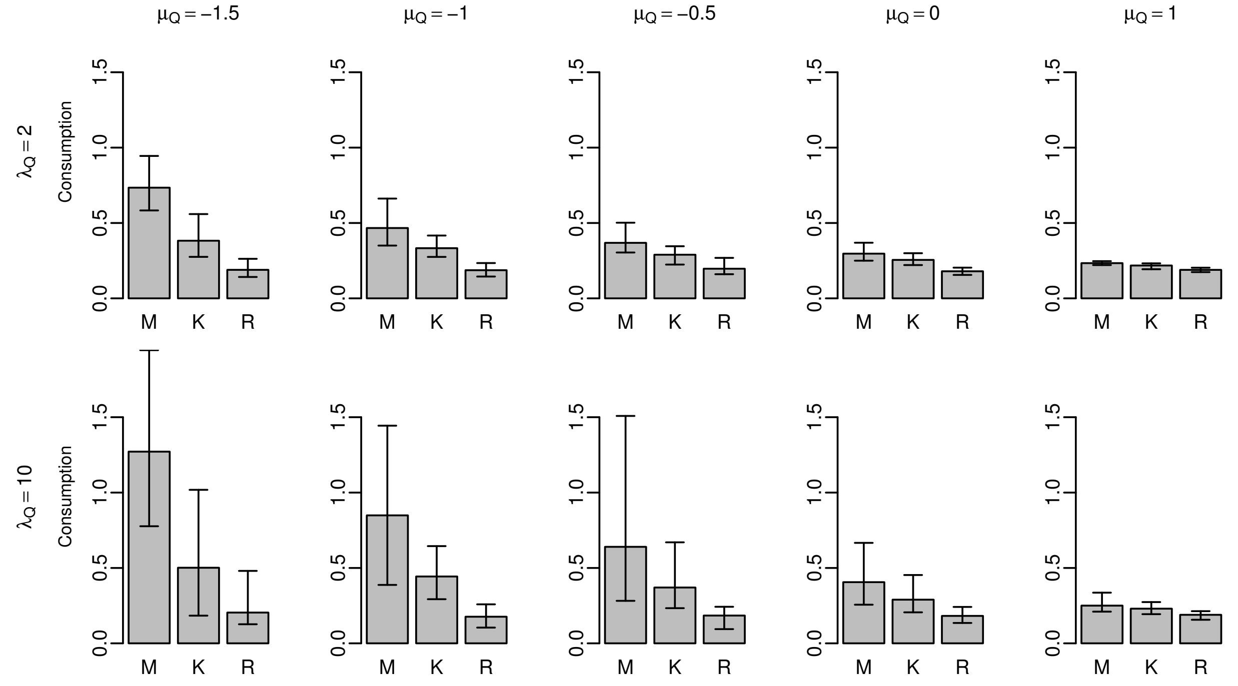

Figure 1.3: Consumption for the three movement models across different landscape parameters patch concentration μ_Q and size γ_Q for medium regeneration rate $\beta_R = 0.01$. Bars show mean consumption values across replicates of landscape parameters while lines show minimum and maximum. Memory is parameterized with best overall parameters, $\phi_L = 0.0001$, $\phi_S = 0.01$, $\psi_M = 2$, $\gamma_Z = 10$. In the figure, M = memory, K = kinesis, R = random walk.

The above results were for a mean update time of $\lambda = 1$ for all movement processes, but simulations were run to compare updating the bias direction (whether from memory or random) more and less frequently. Changes in mean consumption with increasing λ were small (1% random walk, 1–3% kinesis, and 0–6% memory), but in the opposite direction for memory versus the randomly directed movement processes. While memory did best with more frequent directional input, random walk and kinesis both did best with less frequent input and thus more persistent movements.

1.3.2 Memory parameters

Another approach to evaluating memory is to examine how often and by how much memory outperforms kinesis when matching simulations by habitat parameters (Fig. 1.4). The clearest pattern emerges with memory spatial scale, with larger values outperforming smaller values almost exclusively. Faster short decay rates were generally better, with 0.1 and 0.01 the best performing, while the opposite was true for the long decay rates with 0–0.001 performing best. There is some clustering evident with the short memory factor as well. When comparing memory parameterizations for specific landscape parameterizations, the general patterns in parameter values still hold but the differences seen between kinesis and memory mirror Fig 1.3. In patchy environments with large patches ($\mu_Q = -1.5$, $\gamma_Q = 10$), memory outperforms kinesis 77–100% of the time with an increase in consumption of 49–165% over kinesis, while in smooth landscapes with smaller patches ($\mu_Q = 1$, $\gamma_Q = 2$), memory outperforms kinesis 37–95% of the time with an increase in consumption of only -2–8%.

Instead of looking for a single set of memory parameters with the highest overall consumption across different landscapes, the optimum memory parameter combination can be found for each landscape parameter combination (Table 1.4). While there is less variability within memory parameterizations than across movement processes, patterns still emerge. The short decay rate varies consistently with regeneration rate, with the optimum parameter combination tending to include ϕ_S of 0.01, 0.01–0.1, and 0.1–0.5 for slow, medium, and fast regeneration rates respectively. There is less consistency in the long decay rate, other

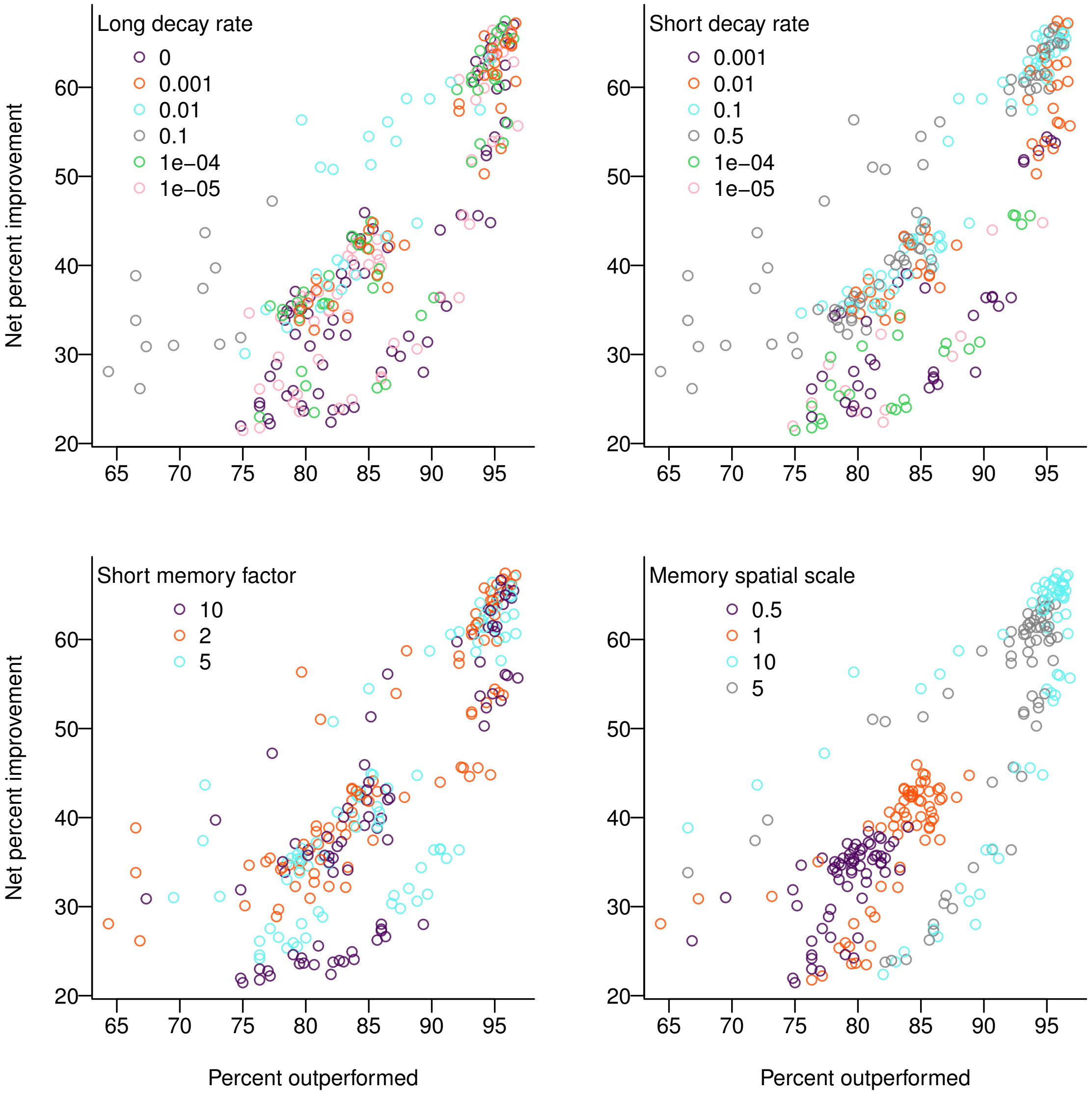

Figure 1.4: Percent of memory simulations that outperform kinesis and net amount of consumption gained using memory. Each point represents a parameterization of the memory movement process. Simulations are matched by landscape and regeneration rate. Percent outperformed shows the percent of simulations for which memory outperformed kinesis for that set of parameters. Net percent improvement shows how much consumption improves with memory over kinesis. It is the sum of the differences between that memory parameterization and kinesis for each simulation divided by the total consumed by kinesis across all simulations. Panels are each color coded by different memory parameters.

		$\beta_R = 0.005$				$\beta_R = 0.01$				$\beta_R = 0.05$			
μ_Q	γ_Q	ϕ_L	ϕ_S	ψ_M	γ_Z	ϕ_L	ϕ_S	ψ_M	γ_Z	ϕ_L	ϕ_S	ψ_M	γ_Z
-1.5	2	1e-04	0.01	2	10	1e-04	0.01	2	10	0.01	0.5	2	5
-1.5	10	0.001	0.01	5	10	0	0.01	2	10	0.01	0.5	2	10
-1	2	0.001	0.1	5	5	1e-04	0.5	5	10	0.01	0.5	5	10
-1	10	1e-05	0.01	5	10	1e-05	0.01	2	5	1e-04	0.1	5	10
-0.5	2	1e-05	0.01	5	10	0	0.1	10	5	0.01	0.5	5	10
-0.5	10	0	0.01	5	10	1e-04	0.1	10	10	0.01	0.1	5	10
0	2	1e-04	0.01	5	5	0.001	0.01	2	10	0.01	0.1	2	10
0	10	0.001	0.01	2	10	1e-05	0.1	5	10	1e-04	0.5	5	10
1	2	0.001	0.01	5	10	1e-05	0.01	10	10	0.01	0.1	2	5
1	10	0	0.01	10	10	1e-05	0.5	10	10	0.01	0.1	5	10

Table 1.4: Best performing memory parameters (ϕ_L, ϕ_S, ψ_M, γ_Z) for each landscape environment, a combination of regeneration rate (β_R), patch concentration (μ_Q), and patch size (γ_Q).

than it tends to be 0.01 for fast regeneration and less than 0.01 for slower regeneration rates. Interestingly, a long decay rate of 0 was selected for only a few combinations, even though resource stability means there is no obvious advantage to decaying the long-term attractive memory stream. Little pattern is apparent with the short memory factor in relation to the landscape parameters, although there appears to be an interaction between the short decay rate and the short memory factor. Larger short memory factors are associated with relatively faster short decay rates. Thus the short-term repulsive memory stream may similarly adjust the overall memory by either a lower weighting of a slowly decaying memory or a higher weighting of a faster decaying memory (Eqs. 1.4 and 1.6). Finally, a value of 10 is favored for the memory spatial scale, meaning a weaker discounting by distance giving more weight to distant patches is preferred.

Comparing variable importance in explaining the differences in consumption, landscape parameters dominate memory parameters (Table 1.5). A conservative rule of thumb to interpret variable importance values is that a variable is informative if its value is greater than the absolute value of the lowest negative value, as irrelevant predictors will randomly

Parameter		Variable importance
μ_Q	landscape patch concentration	1.07e-01
γ_Q	landscape patch size	3.43e-02
β_R	regeneration rate	1.19e-02
ϕ_S	short decay rate	5.19e-03
γ_Z	memory spatial scale	3.52e-03
ψ_M	short memory factor	4.30e-04
ϕ_L	long decay rate	1.61e-04

Table 1.5: Permutation importance scores (mean decrease in accuracy) calculated using random forests for the memory movement process. Results shown treat parameters as continuous variables. Results were similar when parameters were treated as categorical.

vary around zero (Strobl et al. 2009). All parameters had positive variable importance values. Of the landscape parameters, patch concentration is the most important, followed by patch size and regeneration rate at a similar order of magnitude. For the memory parameters, the short decay rate was most important, followed by memory spatial scale at a similar order of magnitude, then short memory factor and long decay rate. Long decay may only be important as a threshold (i.e., just needs to be slow enough), and the bulk of the observations were for smaller long decay rates since the long decay rate must be smaller than the short decay rate.

1.3.3 Behavior

Differences in habitat usage are apparent across the three movement processes and different landscape parameterizations (Fig. 1.5), mirroring the differences observable in individual trajectories (Fig. 1.2). The amount of habitat with zero resources, and thus the remaining area that each quartile of resource quality occupies, varies with patch concentration, from nearly all area having zero resources ($\mu_Q = -1.5$) to nearly all area having some positive amount of resources ($\mu_Q = 1$). As expected, the habitat usage of the random walk matches the distribution of habitat on the landscape. With kinesis, merely by switching states based on consumption rate, the habitat usage is markedly biased towards areas of higher quality.

However, patch size, γ_Q, has no effect and the habitat usage for kinesis is similar across different values. Memory, on the other hand, results in even more time spent in better quality habitat that kinesis, and also differs by patch size as well as concentration. Memory is able to spend more time in better habitat for landscapes with fewer, but high-value, larger patches.

In addition to differences in habitat usage, memory spent less time searching on average than kinesis (Fig. 1.6). For kinesis, time searching decreased with smoother landscapes, that is, as the amount of area with some resources increased. Memory showed a very slight increase in time searching with patchier landscapes, but was generally consistent across differing patch concentration values. On the other hand, kinesis showed increasing variability with increasing patch size, but the median time searching was similar across scales. For memory, time searching decreased substantially with increasing patch size and variability was less impacted than for kinesis.

1.4 Discussion

In this chapter, I present a continuous-time, continuous-space foraging model that incorporates movement with directional preference based on a memory of habitat quality. The habitat memory is composed of two streams, a long-term attractive stream and a short-term repulsive stream, which the forager integrates across the landscape to probabilistically pick a direction. While the different movement processes perform similarly in smooth landscapes, patchier landscapes differentiate them. The concentrated resources in patchier landscapes are both harder to locate and of higher value once located, leading to memory outperforming random walk and kinesis. Similarly, foragers using memory also receive higher rewards with a faster regeneration rate and larger high-value patches, which also provide a stronger signal in memory. In general, landscapes that favor memory are those with higher rewards or higher difficulty for locating resources and are the places best-suited to look for evidence of memory-informed foraging behavior.

While many existing models have utilized a discrete random walk formulation of move-

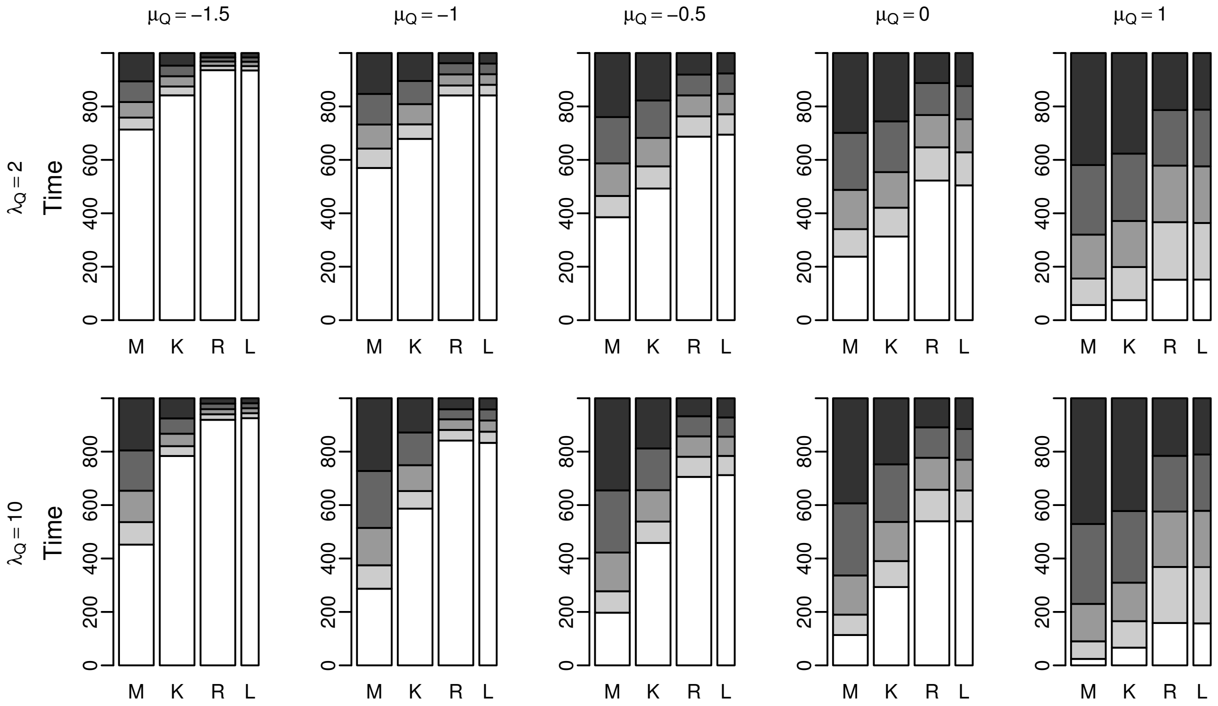

Figure 1.5: Time spent in areas of different resource quality across different landscape parameters patch concentration μ_Q and size γ_Q for medium regeneration rate $\beta_R = 0.01$ compared to the distribution of resources on the landscape. White represents zero resources while shades of gray from light to dark show quartiles of increasing quality. Memory is parameterized with best overall parameters, $\phi_L = 0.0001$, $\phi_S = 0.01$, $\psi_M = 2$, $\gamma_Z = 10$. In the figure, M = memory, K = kinesis, R = random walk, L = landscape.

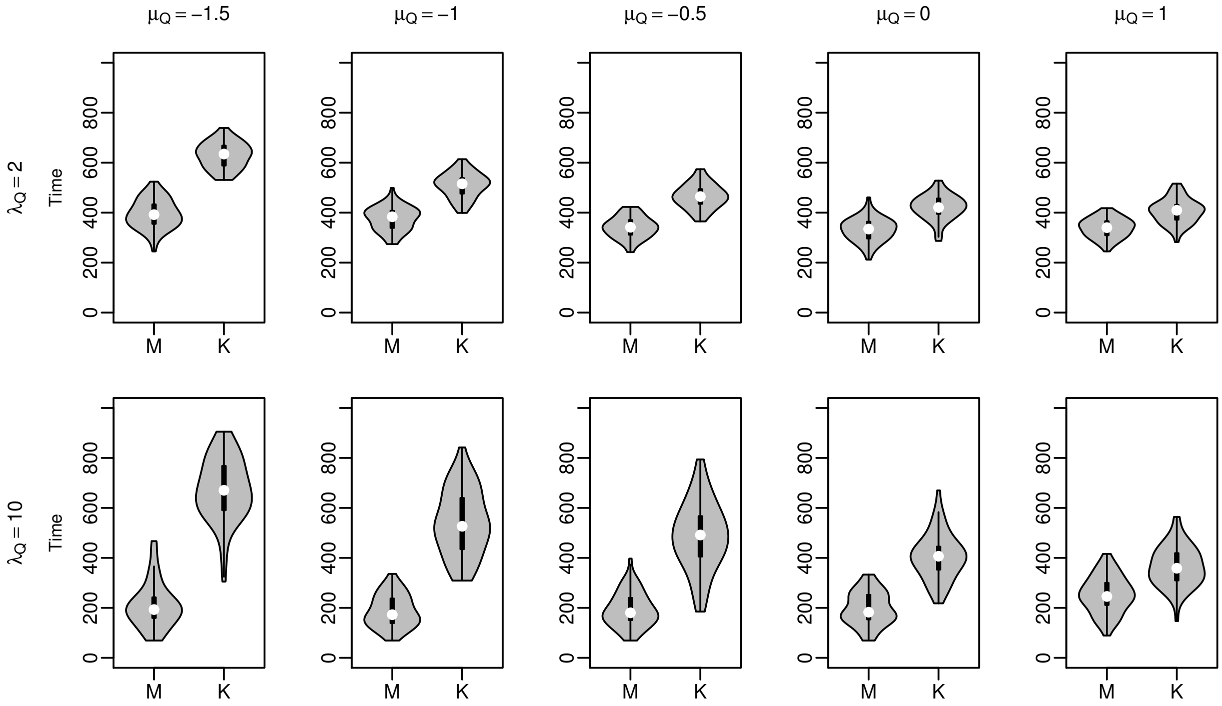

Figure 1.6: Time spent searching (as opposed to feeding) for memory and kinesis movement processes across different landscape parameter values for patch concentration μ_Q and size γ_Q for medium regeneration rate $\beta_R = 0.01$ as a violin plot showing median values and kernel density plot. Memory is parameterized with best overall parameters, $\phi_L = 0.0001$, $\phi_S = 0.01$, $\psi_M = 2$, $\gamma_Z = 10$. In the figure, M = memory, K = kinesis.

ment (e.g., Boyer and Walsh 2010; Mueller et al. 2011; Van Moorter et al. 2009), actual animal movements are a continuous process across a continuous landscape even though they are generally sampled discretely, and recent advances allow continuous movement processes to be parameterized from observed trajectory data points, even when sampled irregularly (Gurarie et al., in review). This also aligns with the push towards continuous-space formulations in spatial population models, which have the advantage of representing spatial heterogeneity from multiple sources and at multiple scales as well as easily associating observed trajectory data despite the mathematical complexity (Morales et al. 2010). The three movement processes modeled here are nested, so that the same underlying movement model is used and additional behavioral complexity, like switching states or using memory-informed directional biases, can be enabled or disabled within the same framework. This allows for better comparisons between movement processes for simulation studies and also for hypothesis testing if the model is fit to data. The memory implementation is both simple and conforms to current knowledge in animal cognition. Two memory streams are a common feature of cognitively-based ecological models (Kacelnik et al. 1987; Anderson 2002; Van Moorter et al. 2009; Anderson et al. 2010) and reflect evidence for multiple parallel memory systems which interact (Poldrack and Packard 2003; Kolling et al. 2012).

The degree to which consumption varied among the three movement processes depended on the landscape characteristics (Fig. 1.3). For smooth continuous landscapes that had a relatively even distribution of low resource levels, the different movement processes performed similarly. However, the patchier the landscape and the larger the amount of space with no resources, then the more that kinesis outperformed random walk and that memory outperformed both. With patchier landscapes, resources are both more difficult to locate and of higher value (due to the total amount of resources being constant across landscapes), thus raising the stakes for finding resource locations. In this situation, any tendency to slow down in the few higher-valued patches is an advantage, as seen by kinesis outperforming random walk, and memory further outperforms other movement processes by directing movement towards hard-to-find patches.

It is not just, however, landscape patchiness that is a factor in differing consumption across movement processes, but also the corresponding relative patch size. While concentration relates to resource scarcity and how high-value those patches are, patch size relates to how large and contiguous patches are (Fig. 1.1). That is, given a location with resources, what is the likelihood that nearby locations are more likely to also have resources of a similar quality. While both memory and kinesis increase their mean consumption differential over random walk with increasing patchiness (μ_Q), memory shows more dramatic improvement with increasing patch size (γ_Q) as well. Kinesis and random walk, on the other hand, mainly increase consumption variability (as does memory), and mean consumption for kinesis only slightly improves in landscapes with relatively larger patches. The underlying reason for this may be search times (Fig. 1.6). Kinesis shows the same mean time searching with increasing patch size, but increased search time variability, which matches consumption differences over those landscape parameters. Memory, however, shows a decrease in search time with increasing patch size, as memory is better able to exploit the larger, more contiguous patches and spend less time traveling between them. Interestingly, with memory, consumption variability increased with patch size, but search time variability did not. For kinesis, larger, more contiguous patches are only slightly advantageous, though variability increases because encounters become more unpredictable compared to many smaller patches. Memory, however, is able to exploit larger patches more efficiently. Larger patches give a stronger signal to the probabilistic direction (Eq. 1.8), and memory is easily able to return to a large patch after wandering off, while kinesis does not.

The spatial scale of memory is also, presumably, related to patch size. Larger values of spatial scale generally performed better, reflecting an advantage to considering food farther away, and providing the ability to make movements towards distant locations noted by Smouse et al. (2010). However, the few landscapes where smaller values of spatial scale were preferred nearly all had smaller-sized patches (Table 1.4). This may be because smaller patches have a smaller signal in memory, making it is advantageous to weight closer resources higher, as well as distant patch being too small to be worth the travel time. Patch size may also relate to a forager's perception abilities, which were not considered here, though other studies (e.g., Mueller et al. 2011) have explicitly modeled perception. Including perception would likely amplify this effect, as more discontinuous patches would be harder to detect and exploit.

Finally, landscape regeneration rate also affects each movement process differently. With higher regeneration rates, differences are more apparent, as there is a stronger reward for returning to patches, favoring memory. With slower regeneration rates, even a random walk can consume the bulk of the resources if the simulation lasts long enough (consider the extreme case of a zero regeneration rate, so that all three movement processes would eventually consume all the resources). Landscape regeneration rate has the biggest effect on the optimal parameterization of the memory model (Table 1.4), with the short-term decay rate ideally increasing as the regeneration rate increases, thus returning the animal to productive patches once enough time has elapsed for them to regenerate. This suggests that animals may track an assessment of the lag time to return to a patch (represented here as the short-term decay rate). This assessment may be inherited or learned based on environmental conditions. However, memory still generally outperforms the other movement processes at non-optimal decay rates in patchy landscapes, suggesting that memory using a single short-term decay rate could be robust to regeneration rates varying seasonally or among resource types.

Thus, these landscape characteristics paint a picture of the types of landscapes where memory would be especially favored over a random walk or even a sensory-driven process like kinesis. In general, a landscape where there is a larger payoff for finding a resource patch, whether in size, value, of difficulty in locating, favors memory. These landscapes would consist of sparse, contiguous patches of high-value resources that regenerate quickly located on a space that was mostly devoid of resources. These then are they types of landscapes one should look to when considering the evolutionary aspects of memory, or when seeking evidence for memory-driven search behavior today. In general these match what has been predicted by other models, even when the conception of memory is very different (e.g., Grove

2013). The conclusion that memory is more useful for lower patch density (Grove 2013) is analogous to the result here for patchier landscapes (those with more zero resource area). In contrast, the previous finding that larger patches decrease the utility of memory (Grove 2013), is less directly comparable, as patch size was increased while maintaining patch density and quality. However, the qualitative conclusion that memory is less useful when patches are more easily discoverable without it is supported. Avgar et al. (2013) suggest that memory should be limited only by physiological constraints in an unchanging environment, but that in a temporally changing environment, forgetting is adaptive and memory capacity should negatively correlate with the rate of change. In these simulations, the available amount of resources varied temporally (though intrinsic quality did not), and the short-term memory decay rate, that is the rate of forgetting, did track the rate of environmental change as represented by the regeneration rate. However, it has been suggested that the utility of memory in high complexity landscapes is reduced due to the high cost of tracking sufficient information (Fagan et al. 2013). Memory costs were not explicitly modeled here, as I took the approach of Grove (2013) that memory must outperform naive or sensory-driven processes to be useful. An interesting extension of this work would be to model memory at different spatial resolutions and determine if an increasing cost for more detailed memory would produce the dome-shaped relationship between memory utility and resource complexity suggested by Fagan et al. (2013).

While evaluated separately here, the differing landscapes could also be thought of as different habitats an animal encounters throughout its life history. For example, different resource distributions could represent the differences between feeding and breeding habitats that an animal migrates between or the seasonally varying differences between summer and winter habitats. In this case, the total amount of resources may also differ, but the general conclusions in terms of the relative performance of different movement processes would still hold. Thus, it may be that memory is most useful in times of resource constraint, such as hard-to-find winter forage, after a habitat perturbation (e.g., Preen and Marsh 1995), or during times of more limited mobility, such as the breeding season. For example, ungulate species on the Isle of Rhum, Scotland all foraged on high-quality, high-biomass areas in the summer during high resource availability, but showed resource partitioning during the winter (Gordon and Illius 1989). The decimation of foraging habitat caused by a cyclone and floods led to changes in dugong (*Dugong dugon*) distribution in the area as well as emigration to other areas (Preen and Marsh 1995).

When looking for systems in which to apply this model, necessary data include heterogeneous resources for which a measure of resource quality (not simply habitat type) is available and movement trajectories of the foragers. One possibility is dugongs foraging on seagrass beds. Seagrass meadows are patchily located in coastal waters, and the meadows themselves are spatially heterogeneous in quality based on biomass density and species composition (Sheppard et al. 2007). Dugongs have been observed to revisit grazing locations and the revisit time has been observed to correlate with regeneration to ungrazed capacity (Preen 1995). In fact, dugong grazing pressure shapes community structure by creating favorable conditions for preferred species, a process known as cultivation grazing (Preen 1995; Aragones et al. 2006). Another possibility is Mongolian gazelles (*Procapra gutturosa*), a wide-ranging species (Olson et al. 2010), for which satellite-derived measures of habitat quality are available (Mueller et al. 2008). Movement processes could by compared by simulating a model trajectory step-by-step based on an animal's trajectory and comparing the actual step with the likelihood of each movement process given the animal's history up to that point.

In conclusion, the model presented here is a robust framework for considering memory in a continuous-space and continuous-time movement model that could be applied to a variety of systems. These results suggest that the best habitats to look for evidence of memory-driven search would be those with concentrated contiguous patches with faster regenerating resources. While separating memory-driven foraging from sensory-driven alternatives is difficult (Fagan et al. 2013), disproportionate space use of higher value areas, higher consumption rates, and consumption variability all point to memory influencing the movement direction.

Chapter 2

INVESTIGATING THE EFFECT OF MEMORY ON PREDATOR–PREY INTERACTIONS

Abstract

Predator–prey interactions are central to fitness as animals seek to avoid death while simultaneously feeding sufficiently to ensure growth and reproduction, thus managing a food–safety trade-off. Predators can also exert strong non-consumptive effects, as prey engage in antipredator behavior such as shifting habitat use. While models of predator–prey dynamics exist, the impact of cognition on movement and predator–prey interactions is largely unexplored despite evidence of learned responses to predation threat. Here, predators are introduced that relocate based on their persistence and that vary spatially in their correlation with the prey's resources. With memory-informed movement, foragers learn from predator encounters as well as resource quality. They balance attraction to food with repulsion from predators in making movement decisions. Memory outperforms simpler movement processes most for patchy landscapes and more predictable predators, which may be more easily avoided once learned. In these cases, memory aids foragers in managing the food–safety trade-off, as particular parameterizations of predator memory reduce predator encounters while maintaining consumption. Non-consumptive effects are highest in landscapes of concentrated, patchy resources and especially when predators are highly correlated with the forager's resources. While smooth landscapes provide more opportunities to consume resources and avoid predators, predators are able to effectively guard all resources in very patchy landscapes. These non-consumptive effects are also seen with the shift away from the best quality habitat compared to foraging in a predator-free environment.

2.1 Introduction

The most obvious effects of predation are consumptive or, in other words, the killing of prey by predators. However, predators can also affect prey behavior, such as movement and habitat use, leading to non-consumptive effects (Lima 1998; Werner and Peacor 2003), which can be as strong or stronger than consumptive effects (Preisser et al. 2005; Cresswell 2008). In fact, even in classic examples of predator–prey dynamics traditionally quantified through changing densities, non-consumptive effects have been shown to be important (Peckarsky et al. 2008). For example, in lakes with a simple four-species food web, habitat shifts due to predation risk can reverse the effect expected from consumption-driven trophic cascades (Carpenter et al. 1987) or amplify the magnitude of the effects of predators on their prey (He and Kitchell 1990).

Prey may alter their behavior to balance the trade-off between foraging and predation risk in many ways including increasing vigilance, spending more time in refuges, changing habitat use, and changing grouping behavior. Observing these responses, while varying predation risk, can provide a better measure of the effects of predation than mortality alone (Brown and Kotler 2004). For example, while predation of marine mammals is rarely observed, marine mammals give up foraging opportunities and spend less time in high-reward patches in the presence of predators (Wirsing et al. 2008). Predation affects microhabitat selection by prey (Main 1987; Pierce 1988). Prey preference shifts away from higher productive ares in the presence of predators (Hammond et al. 2007).

How prey change their movements in response to predation can depend on the scale considered. When prey are in the immediate vicinity of predators, reducing movement can be an antipredator behavior (Lima and Dill 1990). At larger scales, on the other hand, movement can be advantageous as prey seek to relocate to avoid predators (Mitchell and Lima 2002). Brown et al. (1999) investigated the impact of consumptive and non-consumptive effects on the stability of predator–prey systems by using game theory to model predator–prey dynamics. They found that introducing fear through increased vigilance that reduces prey foraging generally stabilizes otherwise extinction prone predator–prey systems by allowing predators to be efficient at low densities but inefficient at high densities. Non-consumptive effects (the 'ecology of fear') therefore explain why big fierce carnivores are rare (Brown et al. 1999). Applying a game theoretic approach to predator and prey spatial distribution across patches that differ in productivity and riskiness showed that prey distribution was solely dependent on patch riskiness, while the predator's distribution was determined by both riskiness and productivity (Hugie and Dill 1994). This implies that changing resource levels may not affect prey distribution if predators are free to relocate (Hugie and Dill 1994), though in this case both predators and prey had perfect information on each other's distributions.

Risk encapsulates one of the key trade-offs prey make in a predator–prey relationship, balancing the competing goals of consuming enough food to avoid starvation (as well as grow and reproduce) yet also avoiding predation. Risk is not invariant in space when predators can move across the landscape (Lima 2002). One way to quantify predation risk is through measures of predator avoidance, with examples ranging from snails (Turner et al. 2006) to insects (Sih 1982) and fish (Neill and Cullen 1974; Magurran and Seghers 1990), many of which indicate a learned response. While there is a wealth of information on animal learning (Pearce 2008), memory and cognition have frequently been omitted from predator–prey interactions. For example, models have assumed predators and prey had perfect information on each other's distributions (e.g., Hugie and Dill 1994) or that animals have perfect or imperfect knowledge of local conditions (e.g., Brown et al. 1999; Persson and De Roos 2003).

However, simple models of learning and memory have been incorporated into an agent-based model of foraging (Anderson 2002) as well as a model of home-range formation (Van Moorter et al. 2009). Despite memory having been shown to be important to explaining aspects of foraging behavior, it has generally been omitted from predator–prey models. Modeling of memory-based movement, complete with managing multiple potentially competing goals, is one of the open challenges in studying spatial memory and animal movement (Fagan et al. 2013).One approach is to maintain multiple layers for different habitat components, such as resource quality or predation risk (Avgar et al. 2013). Given the enormous span of cognitive abilities ranging from single-celled organisms to wide-ranging forager to apex predators, this raises the question of what advantages cognitive complexity brings and in what circumstances is it most effective.

Including memory in models of predator–prey interaction provides a method to investigate these questions, which are difficult to do experimentally since memory cannot be measured directly. It is plausible to assume memory could affect these dynamics given research on memory and foraging behavior (Kamil and Roitblat 1985; Shettleworth 2001; Stephens et al. 2007) and the higher consequences for poor decisions in the context of predation compared to foraging. Animals can learn negative stimuli faster and retain those memories longer (Quirk 2002; Wiedenmayer 2004; Ferrari et al. 2006). Avoidance of areas of high predation risk is one antipredator strategy (Lima and Dill 1990) and can imply spatial learning. For example, stickleback (*Culaea inconstans*) continue avoid areas after the predator cue is removed though they will eventually return to those areas (Wisenden et al. 1994).

The goal of this chapter is to investigate the effect of memory on the food–safety tradeoff foragers must make under the risk of predation. We do this with a spatially explicit continuous-time, continuous-space model of forager behavior with predators as a dynamic component of the system (Lima 2002). Three movement processes are compared: a random walk, kinesis (a two-state random walk), and memory-informed movement. With memory, the forager learns about food resources and encountered predators, combining both pieces of information to make movement decisions. The predator environment encompasses the predator's correlation with the forager's resource and the predator's predictability in time. The resulting movement behavior of the forager is analyzed to address several questions: (1) are there predator or landscape environments where using memory is particularly useful compared to alternatives, (2) how do characteristics of the predators affect the parameterization of memory, and (3) what non-consumptive effects can be observed by comparing foraging with and without predation?

2.2 Methods

When adding predation to the foraging model (Chapter 1), foragers have two competing objectives: obtaining food and avoiding predators. The foraging model encompasses the regenerating resources consumed by foragers moving according to one of three movement processes: memory, kinesis, and random walk. Resources regenerate logistically to a maximum intrinsic quality that varies spatially but not temporally. Foragers consume resources in their vicinity according to a spatial kernel. Foragers move according to an autocorrelated, directed, continuous movement process. For random walk, this is a single-state process with the bias vector set randomly. For kinesis, foragers switch between a slower, more tortuous feeding state and a faster, more linear searching state based on their consumption rate with the bias vector still set randomly. For memory, foragers switch between feeding and searching states, and the bias vector is set probabilistically based on the forager's spatial memory of the resources. The memory consists of attractive and repulsive streams that decay at different rates, serving to drive the forager away from recently visited, depleted areas but return them to high-quality area that have regenerated.

To extend the model to include predation, several pieces were added. For all three movement processes, a new escape behavior sends the forager in the opposite direction when encountering a predator. When using memory, the foragers now also learn about predators in a separate predator memory stream. Foragers use that information to asses safety from predation and combine it with the resource memory to inform movement direction.

Rather than explicitly modeling the movement and learning of predators, they are represented as a Poisson process. That is, the predator appears at a particular location, remains there for a period of time, then disappears. The predators can thus be thought of as sit-and-wait predators or predators with a small home range corresponding to the encounter radius. The length of time the predator remains therefore represents the activity time or time before relocating, and the 'movement' of the predator is increased by decreasing the predator duration. While random movement is a simplistic assumption, it is important to remember that random movement can be an adaptive strategy if it is advantageous for a predator to appear unpredictable (Roth and Lima 2007). Additionally, sit-and-wait and sit-and-pursue predators induced stronger non-consumptive effects including changes in prey activity compared to wide-ranging actively hunting predators (Preisser et al. 2007), suggesting this predator hunting mode is well-suited for examining the effects of forager memory.

2.2.1 Predators

Predator presence is modeled as a Poisson process in time and space with two main tunable parameters: predator persistence (duration) and predator spatial randomness (space use). Predator persistence refers to the length of time a predator remains after appearing and affects the forager's likelihood of subsequent encounters with a predator after learning about it. Predator spatial randomness refers to the extent to which the distribution of predators is correlated with the resource distribution, which affects the degree of trade-off a forager must make.

The location of the predator appearances is a spatial Poisson process. For random predators, this is simply a random location in the landscape using a homogeneous Poisson process. To increase the food–safety trade-off, predators are more likely to appear in areas of high quality food which is accomplished using an inhomogeneous Poisson process. A parameter ρ controls the transition from random predator appearances in space to predator appearances proportional to resource quality. Thus, for random predators, the intensity of the spatial generation process at all points is uniform, while for non-random predators, the intensity of the process is proportional to landscape quality at that point, $Q_0(z)$. The parameter ρ controls the shift between these two extremes with $\rho \in (0, 1)$ for the intensity function used to generate predator locations,

$$\lambda_p(z) = \rho \bar{Q_0} + (1 - \rho) \frac{Q_0(z)}{\max\limits_{z} Q_0(z)}, \tag{2.1}$$

where $\bar{Q_0}$ is the average habitat quality.

Thus, two parameters govern the predator environment that the foragers experience: predator duration, $\delta = \Delta t$, or the predator's predictability in time, and predator spatial randomness, ρ, or the predator's predictability in space. Note that this formulation does include predator movement. The predator's movements are unaffected by the foragers, though the model could be extended to allow for this possibility.

Escape behavior

The escape behavior when encountering predators is the same across all three movement processes. In the case of a single predator encounter, the velocity V is instantaneously and discontinuously changed at the moment of encounter to be directly away from the predator. The angle is given by $\angle(Z - Z_p)$, where Z is the forager's location and Z_p is the predator's location, and the speed by ν (recall that ν is the magnitude of the μ bias vector, Chapter 1, Eq. 1.7). In the case of multiple predators encountered simultaneously, the escape angle is the sum of the angles away from the i predators weighted by distance, i.e., $\angle V = \sum_i \angle(Z - Z_{p,i})/||Z - Z_{p,i}||$ and the speed is ν still. Further, there is no consumption when escaping a predator.

2.2.2 Predation risk learning

Foragers using the memory movement process must now store information on predators in addition to resource quality, which is accomplished by adding another layer for predator memory in addition to a layer for resource quality. The memory for predator encounters only requires a single stream, in contrast to the resource memory with its short- and long-term memory streams, as the function of the predator memory is always repulsive. The forager learns about predators in its vicinity, and this memory decays with time. Similar to the resource memory, where the memory decay rates are related to the resource regeneration and persistence time scales, the decay rate for the predator memory is presumably related to the predator persistence and predictability in a location.

The predator memory and resource memory are maintained in parallel in separate layers. This approach was suggested by Fagan et al. (2013) as a way to deal with multiple objectives, such as finding food and avoiding predation. In addition, a similar approach of multiplicatively combining multiple layers was used by (Avgar et al. 2013) to calculate a redistribution kernel to model an animal moving discretely in time and space with a biased random walk. Experimental evidence also suggests that foraging and defensive behaviors are likely independent, such as the lack of correlation in response thresholds for positive and negative stimuli (sucrose and shock in honeybees) in the same individual (Roussel et al. 2009). The consequences of mistakes with aversive stimuli such as predator encounters are clearly higher than reward stimuli, and animals can learn predator threats after only one encounter (Wiedenmayer 2004; Ferrari et al. 2006). Fear-conditioned responses tend to be long-lasting (Quirk 2002).

Specifically, the forager detecting the predator is a boolean event, $E(t)$, depending on whether a predator is present in the forager's encounter radius ϵ, $E(t) = I(|Z_p - Z_f| < \epsilon)$, where Z_p and Z_f are the predator and forager locations respectively and I is the indicator function. If the forager detects a predator, it learns about the predator with a spatial kernel centered on the predator's location. While this is currently implemented deterministically (any predator within the encounter radius is detected), it could also be probabilistic, with the detection probability determined by the distance between predator and prey or by the prey's vigilance level.

The equation governing the learning and decay of the predators by the prey is

$$\frac{\partial P}{\partial t} = \beta_P f_P(|z - Z|)(P_0 - P) - \phi_P P, \tag{2.2}$$

where β_P is the learning rate, f_P is the spatial kernel centered on the predator's location, and $P_0 = 1.0$ describes the maximum learning threshold. Because predators are a point location and are dangerous throughout their encounter radius, the kernel function for f_P is the top-hat kernel with length scale (i.e., radius) γ_P (Table 2.1). In these simulations γ_P is matched to the predator encounter radius. If multiple predators are encountered at the

Table 2.1: Spatial kernels used in the predation model.

Description	Equation
Predator learning kernel	$f_P(\lvert z-Z\rvert) = \begin{cases} \frac{1}{\pi\gamma_P^2} & \text{if } \lvert z-Z\rvert < \gamma_P \\ 0 & \text{otherwise} \end{cases}$
Predator safety kernel	$f_R(\lvert z-Z\rvert) = \frac{1}{\gamma_Z}\exp\left(\frac{-\lvert z-Z\rvert}{\gamma_R}\right)$

same time, they are treated additively (assuming no predator interference with one another or possible multiplicative effects). Note that learning rates greater than one are considered, reflecting the rapid learning of negative stimuli such as conditioned fear (Fendt and Fanselow 1999) and novel predator cues (Brown 2003).

Decision rules

How foragers combine their information on both resource and predator location gets to the heart of the food–safety trade-off. Here we take the approach that foragers are attracted in the direction of high-quality habitat as before, but that attraction is tempered by the perceived risk in that direction. We realize this trade-off by first calculating the resource probability distribution, $g(\theta)$, as in Chapter 1, Eq. 1.8. Next the predator risk is calculated similarly to the resource probability distribution by integrating transects of the predation memory map, P, radiating out from the forager's location with the memory value at each point weighted by a spatial kernel. The predation risk values are transformed into a predator safety metric, $p(\theta)$, which ranges between 0 (low safety) and 1 (high safety).

$$p(\theta) = 1 - \max(1, \int_0^r \psi_P P(r,\theta) f_R(r) dr) \tag{2.3}$$

where ψ_P is the predator memory factor, $r = |z - Z|$, and $f_R(r)$ is a distance-dependent two-dimensional kernel, here the exponential kernel with length scale γ_R (Table 2.1). This predator safety metric is also a circular function of θ with values in $[0, 1]$ but not a probability density function. Finally, the resource probability distribution is multiplied by the predator safety metric and re-normalized to create a new probability distribution that incorporates attraction to resources and aversion to areas where predators were previously encountered,

$$h(\theta) = \frac{g(\theta)p(\theta)}{\int_0^{2\pi} g(\theta')p(\theta')d\theta'}. \tag{2.4}$$

The angle of the bias term, $\mu(t)$, in the movement process is then drawn from $h(\theta)$ as described in the 'Behavior states' section of Chapter 1.

2.2.3 Simulations

Parameter values for simulations are shown in Table 2.2. Simulations were run for the three movement processes (memory, kinesis, and random walk) across landscape environments (the same landscapes as Chapter 1) and predator environments (δ and ρ). For memory, simulations were run across parameterizations of predator memory with resource memory parameters set according to the best performing values from Chapter 1.

The simulations were run across the environments defined by the resource parameters of μ_Q and γ_Q and the predation parameters δ and ρ. However, in order to avoid escape behavior sending foragers outside the landscape boundary, an empty border with no predators or resources was added around the landscapes. Because the escape behavior is simple, it is possible for a forager to be stuck between predators, escaping one only to encounter the other, and repeat. In order to avoid biasing the results with the resulting large number of encounters, simulations were restarted with a new random seed if there are five or more repeated encounters.

Encounters happen deterministically within an encounter radius, ϵ. The total number of encounters during the simulation was tracked, but the simulation was never terminated early due to encounters. Encounters are thus dynamic, non-destructive, and hard (Gurarie and Ovaskainen 2013). The highest fitness would come from high consumption and low encounters, while the lowest fitness would come from low consumption and high encounters. A quantitative measure of fitness was computed as consumption $* \, s^{\text{encounters}}$ where s is the survival rate. Two survival rates were compared for a high and low probability of a forager surviving an encounter with a predator. The fitness metric collapses the competing trade-offs

Table 2.2: Parameters used in the predation model and values for simulations. Because units are arbitrary in the simulations, L is used for generic length units and T is used for generic time units.

	Parameter	Definition	Units	Values
Simulations				
	Δt	model time step	T	1
	T	simulation length (time steps)		1000
Landscapes				
	μ_Q	patch concentration		-1.5, -1, -0.5, 0, 1
	γ_Q	patch size		2, 10
Predator environment				
		total predation pressure	T	5000
	δ	predator duration	T	10, 300, 1000
	ρ	predator spatial randomness		0, 0.5, 1
	ϵ	encounter radius	L	5
	s	encounter survival rate		0.8, 0.99
Consumption				
	β_R	regeneration rate	1/T	0.01
	β_C	consumption rate	1/T	1
	γ_C	consumption spatial scale	L	1
Memory[a]				
	ψ_M	short-term memory factor		2
	β_L, β_S	learning rates	1/T	1, 1
	ϕ_L, ϕ_S	decay rates	1/T	0, 0.01
	γ_L, γ_S	learning spatial scale	L	1, 1
	γ_Z	memory spatial scale	L	10

[a] L = long-term memory, S = short-term memory

Table 2.2: (continued)

	Parameter	Definition	Units	Values
Predator memory				
	ψ_P	predator memory factor		1, 10, 100
	β_P	predator learning rate	1/T	1, 10, 20
	ϕ_P	predator decay rate	1/T	0, 0.001, 0.01, 0.1
	γ_P	predator learning spatial scale	L	5
	γ_R	predator risk spatial scale	L	1, 10, 20
Movement[b]				
	τ_S, τ_F	autocorrelation time scale	T	4, 2
	ν_S, ν_F	length of μ	L/T	6, 1
	λ	mean time to update θ	T	1

[b] S = searching, F = feeding

of maximizing consumption and minimizing predator encounters but depends additionally on defining the survival rate.

Predator generation

A set of predator appearance times and locations was generated for each combination of δ, ρ, and landscape (and also depends on total simulation time T and total predation pressure which were not varied). These predator sets were cached across simulations so that different parameter combinations and movement processes experience the same predator environment.

When changing predator duration, constant predation pressure across simulations was maintained by altering the number of predator appearances, such that total predation pressure was $\sum_{i=0}^{p} \Delta t$, where there are p predator appearances that each last $\delta = \Delta t$ amount of time. The Poisson process has the property that given an interval $(0, t)$ and the number of arrivals in the interval $N(t) = n$, then the n arrivals are uniformly distributed on the interval. While in a Poisson process the number of arrivals is Poisson distributed (i.e., $N(t) \sim \text{Poisson}(\lambda t)$), in order to maintain constant predation pressure, the number of predator appearances p was set based on δ (thus a quasi-Poisson process). Then p predator appearance times were independently drawn from the uniform distribution on the interval $(0, T - \delta)$ where T is the total amount of time in a simulation. Altering the predator duration δ moved the predator appearances along the gradient from persistent to ephemeral.

The predator spatial randomness is controlled by transitioning between a homogeneous and inhomogeneous Poisson process when generating spatial locations. One way to simulate an inhomogeneous Poisson process with an intensity function (Eq. 2.1) that varies over a surface (the two-dimensional landscape in this case), is to simulate a homogeneous process with an intensity equal to that of the maximum intensity of the surface. Random appearances (i.e., a homogeneous process) can be simulated with the algorithm by having the probability of location retention be uniform across the landscape. The simulated points are thinned using a retention probability equal to the intensity at that point divided by the maximum intensity. I applied this method by creating a probability surface for the grid points in the landscape. For each of the p predator appearance times, a location was generated by sampling the x and y coordinates independently from a uniform distribution. The location was retained with probability corresponding to the grid square in which it is located (see Eq. 2.1). This process was repeated until a location is accepted for that appearance time.

2.3 Results

2.3.1 Comparing consumption and encounters

Overall, predator environment strongly affects both consumption and encounter rates, though more so for memory than other movement processes (Fig. 2.1). Predator predictability affects predator encounters with more encounters for ephemeral predators ($\delta = 10$) compared to more stationary predators ($\delta = 300, 1000$). Consumption decreases as predators become more correlated with resource abundance with increasing spatial randomness (ρ).

Random walk is relatively less sensitive to both predator and landscape environment. When predators are correlated with the resource ($\rho = 0$), there is some food–safety trade-off with lower consumption and encounters for landscapes with large high-value patches and vice versa for landscapes with smaller patches. The interaction of predators co-located with food resources that are more diffuse (smaller patches) is necessary to produce the trade-off across landscapes with a random walk. Whereas encounters decrease for memory with increasing predator spatial randomness, the opposite is true for random walk, where encounters slightly increase.

With kinesis, on the other hand, a food–safety trade-off with landscape parameters occurs across all predator environments. Patchiness is the most important to the food–safety trade-off for kinesis, and increasing patchiness leads to increasing encounters and higher consumption. Interestingly, kinesis evinces this trade-off across all predator environments, unlike random walk and memory. However, predator environment, especially predator spatial randomness, does not vary consumption and encounters much for kinesis compared to the other movement processes, with the exception of higher encounters with ephemeral predators.

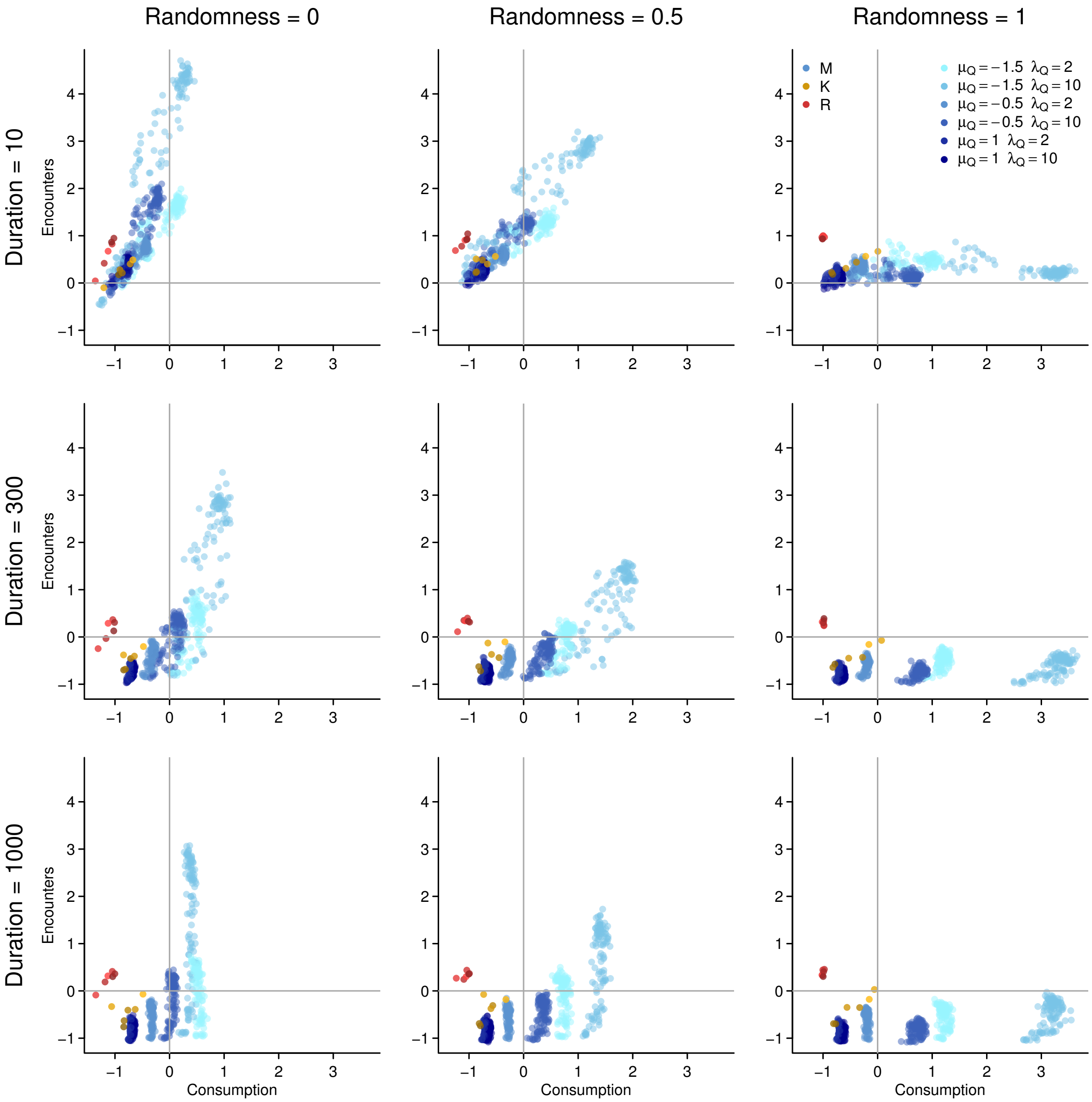

Figure 2.1: Predator encounters versus consumption for the three movement processes, random walk (red), kinesis (orange), and memory (blue) across the predator environments described by predator duration and spatial randomness. Different color shades show results for different landscape environments described by patch concentration and size (legend provided for memory only). Multiple points for different landscape environments for memory show different parameterizations of predator memory (Table 2.2). Encounters and consumption are normalized by mean and standard deviation, so positive values are above average and negative values are below average.

For memory, the food–safety trade-off manifests both across landscape environments as well as across parameter combinations within a specific landscape environment. In both cases, the trade-off is more muted as predator spatial randomness increases, meaning memory is able to increase consumption in some cases (i.e., certain landscapes or predator memory parameterizations) without necessarily increasing encounters at all or to the same degree. Similarly, as the food–safety trade-off diminishes with increasing predator spatial randomness, encounters decrease and the variability among predator memory parameterizations decreases as well. In essence, by using memory to exploit food resources, foragers are able to 'avoid' predators randomly located in unsuitable habitat.

When there are two competing objectives, maximizing consumption and minimizing encounters, there is not always a clear optimal strategy; however, a result that has more encounters for similar or less consumption (or conversely, lower consumption for a given number of encounters) is clearly worse. Kinesis outperforms random walk across all predator and landscape environments. Memory outperforms random walk and kinesis when predators are randomly located and more persistent, though in other cases there are some parameterizations of predator memory that lead to higher encounters but also higher consumption. With ephemeral predators ($\delta = 10$), some memory parameterizations are demonstrably worse than kinesis though not random walk. Encounter rates range higher for memory when predators are on resources ($\rho = 0$) because the resource memory attracts foragers to these locations. This is exacerbated by patchy landscapes, which concentrate predators much more than smooth landscapes. When predators are random, memory has lower encounter rates than random walk or kinesis across all landscapes, as memory is able to exploit resources away from predators across all parameterizations of the predator memory.

2.3.2 Differing survival rates

Given these competing objectives, another way to compare movement processes and parameterizations is with a measure of fitness using high and low survival rates. At high survival, all predator memory parameterizations outperform random walk and nearly all outperform

Environment		High survival				Low survival			
δ	ρ	ϕ_P	β_P	ψ_P	γ_R	ϕ_P	β_P	ψ_P	γ_R
10	1	0.1	10	1	1	0.1	20	100	1
10	0.5	0.1	20	1	1	0	20	100	20
10	0	0.1	20	10	10	0	20	100	10
300	1	0.01	20	10	10	0.001	10	100	10
300	0.5	0.01	10	100	10	0	20	100	20
300	0	0.01	10	100	10	0.001	20	100	10
1000	1	0	20	100	1	0.001	20	100	10
1000	0.5	0	20	10	10	0	20	100	10
1000	0	0.001	10	100	10	0.001	20	100	10

Table 2.3: Best performing predator memory parameters in different predator environments using fitness under high and low survival as a metric. Best performing parameters were the same across all landscape environments for a given predator environment. Predator environment parameters are duration δ and spatial randomness ρ. Predator memory parameters are decay rate ϕ_P, learning rate β_P, memory factor ψ_P, and spatial scale γ_R.

kinesis as well. At low survival, the percent of parameterizations that outperform, analogous to the importance of parameterizing the predator memory correctly, varies. For example, in a landscape of spatially correlated persistent predators ($\delta = 1000, \rho = 0$), 76% of memory parameterizations outperform kinesis while 93% outperform random walk, while with less correlated ephemeral predators ($\delta = 10, \rho = 0.5$) 19% and 80% outperform, respectively. Landscape environment is important too: the percent outperforming kinesis varies from 36–97% in the first case and 6–56% in the second across landscapes. How the predator memory is parameterized is most important with low survival, and landscapes with large high-value patches.

Similarly, the optimal parameterization of predator memory depends both on the survival rate as well as the predator environment (Table 2.3). For a given predator environment and survival rate, the ordering of predator memory parameterizations from best to worst is consistent across landscape environments. However, the landscape environment does affect the magnitude of consumption and encounters and thus fitness, as well as how differentiated the parameterizations are. The optimal decay rate decreases with increasing predator duration and is lower for low survival compared to high survival. The other memory parameters do not follow as clear a pattern, but values are generally larger with lower survival and when predators are more correlated with the resource. The optimal parameterizations are more similar for low survival and the increased importance of avoiding encounters.

In the case of persistent predators ($\delta = 1000$) correlated with patchy resources (Fig. 2.2), the best performing parameters are a small decay rate and large values for learning rate, memory factor, and spatial scale. Here the amount consumed is similar across parameterizations, and the main difference is number of encounters, so there is an increase in fitness for both high and low survival as encounters drop. Thus, in comparison to other movement processes, in which a decrease in movement would decrease both consumption and encounters, memory reduces the food–safety trade-off. Predator encounters can be reduced without changing consumption. While the memory parameterizations with lower fitness have more encounters than random walk and kinesis, fitness is still similar or higher. This holds true as predator spatial randomness increases, except that memory reduces encounters below that of random walk and kinesis for all parameterizations. With increasing landscape smoothness, there is less differentiation across memory parameterizations.

On the other hand, ephemeral predators ($\delta = 10$) result in a food–safety trade-off within memory parameterizations: the same parameters that maximize fitness under high survival conditions are the worst performing under low survival conditions (Fig. 2.3). The best performing parameterization for low survival is the same as above with persistent predators. The best parameters for high survival tend to be either a fast decay rate with larger values for the other parameters or a slow decay rate and at least some small values for the other parameters. Random walk and kinesis fall in the middle with kinesis providing a better compromise for maximizing both high and low survival than nearly all memory parameterizations (except $\phi_P = 0, \beta_P = 10, \psi_P = 10, \gamma_R = 10$), although memory clearly outperforms for high or low survival taken individually. As the landscape patch concentration and/or size decreases, this trade-off persists, but the differences between parameterizations again decrease. The trade-off increases with predator correlation with the resource, and disap-

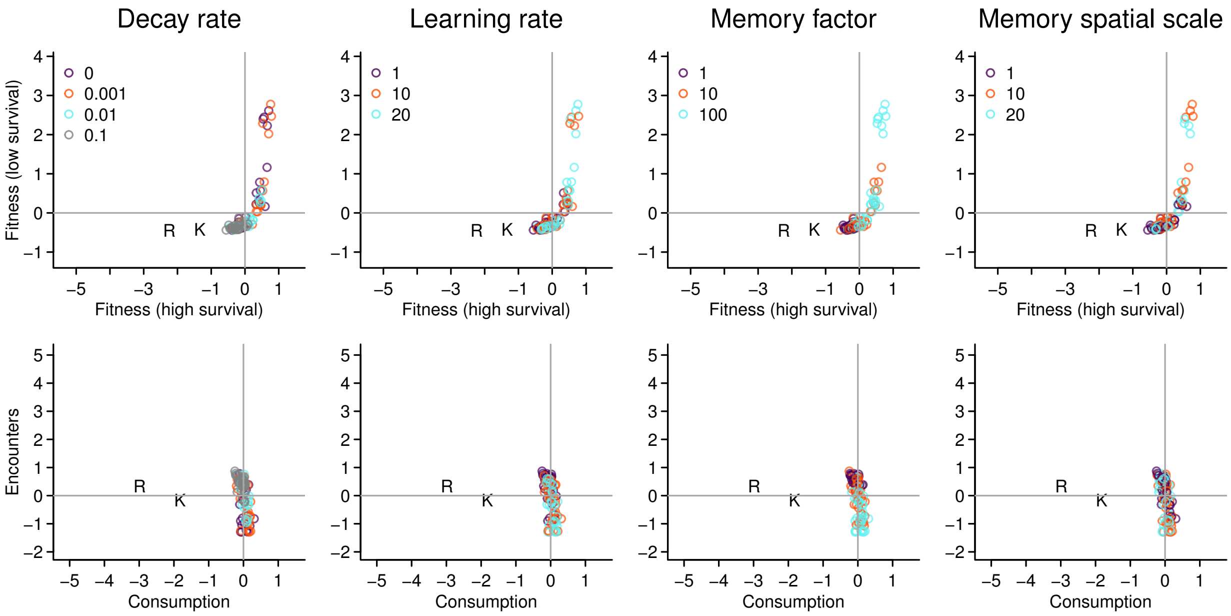

Figure 2.2: Performance of different parameterizations of predator memory in a predation environment of persistent predators correlated with patchy resources ($\delta = 1000, \rho = 0, \mu_Q = -1.5, \gamma_Q = 2$). Points are color-coded by predator memory parameters (left to right) decay rate ϕ_P, learning rate β_P, memory factor ψ_P, and spatial scale γ_R. Consumption, encounter, and fitness values are normalized by mean and standard deviation, so positive values are above average and negative values are below average for this particular environment.

pears when the predators are randomly located. With low survival, a decay rate of zero is optimal, even though predators are ephemeral, as long as they are correlated with the resource. Once the predator location is random, a large decay rate is favored. High survival always favors a large decay rate, though a similar pattern can be seen with the decrease in the other memory parameters as predators are more randomly located.

2.3.3 Predator memory parameters

Evaluating the variable importance of parameters, the environment parameters dominate the predator memory parameters though the ordering of the parameters by importance depends on the metric considered (Table 2.4). A conservative rule of thumb for interpreting variable

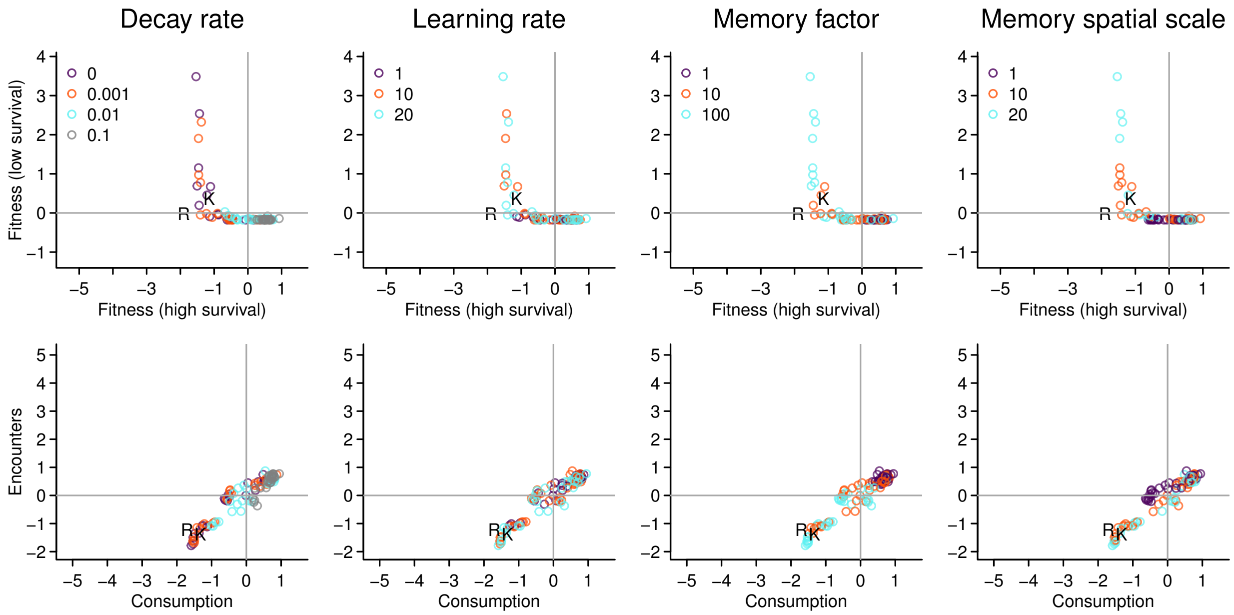

Figure 2.3: Performance of different parameterizations of predator memory in a predation environment of ephemeral predators moderately correlated with patchy resources ($\delta = 10, \rho = 0.5, \mu_Q = -1.5, \gamma_Q = 10$). Points are color-coded by predator memory parameters (left to right) decay rate ϕ_P, learning rate β_P, memory factor ψ_P, and spatial scale γ_R. Consumption, encounter, and fitness values are normalized by mean and standard deviation, so positive values are above average and negative values are below average for this particular environment.

Parameter		Consumption	Encounters	Fitness (high s)	Fitness (low s)
μ_Q	landscape patch concentration	4.34e-02	2.41e+02	2.46e-02	1.21e-03
γ_Q	landscape patch size	1.15e-02	9.76e+01	8.06e-03	1.41e-03
δ	predator duration	4.76e-03	3.04e+02	8.81e-03	2.60e-03
ρ	predator spatial randomness	1.58e-02	1.86e+02	1.89e-02	2.63e-03
ψ_P	predator memory factor	1.88e-03	9.29e+01	6.07e-04	3.33e-04
β_P	predator learning rate	3.00e-04	2.10e+01	5.69e-05	8.62e-05
ϕ_P	predator decay rate	1.39e-03	3.72e+01	4.00e-04	1.99e-04
γ_P	predator risk spatial scale	3.26e-05	2.14e+01	-7.85e-05	5.24e-07

Table 2.4: Permutation importance scores (mean decrease in accuracy) calculated using random forests for the memory movement process for four metrics: consumption, encounters, and fitness with high and low survival. Results shown treat parameters as continuous variables. Results were similar when parameters were treated as categorical. Magnitudes of scores depend on the values of the metric, and thus vary among metrics.

importance values is that a variable is informative if its value is greater than the absolute value of the lowest negative value, as irrelevant predictors will randomly vary around zero (Strobl et al. 2009). Using this criterion, all parameters are informative in explaining the variance in the metrics, with the exception of memory spatial scale for high survival. For consumption, landscape patch concentration and size (which switch order from the case with no predators, Chapter 1) and predator spatial randomness are the most important environmental parameters, while predator memory factor and decay rate are the most important memory parameters. For encounters, predator duration, landscape patchiness, and predator spatial randomness are the most important environmental parameters, and predator memory factor and decay rate are still the most important memory parameters. When combining consumption and encounters into fitness, the ordering of the memory parameters is the same. Predator environment is most important under low survival, while landscape patchiness and predator spatial randomness are most important under high survival.

The different components of predator memory can also be evaluated by looking at the effects of one parameter across predator environments while averaging over the other memory parameters and landscape environments (Fig. 2.4). Taking the parameters in order of importance, increasing the predator memory factor serves to decrease consumption and encounters. This is particularly important when encounter survival is low, as fitness generally increases with increasing memory factor values. Predator decay rate has a stronger effect on consumption for shorter predator durations and on encounters for more spatially correlated predator locations. Small decay rates are strongly favored under low survival, while values vary more by predator environment under high survival. Learning rate and spatial scale both exhibit a threshold effect for encounters: there is a difference between one and larger values, but less difference among larger values. Low survival tends to favor larger values for those parameters while high survival is less sensitive.

2.3.4 Changes to resource

One way to consider the non-consumptive effects of predation is to examine the effect on the resource. All movement processes consume less resources with predation compared to without, though the effect is most pronounced for memory, followed by kinesis then random walk (Fig. 2.5). Not surprisingly, consumption is most reduced as spatial randomness decreases and predators are more correlated with resources. Similarly, consumption is also reduced for ephemeral predators. For landscape environment, consumption is most reduced for patchy landscapes with large high-value patches (Fig. 2.6, the same pattern occurs with kinesis), with the effect of patch size being much larger than patch concentration. Across memory parameterizations, the parameters that most reduce encounters (i.e., small decay rate and large values for learning rate, memory factor, and spatial scale) are also those that result in the biggest change in consumption. The variability in the consumption change across predator memory parameterizations is highest for very short duration predators and minimal for long duration predators.

When looking at the underlying causes of this change, the habitat use also changes dramatically when there is a strong drop in consumption (Fig. 2.7). In patchy landscapes (Fig. 2.7, top and middle), time spent in the best habitat is dramatically reduced for memory,

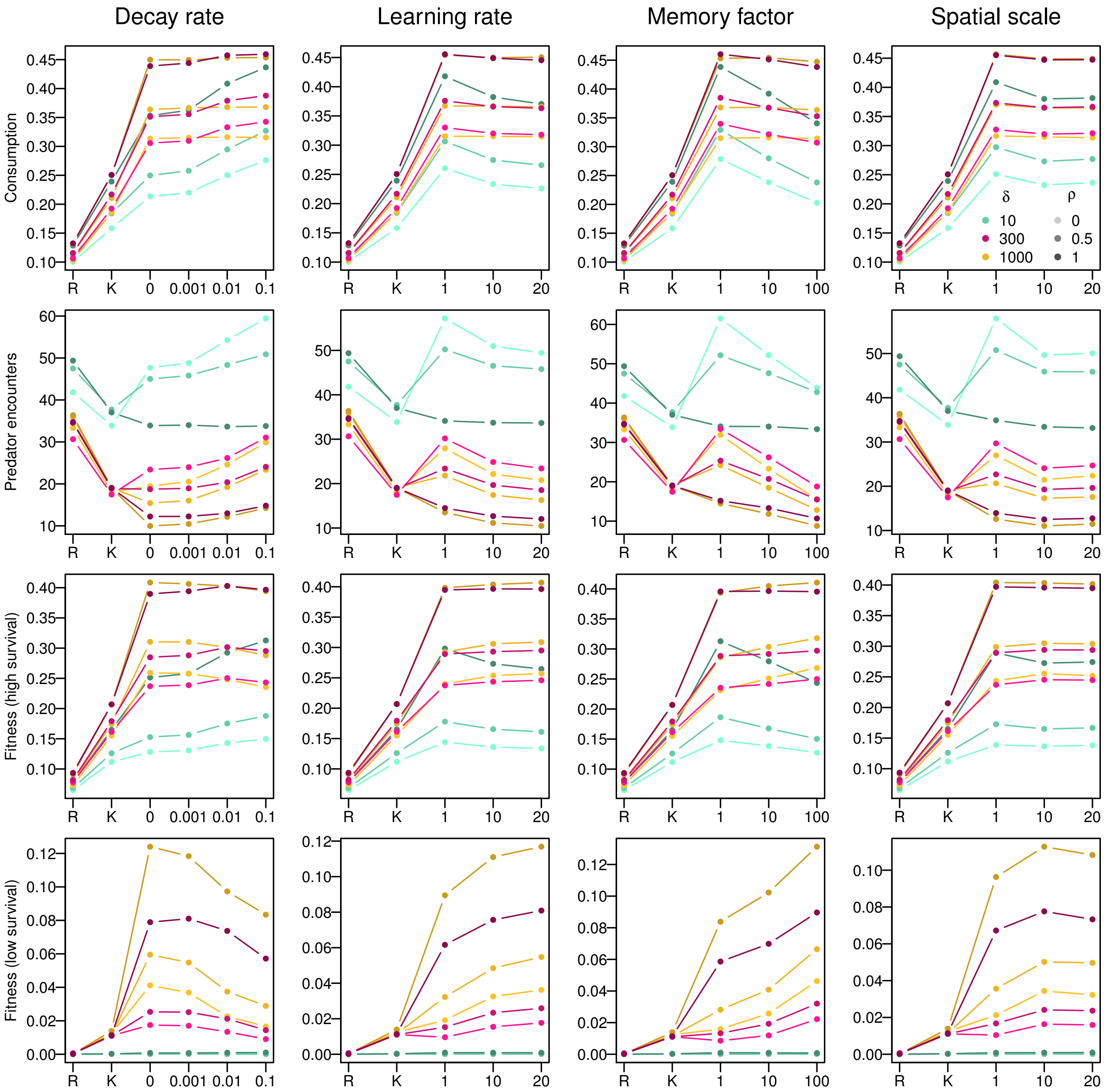

Figure 2.4: Metrics consumption, encounters, and fitness compared across parameter values of predator memory and kinesis and random walk. For each predator memory parameter, results are averaged across all other predator memory parameters. Results are shown for individual predator environments (δ, ρ), but averaged across landscape environments (μ_Q, γ_Q).

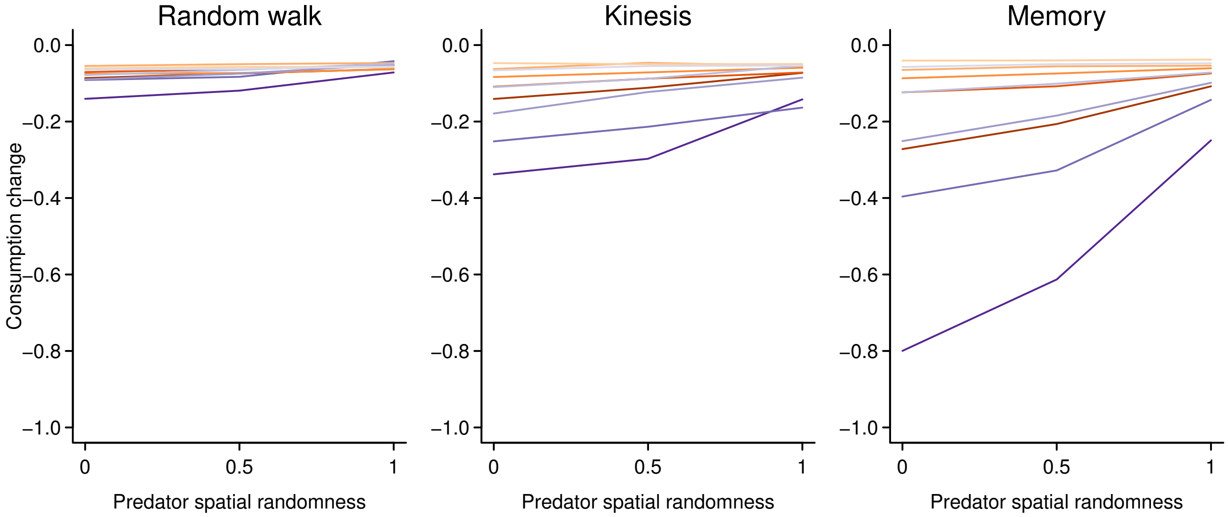

Figure 2.5: Decrease in consumption for different movement processes across predator spatial randomness comparing average total consumption on that landscape with predators to that without predators. Color shows landscape environment, $\gamma_Q = 2$ (orange) and $\gamma_Q = 10$ (purple), with darker colors indicating increasing patchiness (i.e., decreasing μ_Q). Predator duration is 300. Memory results are averaged across parameterizations of predator memory (but see Fig. 2.6).

though it is still well above the landscape distribution. Habitat usage is similar between high and low survival, except in the case of ephemeral, spatially correlated predators, which also show the largest change in habitat usage. Time spent in the highest quality areas decreases precipitously when predators are spatially correlated with resources. Even under predation, foragers still spend more time in higher quality resources in landscapes with large high-value patches compared to either smoother landscapes or those with smaller patches, despite the large declines. In smooth landscapes (Fig. 2.7, bottom), time spent in high quality areas is higher, but those areas are more diffuse and of lower quality than in patchy landscapes. There are more differences in habitat usage between high and low survival for ephemeral predators compared to persistent predators. In fact, foragers using memory under low survival conditions spends less time in high quality habitat than kinesis with ephemeral predators.

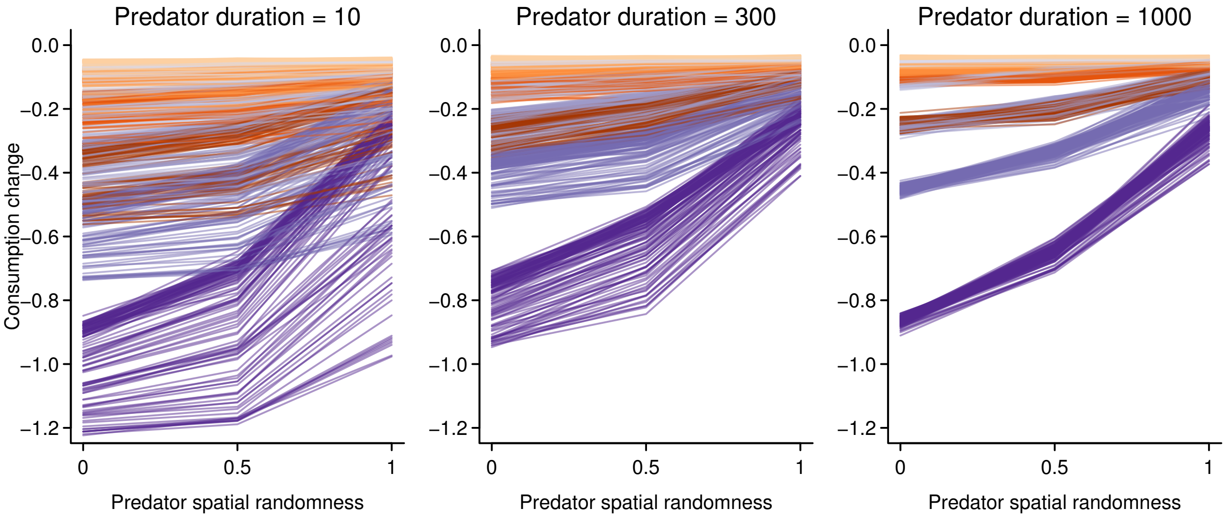

Figure 2.6: Decrease in consumption for different predator memory parameterizations in different predator environments comparing average total consumption on that landscape with predators to that without predators. Color shows landscape environment, $\gamma_Q = 2$ (orange) and $\gamma_Q = 10$ (purple), with darker colors indicating increasing patchiness (i.e., decreasing μ_Q). Each line represents a predator memory parameterization (Table 2.2).

2.4 Discussion

In this chapter, the foraging model presented in Chapter 1 is extended to include predation in a dynamic, spatially explicit way (Lima 2002). Predators encounter foragers and are able to relocate, rather than being abstracted into a measure of risk. Foragers learn by encountering predators, then combine layers of information on resource quality and predation risk to make movement decisions. This framework allows the investigation of the food–safety trade-off experienced by foragers at risk from predation, which is challenging to do experimentally given the unobservable nature of memory (Fagan et al. 2013). Across landscape and predator environments, memory is particularly useful with longer duration predators and patchy landscapes. These same landscapes are also those with the highest non-consumptive effects of predation, seen in the changes in resource consumption with and without predation. The longer predators persist, the better memory is able to aid foragers

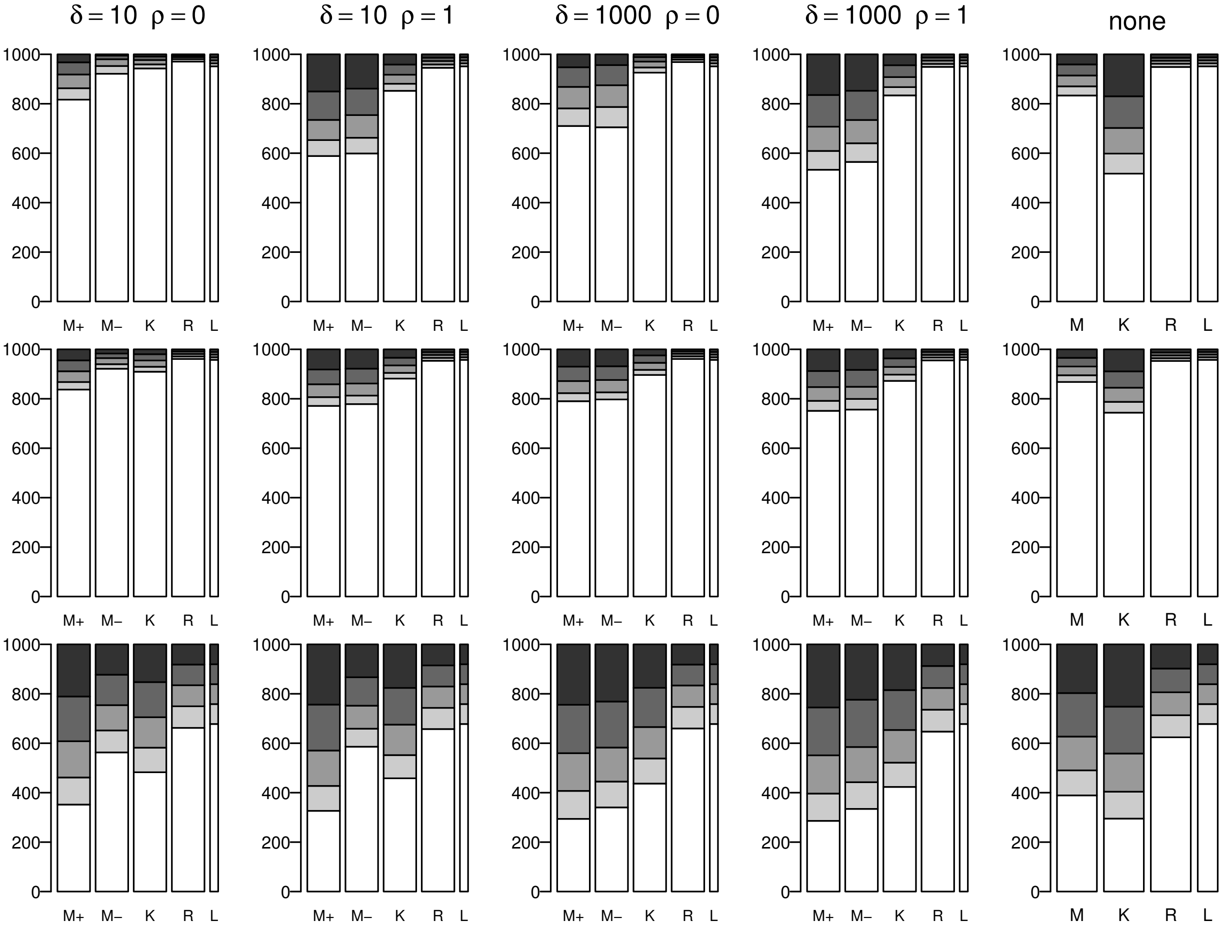

Figure 2.7: Time spent in areas of different resource quality across different predator environments compared to the distribution of resources on the landscape. Rightmost column (none) is no predators. Landscape environments are $\mu_Q = -1.5, \gamma_Q = 10$ (top), $\mu_Q = -1.5, \gamma_Q = 2$ (middle), and $\mu_Q = 0, \gamma_Q = 2$ (bottom). White represents zero resources while shades of gray from light to dark show quartiles of increasing quality. In the figure, M+ = memory (high survival), M– = memory (low survival), K = kinesis, R = random walk, L = landscape. Memory is parameterized with best parameters according to fitness in Table 2.3.

in managing the food–safety trade-off.

While multiple competing goals make comparisons more difficult, it is clear that memory provides a survival advantage in most predator environments. The size of that advantage depends on the environment. More persistent predators are easier to learn to avoid. However, even if the predators themselves are not persistent, it is still possible to avoid them using learning if they are correlated with some other measure, e.g., resource quality, that varies spatially. Like foraging without predation risk (Chapter 1), memory provides the most benefit in patchy landscapes where it is better able to exploit resources. When predators are correlated with resources, encounters go up as well. Here the patch size works differently than with no threat of predation. In a predator-free landscape, larger and more contiguous patches are a huge advantage for memory, which fully utilizes those patches and minimizes travel time. However, with low predator spatial randomness and fewer but larger high-value patches, predators in effect 'guard' those resources. Smaller patches, on the other hand, are more numerous, giving foragers alternative resources to utilize, as the predators cannot occupy all of them.

These same effects of landscape environment also relate to the non-consumptive effects of predation. Not surprisingly, consumption is most reduced in landscape environments where it was the highest without predation. These landscapes with large high-value patches are also the same ones where predators can effectively monopolize resource locations. In smoother landscapes or those with smaller patches, consumption decreases less from a smaller starting point. The parameters that are best for low survival of encounters also reduce consumption the most. This suggests that even though encounters might be rare in these contexts, the effects of predation can still be significant on the ecosystem. Indeed, the potential strength of non-consumptive effects of predation compared to consumptive effects has been noted (Lima and Dill 1990; Preisser et al. 2005; Cresswell 2008). In the case of changes in habitat, avoidance could be due to sensory predator cues (e.g., Brown 2003). However, it is also likely that memory plays a role in some of these observed non-consumptive effects as well.

One notable point is that the effects of predator environment are non-linear for memory (see Fig. 2.4). For example, consumption is much higher and encounters lower for spatially random predators ($\rho = 1$) than any degree of correlation with the resources ($\rho = 0, 0.5$). Similarly, predators with any degree of persistence ($\delta = 300, 1000$) are much more similar to each other than more ephemeral predators ($\delta = 10$). This suggests that while memory is not useful in some extreme environments such as very ephemeral predators, it may not take a large increase in persistence to switch to a state in which memory is favored. On the other hand, it may not take a large degree of correlation between the predator's locations and the forager's food resources before increasing effects of predation are felt in terms of increased encounters and decreased consumption. It is advantageous for the predator to be unpredictable in time, but not in location, especially if a forager's resources are sparsely located rather than broadly distributed.

Of the predator memory parameters, predator memory factor explains more of the variation in consumption, encounters, and fitness, followed by predator decay rate (Table 2.4). Notably, the ordering of variable importance was consistent across metrics even if optimal values differed. Predator decay rate has the clearest pattern with predator environment, with the optimal decay rate decreasing as predators are more persistent (Table 2.3). Because memories of a predator encounter will steer a forager away from that location whether that predator is still there or not, a balance must be struck between a decay rate small enough to avoid future encounters while at the same time not unnecessarily forgoing future feeding opportunities. This balance depends on both the predictability of the predators and the survivability of encounters. The predator memory factor was always at its largest value under low survival, and tended to decrease with less persistence and spatial randomness under high survival. The memory factor serves to scale the integrated measure of predation risk when calculating predator safety in a particular direction (Eq. 2.3). Larger memory factor values give greater weight to the riskiness of a particular direction. Larger values thus increase the likelihood that the safety value, $p(\theta)$, in the direction of a previously encountered predator will be zero, so there is no chance of going in that direction. Larger values were always preferred for the learning rate, which reflects the need to learn quickly after a single encounter. In contrast, a forager can learn more slowly about resources as it moves through an area. Finally, the memory risk spatial scale reflects the degree to which predator risk is weighted by distance, i.e., should the forager only be concerned with nearby predators or also those farther away. In general a medium value performed best, reflecting a compromise between avoiding getting too close to predators, even those not in the immediate vicinity, and exploiting feeding opportunities between the forager and a more distant predator.

Animals face a food–safety trade-off in their quest for food under threat of predation. Many predator avoidance strategies also reduce consumption, such as limiting foraging time or increasing vigilance. Here, using memory gives the forager the ability to reduce encounters without necessarily reducing consumption. Namely, when predators are persistent and less correlated with resources. While example exist of predators being spatially random and not correlated with the prey's resource quality, the predators in this case are temporally unpredictable as well, such as hawks (*Accipiter striatus*) preying on other birds (Roth and Lima 2007). Evidence suggests this is a deliberate strategy rather than due to cognitive limitations of the hawks. This makes it unlikely that memory could mitigate the food–safety trade-off in this case, and indeed, Roth and Lima (2007) surmise that the predator unpredictability is due to a behaviorally response prey. Another example of a predator uncorrelated with its prey's resource could be a generalist predator feeding on multiple prey with non-overlapping diet preferences. In the terminology of Preisser et al. (2007), this would be a broad-domain predator, and temporal predictability would necessitate that the predator use a sit-and-wait or sit-and-pursue hunting mode. This combination was relatively uncommon, however, perhaps because prey with spatial memory capabilities could employ highly effective counter measures.

Other predator environments, particularly ephemeral predators, reduce the usefulness of memory. Foragers still face a trade-off when using memory, i.e., different parameterizations of memory tend to increase consumption and encounters in tandem. However, even when memory can help mitigate the food–safety trade-off, this is in relation to other movement processes or parameterizations of memory. There can still be strong non-consumptive effects, even with fewer encounters. It would also be possible to consider the food–safety trade-off more dynamically, where predator memory and possibly other parameters would depend on the forager's state and goals (McNamara and Houston 1986; Higginson et al. 2012). That is, a hungry animal might take more risks to obtain food than a satiated one. How the different pieces of information are weighted could depend on a variety of factors such as vigilance levels or bioenergetic criteria such as food reserves or recency of feeding. In this case, how much an animal pays attention to its memory of previous encounters would become another strategy to manage the food–safety trade-off.

Although particular parameterizations of memory can help the forager manage the food–safety trade-off in terms of reducing encounters without reducing consumption, consumption is still reduced compared to foraging without predators. In fact, the reduction in consumption is generally larger for memory compared to other movement processes given memory's higher starting point. These reductions are present even with minimal encounters, showing that strong non-consumptive effects are possible, particularly when encounter survival is low. While changes in habitat use (i.e., spending less time in good areas) were greater under low survival with the greater emphasis on avoiding encounters, this was particularly the case for ephemeral non-random predators (Fig. 2.7). Because the optimal predator memory parameterization in this case included no decay of the predator memory (Table 2.3), the forager essentially tries to avoid predators everywhere they have been encountered. This minimally works to reduce encounters when predators are spatially correlated, but also strongly affects habitat usage. Spatially random or temporally persistent predators, on the other hand, are much easier for a forager using memory to avoid, and consequently the observed habitat usage changes are smaller.

In conclusion, modeling provides a unique perspective in being able to control aspects of memory and compare memory-informed movement to other movement processes under the same circumstances, both predator environment and landscape environment. This model demonstrates one way to include predators as a dynamic part of the system. This allows one to investigate the food–safety trade-off inherent to foraging under risk of predation while manipulating the forager's memory. The results suggest that the types of landscapes where one is most likely to find memory-driven movement in search of resources (Chapter 1) are also those where memory provides the most benefit when predators are considered as well. Unlike many antipredator strategies in which reducing predator encounters also reduces consumption (e.g., reduced movement, increased vigilance), memory allows the forager to reduce encounters while still maintaining consumption when predators are temporally predictable and alternative foraging locations exist. However, even when using memory, non-consumptive effects from predation are still found, as foragers reduce consumption and shift their habitat use compared to foraging without predators.

Chapter 3

EFFECTS OF MEMORY AND LEARNING ALONG THE EXPLORATION–AVOIDANCE AXIS FOR RELOCATED ANIMALS

Abstract

Conservation biologists use animal relocations to reintroduce extirpated populations and augment existing populations. One factor that can affect relocation success is animal temperament, or where individuals fall on axes such as bold–shy and exploration–avoidance. These same axes correlate with the fast–slow cognitive styles underlying learning, memory, and decision-making. I ran simulations introducing naive animals to new landscapes (good and poor release sites). Parameters explored include the learning rates for spatial memory (used to locate resources), average consumption rates (used in behavior switching), and the memory value along the exploration–avoidance axis (used for new habitat). Foragers were relatively insensitive to the consumption rate at their previous location negatively impacting their ability to adapt to their new environment. Likewise, most non-extreme learning rates for average consumption effectively provide the forager with the necessary information to switch between feeding and searching behaviors. Performance along the exploration–avoidance spectrum was habitat-dependent, though in general, foragers that are low to moderately exploratory in new habitats are successful. These results suggest that memory and an animal's ability to learn about its environment could be important for relocation success, and that variability in exploratory tendency could help animals adapt to a range of new habitat conditions.

3.1 Introduction

Animal relocations encompass reintroductions, the re-establishing of a locally extirpated species; translocations, moving wild animals from one part of their range to another; and supplementations, augmenting the number or genetic diversity of an existing population (Fischer and Lindenmayer 2000). Examples include conservation efforts to reintroduce endangered or threatened populations (Fritts et al. 1997; Zidon et al. 2009), supplementing small relict population to aid species recovery (Weinberger et al. 2009), managing problematic animals in human–animal conflict (Linnell et al. 1997; Athreya et al. 2011), and assisted colonization to attempt to prevent extinctions of species threatened by climate change (Shirey and Lamberti 2010).

Animals released into novel environments, where they have no knowledge of the resource availability and quality or habitat structure, can learn about this new environment as they explore their new surroundings. One factor affecting relocation success is preference for habitat conditions similar to their natal habitat (Stamps and Swaisgood 2007). This preference is predicted to occur when previous habitat was high quality and when it is difficult for the animal to estimate the quality of newly encountered habitat, and it can lead to relocated animals dispersing long distances rather than settling in the vicinity of the release site (Stamps and Swaisgood 2007). In a study of translocated elk (*Cervus elaphus*), for example, animals showed a preference for previously visited sites of high quality, showing the importance of spatial familiarity in habitat selection (Wolf et al. 2009). Releasing animals in high quality habitat was one factor that contributed to the successful reintroduction of black bears (*Ursus americanus*) to Arkansas (Smith and Clark 1994). Another study of translocated elk found forage biomass directly influenced release-site fidelity (Frair et al. 2007).

Animal temperament has been suggested as an important consideration in reintroduction programs, both through potential changes induced by captive breeding programs or as a way to increase the success of animal relocations (McDougall et al. 2006). Temperament refers to individual differences which are consistent across time and between situations in traits such as aggressiveness or exploration (Réale et al. 2007). This concept is important because it shows behavioral plasticity may actually be more limited than previously thought, and variation in temperament can maintain variation in behavior across individuals (Sih et al. 2004). Limited behavioral plasticity is one explanation for animals engaging in non-optimal behavior in some contexts (Sih et al. 2004).

Personality traits, or behavioral types, are frequently described along a continuum or axis, such as shyness–boldness, exploration–avoidance, activity, sociability and aggressiveness, and evidence suggests these traits are ecologically important (Réale et al. 2007). Behavioral types can also be considered in relation to cognition where the speed–accuracy trade-off is fundamental to individual differences (e.g., in perception, learning, memory, and decision-making) (Sih and Del Giudice 2012). Many behavioral-type axes can be mapped onto a fast–slow continuum, with bold, aggressive, proactive, and fast-exploring types being 'fast types' and cautious, nonaggressive, reactive, and slow-exploring types being 'slow types.' Fast types are considered high risk and high reward, and this risk–reward trade-off links behavioral types to the speed–accuracy trade-off of cognitive styles.

Behavioral types and individual differences in cognitive style can affect memory in three phases: encountering new situations, assessing new situations, and altering behavior in response to new assessments. Fast behavioral types, such as bold or fast-exploring individuals, are likely to encounter new situations more quickly than slow behavioral types, and thus appear to learn more quickly. However, they are also more likely to rely on prior assessments (particularly proactive individuals) and thus slower to learn changes in the environment or alter their behavior in response to new information (Sih and Del Giudice 2012).

While individual differences in behavioral type are likely to relate to differences in how individuals process and store information, memory is also something that will differ both among individuals and through time for a single individual as a result of an individual's experiences. A clear distinction in memory is between naive, newly introduced animals and experienced individuals that have been resident for some period of time. In a study of elk introduced to a novel environment, Fryxell et al. (2008) analyzed movements, which were initially dispersive and then transitioned to home range behavior, where movement modes can be thought of as structured by the relationship between an animal's internal state and the external state of the environment (Owen-Smith et al. 2010). Home-range movement patterns showed a preference for areas that were nearby, familiar, and attractive habitat. Dispersal distance and time varied by individual. These dispersal distances were likely mediated by individual differences in behavioral type, as social animals were more sedentary than solitary individuals (Fryxell et al. 2008).

Managers have also tried manipulating or selecting for behavioral types to improve relocation success. For example, selecting against boldness in both breeding stock and animals to release has been suggested, as bold captive-bred swift foxes (*Vulpes velox*) were more likely to die soon after reintroduction (Bremner-Harrison et al. 2004). In a meta-analysis on the fitness effects of temperament, exploration had a positive effect on survival but no effect on reproductive success, and boldness increased reproductive success (especially for males) but at the cost of reduced survival (Smith and Blumstein 2008). This suggests that variation in boldness may be maintained through trade-offs, where fitness varies depending on the environment. Additionally, releasing only shy individuals may increase short-term success, but with long-term consequences for reproductive success (Smith and Blumstein 2008).

While it has been suggested that issues with animals learning and remembering resources in their new environment may be an important underlying cause of relocation failures (Teixeira et al. 2007), this issue has been largely unexplored. Behavioral type correlates to dispersal tendency with important implications for relocations (Sih et al. 2012). Simulation modeling provides a means to explore interactions of memory, learning, and exploratory tendency which are difficult to control experimentally.

This chapter examines how individual differences on the fast–slow spectrum, such as learning rates (speed) and exploration–avoidance, affect relocation success, memory formation, and habitat use. Total consumption over the simulation is used as a proxy for the animal finding suitable habitat as a measure of relocation success. In simulations, I vary learning rates and memory parameters for naive relocated animals. How animals learn unfamiliar habitat quality is also considered through explicitly modeling foragers learning the average consumption rate with different start values. For comparison, simulations are also run with fully informed individuals already habituated to their environment and animals using kinesis rather than memory. With kinesis, foragers learn the average consumption rate used for behavior switching, but do not form spatial memories.

3.2 Methods

In this chapter, animals are introduced to a new landscape and tracked as they explore their new habitat. In Chapters 1 and 2, foragers using memory were assumed to already have a spatial map of habitat quality in the area, and foragers were additionally assumed to 'know' the average landscape quality under optimal foraging theory (Charnov 1976). Foragers using the memory and kinesis movement processes used this average consumption rate, $\overline{C}$, to switch between searching and feeding behaviors. However, after being introduced to a new landscape, a mismatch between an animal's previous average consumption rate and the new habitat quality is possible. This previous average consumption rate could remain fixed, or the animal could adjust it by learning from their experience in the new habitat. The Marginal Value Theorem (MVT), that the forger should leave a patch when the consumption rate within the patch declines to the average consumption rate in the environment including travel time, assumes discrete patches and knowledge of the average consumption rate as originally formulated (Charnov 1976). However, the MVT has been extended to show animals could estimate the average consumption rate by summing their consumption and foraging time or using an exponentially weighted estimate in stochastic environments (McNamara and Houston 1985) and to apply to continuously distributed resources (Arditi and Dacorogna 1988).

Relocated individuals have no way of knowing the average consumption rate of their new environment. Thus, they presumably use the value from their prior experience or perhaps some default value to switch between behaviors when exploring a new environment. Here the learning is modeled as a exponentially weighted moving average,

$$\overline{C}(t) = \alpha C(t) + (1 - \alpha)\overline{C}(t - 1), \tag{3.1}$$

where α is the average consumption learning rate and $\overline{C}(0)$ is the average consumption start value. Note that $\alpha = 1 - \exp(-\Delta t\ \tau)$ if the consumption rate is sampled irregularly where τ is the filter time constant, though here the sampling is assumed to be regular for simplicity. This is a reasonable assumption for this model when the animal is consuming continuously, but might not apply to more discretely distributed resources. A learning rate of zero corresponds to an average consumption rate set genetically or at some specific developmental period, while non-zero values correspond to a plastic average consumption rate set through the forager's experience of the landscape. The larger the learning rate, the more heavily weighted the average consumption rate is to recent experience. Thus $\bar{C}$ is now dynamic quantity rather than the fixed value based on assumed knowledge of average habitat quality used in Chapter 1. This is the same equation used to model a forager learning the search time or energy intake thresholds for patch leaving with discretely encountered prey (Esposito et al. 2010).

Those foragers using memory are released into the new landscape naive, with no knowledge of their environment, in contrast to the fully informed individuals considered earlier (Chapters 1 and 2). Previously, the long-term stream was initialized to the habitat quality and the short-term stream to zero (see Eq. 1.4), meaning the forager already knew the locations of food patches. The question then, in a brand new environment, is how do foragers initialize their spatial memory M, and in particular the long-term attractive stream L. That is, how exploratory or not is the animal about the potential resources in unknown areas? This parameter is $M*$, the uninformed memory value or attractiveness of unexplored habitat. $M*$ sets the value assigned to L at the start of the simulation (S is still initialized to zero). As the forager moves about its new habitat, it learns in the area in its vicinity using a bivariate normal learning kernel for the short- and long-term memory streams (Chapter 1, Eqs. 1.5 and 1.6).

Based on the results of previous chapters, here the focus is on patchy landscapes with

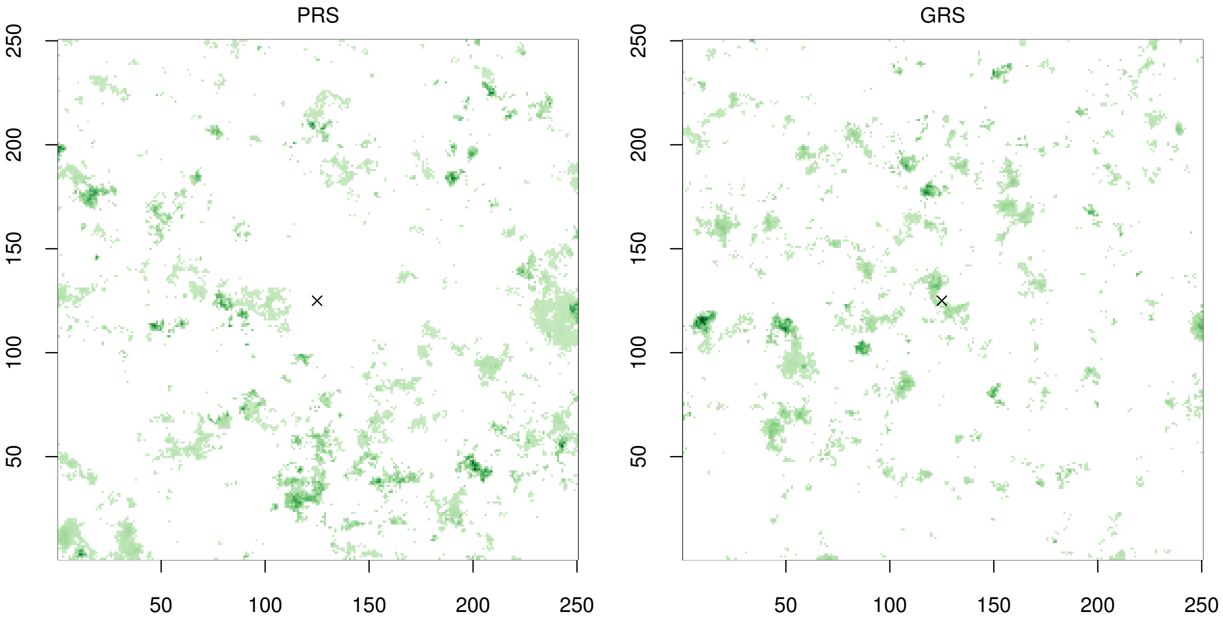

Figure 3.1: Landscapes used in simulations: poor release site (PRS, left panel) and good release site (GRS, right panel). White indicates areas of no resources and resource quality increases with darker shades of green. Release site marked with x.

large high-value patches where memory is more likely to show interesting differences among parameterizations and with other movement processes. Two landscapes were created (Fig. 3.1), to simulate a common practice of releasing relocated animals in areas of presumed high quality habitat (e.g., Smith and Clark 1994), as well as a second case in which better quality habitat is located farther from the release site. The landscapes are 25 time bigger than those used in Chapters 1 and 2 to allow for the examination of the dispersal process. In order to create patches of varying quality, four landscape layers were created with different parameterizations: 1) $\mu_Q = -2, \gamma_Q = 10, \sum Q = 10$, 2) $\mu_Q = -2, \gamma_Q = 10, \sum Q = 7.5$, 3) $\mu_Q = -1.5, \gamma_Q = 10, \sum Q = 5$, and 4) $\mu_Q = -1.5, \gamma_Q = 10, \sum Q = 2.5$, where μ_Q is patch concentration, γ_Q is patch size, and $\sum Q$ is total quality (see Chapter 1). For the good release site (GRS), the layers were added together for a total $\sum Q = 25$. For the poor release site (PRS), the center 1/25 square of habitat (forager release location) was set to 0 for the best quality layers 1 and 2, then the layers were added together and renormalized to sum to 25 like the good release site landscape.

In order to characterize the value of learning in a new landscape by relocated individuals, parameterizations of memory were compared to the kinesis movement process. For both memory and kinesis, different values for the average consumption learning rate and start value were examined. For memory, the short and long learning rates and the value for uninformed memory were also varied. Each parameter combination (Table 3.1) was repeated 20 times to account for the variability in exploration of a novel habitat across both the good and poor quality release site landscapes. The main metric tracked is total consumption over the simulation. Consumption is a proxy for the animal finding suitable habitat as a measure of relocation success. In order to better understand the mechanisms leading to differences in consumption among scenarios, forager trajectories are also recorded. This allows the examination how foragers explored the landscape and how that exploration varied depending on the movement process and underlying parameterization of that process.

3.3 Results

3.3.1 Learning rates

There are two classes of learning rates manipulated in this chapter: the average consumption learning rate (and associated start value) used by both kinesis and memory and the short- and long term learning rates for habitat quality for spatial memory. We first consider the latter.

Memory learning rates

The differentiation of performance across the short- and long-term learning rates for the respective resource memory streams varied by landscape (Fig. 3.2). For the PRS, there was little variation in consumption with learning rates. For the GRS, on the other hand, there was a clear increase in consumption with both higher long-term learning rates and lower short-

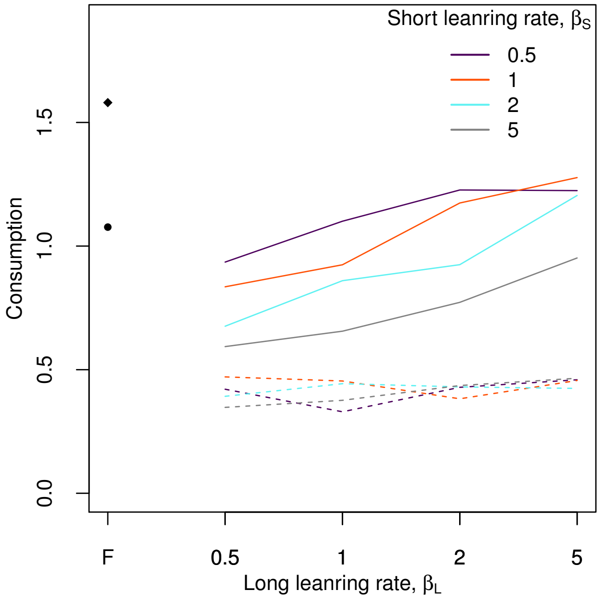

Figure 3.2: Consumption amounts across values of short-term learning rates (colors), β_S, and long-term learning rates (x-axis), β_L, and landscapes, GRS (solid) and PRS (dashed). For comparison, fully informed memory (F) shown with points, GRS (diamond) and PRS (circle). Other parameter values in Table 3.1.

Table 3.1: Parameters used in the model and values for relocations simulations. Because units are arbitrary in the simulations, L is used for generic length units, T is used for generic time units, and R is used for generic resource biomass units.

	Parameter	Definition	Units	Values
Simulations				
	Δt	model time step	T	1
	T	simulation length (time steps)		1000
Consumption				
	β_R	regeneration rate	1/T	0.01
	β_C	consumption rate	1/T	1
	γ_C	consumption spatial scale	L	1
	α	average consumption learning rate		1
	$\overline{C}(0)$	average consumption start value	R	0, 1e–6, 1e–4, 1e–2
Memory[a]				
	ψ_M	short-term memory factor		2
	β_L	long-term learning rate	1/T	0.5, 1, 2, 5
	β_S	short-term learning rate	1/T	0.5, 1, 2, 5
	ϕ_L, ϕ_S	decay rates	1/T	0.0001, 0.01
	γ_L, γ_S	learning spatial scale	L	1, 1
	γ_Z	memory spatial scale	L	2, 10, 100
	$M*$	uninformed memory	R	0, 1e–14, 1e–12, 1e–10, 1e–8, 1e–6, 1e–4, 1e–3, 1e–2, 0.1
Movement[b]				
	τ_S, τ_F	autocorrelation time scale	T	4, 2
	ν_S, ν_F	length of μ	L/T	6, 1
	λ	mean time to update θ	T	1

[a] L = long-term memory, S = short-term memory

[b] S = searching, F = feeding

term learning rates, though there was no interaction between short- and long-term learning rates. However, even the best-performing learning rates did not match the performance of fully informed memory (points in Fig. 3.2), which has the advantage of complete knowledge of resource locations.

The same ordering of the performance of short-and long-term learning rates remained across the range of exploration–avoidance for the GRS (Fig. 3.3). However, for low exploratory individuals (small $M*$), naive foragers approached the consumption rates of fully informed individuals. For the PRS, the picture was more complicated. For more extreme values of $M*$, whether on either end of the exploration–avoidance spectrum, consumption was largely unaffected by learning rates (i.e., similar to Fig. 3.2). For midrange values closer to the true average landscape quality ($\bar{Q}_0 = 4e - -4$), the patterns with both short- and long-term learning rates matched those of the GRS. The remaining simulations used $\beta_S = 1$ and $\beta_L = 5$, the optimal learning rate parameterization across values on the exploration–avoidance spectrum.

Learning the average consumption rate

Both memory and kinesis displayed a dome-shaped relationship between consumption and the average consumption value learning rate, α (Fig. 3.4). This learning rate is used by foragers to learn the average consumption rate, $\bar{C}$, used to switch between searching and feeding behaviors (Eq. 3.1). The optimum values were similar for both, with a slightly smaller α preferred for kinesis for the GRS. In general, the starting value, $\overline{C}(0)$, the forager's uniformed guess at the average habitat quality, was unimportant, except when it was never updated ($\alpha = 0$). In that case, values closer to the true average quality (4e–4) performed best for kinesis and memory. However, a large value (0.01) did nearly as well or better than the near-true value (1e–4) for memory but was the worst performing value for kinesis.

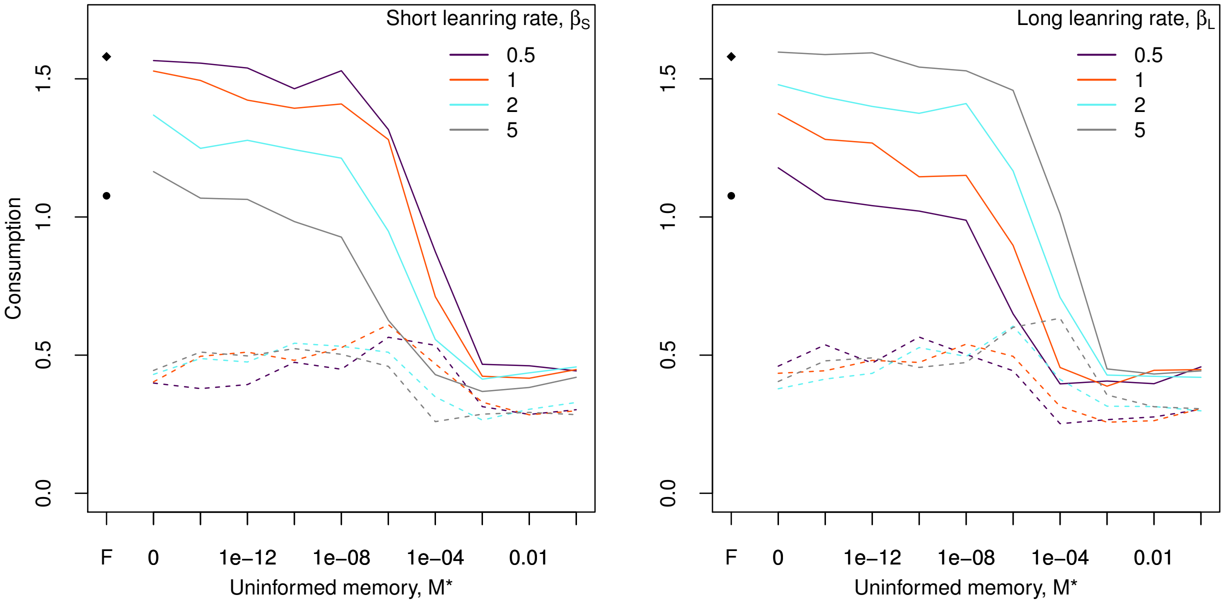

Figure 3.3: Consumption rates for short-term learning rates (colors, left panel) and long-term learning rates (colors, right panel) across values of unexplored memory values (x-axis), $M*$, and landscapes, GRS (solid) and PRS (dashed). For comparison, fully informed memory (F) shown with points, GRS (diamond) and PRS (circle). Other parameter values in Table 3.1.

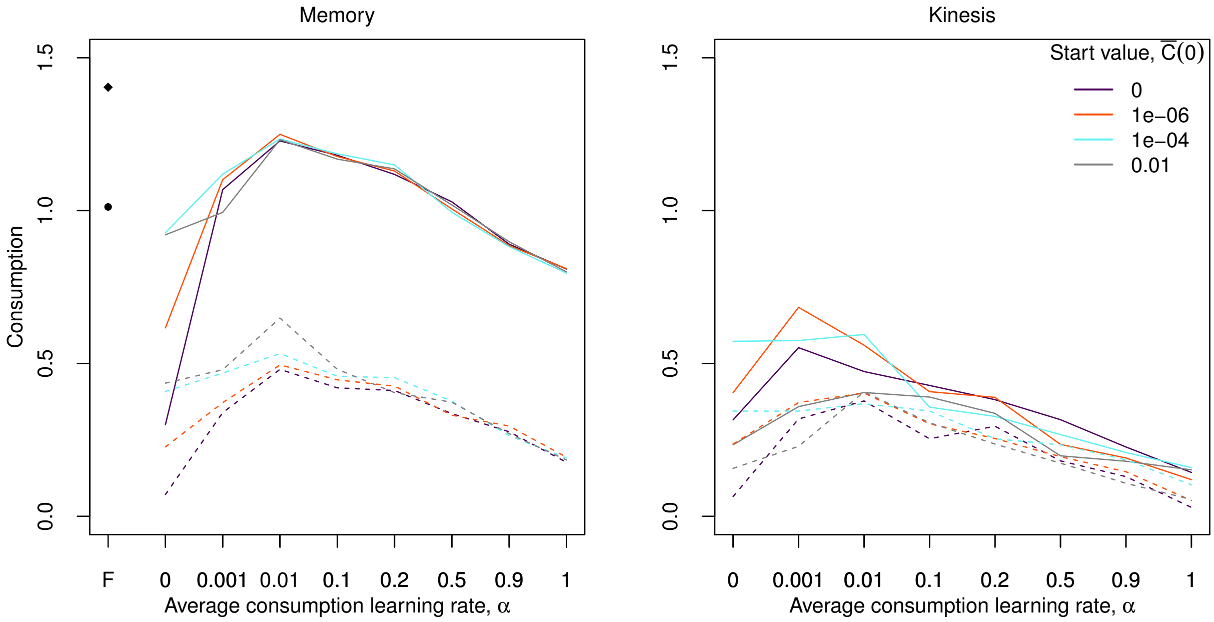

Figure 3.4: Consumption rates for memory (left panel) and kinesis (right panel) across values of average consumption learning rates (x-axis), α, and average consumption start values (colors), $\overline{C}(0)$, and landscapes, GRS (solid) and PRS (dashed). For comparison, fully informed memory (F) shown with points, GRS (diamond) and PRS (circle). Other parameter values in Table 3.1 and $\beta_L = 5, \beta_S = 1$.

Interactions with exploratory tendencies

Returning to the exploration–avoidance spectrum of memory values for new habitat, the patterns across landscapes seen with learning rates (Fig. 3.2) occurred across other parameters such as average consumption learning rate, α, and memory spatial scale, γ_Z (Fig. 3.5). For the GRS, there was a plateau across low to moderate exploration values, followed by a steep decline in consumption with more exploratory values. For the PRS, consumption values were generally smaller (true also for kinesis and fully informed memory), and peak consumption occurred with moderately exploratory values of uninformed memory. The ordering of performance of the learning rate α was consistent across the exploration–avoidance spectrum ($M*$) and between landscapes. A relatively slow learning rate performed best, meaning a longer-term consumption average is preferred. The exception was the case with no learning ($\alpha = 0$), which was the worst performing option by far for the GRS, but did better than 'decide based on the last experience' ($\alpha = 1$) for PRS (no learning also outperformed faster learning rates for kinesis).

For γ_Z, large spatial scales ($\gamma_Z = 10$ and 100) performed similarly and better than small spatial scales ($\gamma_Z = 2$) for the GRS. This ordering was consistent with fully informed memory, though the largest spatial scale ($\gamma_Z = 100$) was more strongly preferred. For the PRS, there were not large differences among values, but a small spatial scale ($\gamma_Z = 2$) was best with low exploration values for uninformed memory, a larger spatial scale ($\gamma_Z = 10$) was best with exploratory values, and the largest spatial scale ($\gamma_Z = 100$) underperformed. This was in marked contrast to the fully informed memory, where the smallest spatial scale ($\gamma_Z = 2$) was the worst performing.

3.3.2 Space use

Trajectories

How foragers explored their new habitat changes considerably across movement processes and memory state. With kinesis (Fig. 3.6), trajectories tended to be wide-ranging and

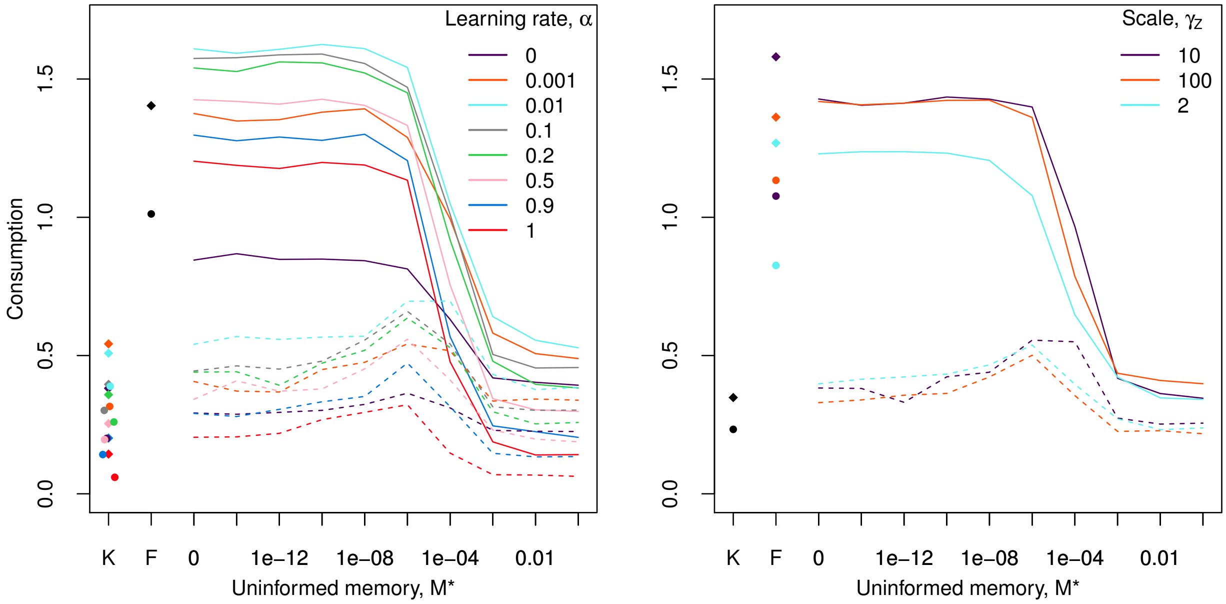

Figure 3.5: Consumption rates for average consumption learning rate (colors, left panel) and memory spatial scale (colors, right panel) across unexplored memory values (x-axis), $M*$, and landscapes, GRS (solid) and PRS (dashed). For comparison, kinesis (K) and fully informed memory (F) shown with points, GRS (diamond) and PRS (circle). Other parameter values in Table 3.1 and $\beta_L = 5, \beta_S = 1$.

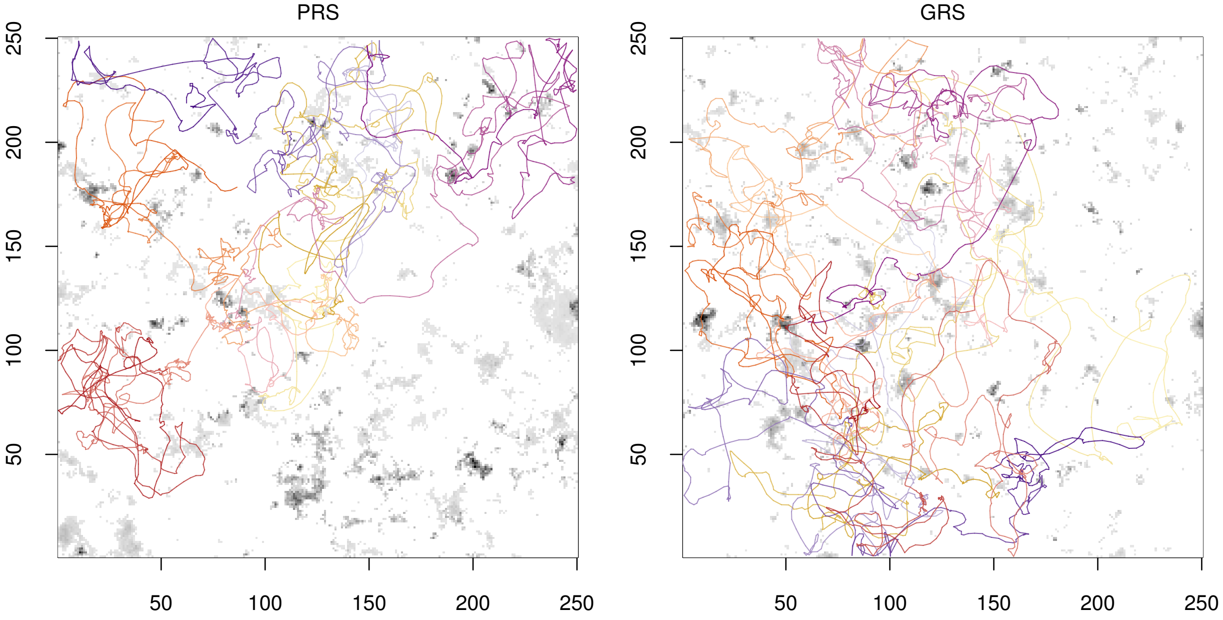

Figure 3.6: Sample trajectories for foragers using kinesis for the PRS (left panel; $\alpha = 0.01, \overline{C}(0) = 0.01$) and GRS (right panel; $\alpha = 0.001, \overline{C}(0) = 1\text{e–}6$). Colors (red, orange, yellow, purple, pink) denote separate trajectories with gradient increasing from light to dark with time. Other parameter values in Table 3.1.

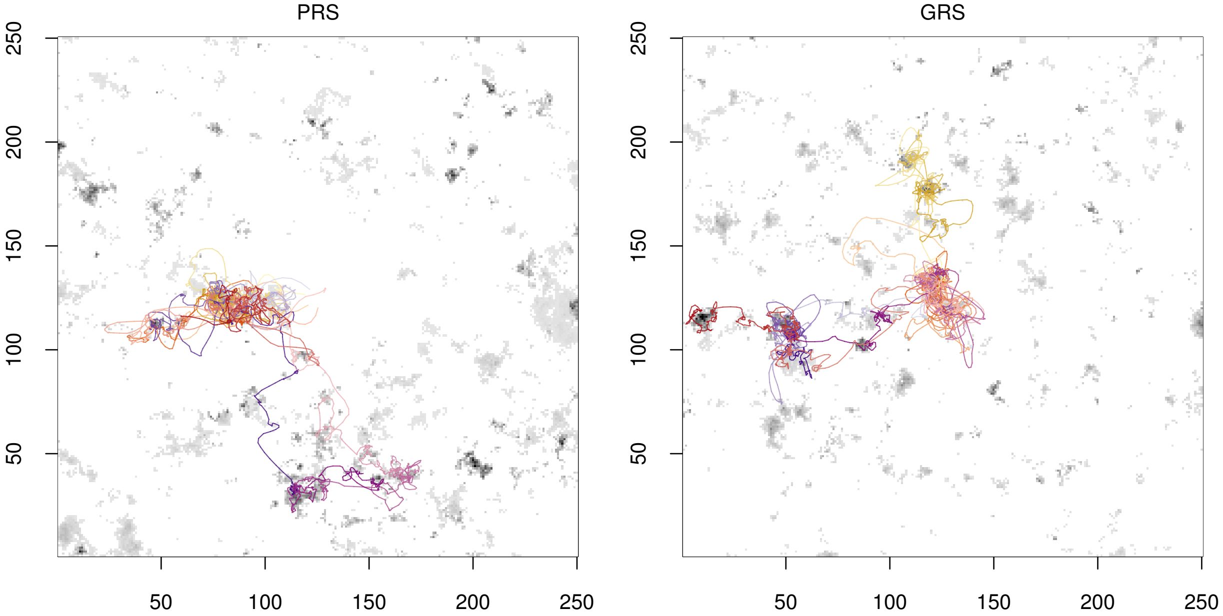

Figure 3.7: Sample trajectories for foragers using fully informed memory for the PRS (left panel) and GRS (right panel). Colors (red, orange, yellow, purple, pink) denote separate trajectories with gradient increasing from light to dark with time. Other parameter values in Table 3.1 and $\gamma_Z = 10, \beta_L = 1, \beta_S = 1$.

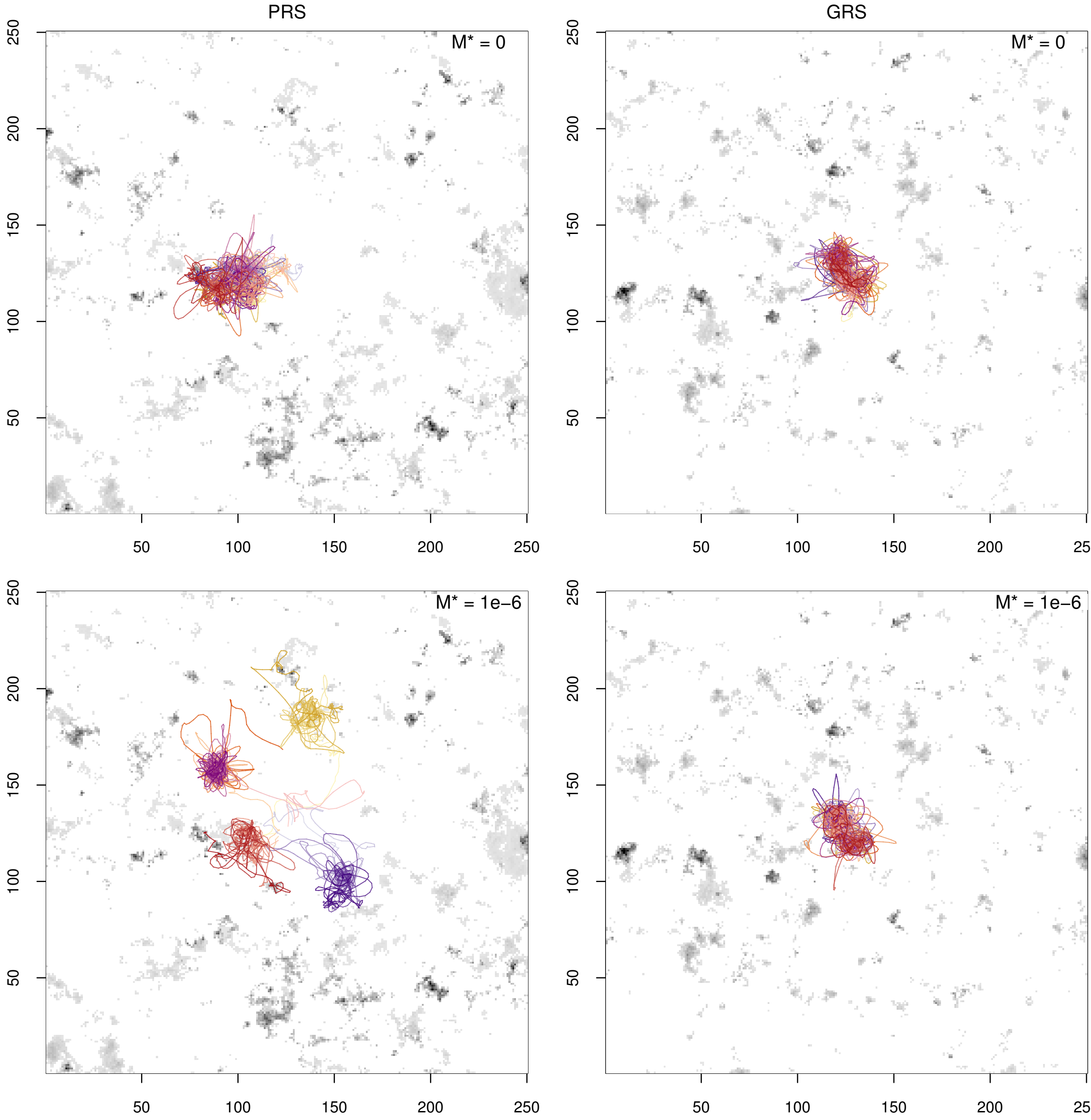

Figure 3.8: Sample trajectories for foragers using uninformed memory for the PRS (left panels) and GRS (right panels). Top row is low exploration foragers ($\alpha = 0.01, \overline{C}(0) =$ 1e–6, $\gamma_Z = 10, M* = 0$), and bottom row is moderate exploration foragers ($\alpha = 0.01, \overline{C}(0) =$ 1e–6, $\gamma_Z = 10, M* =$ 1e–6). Colors (red, orange, yellow, purple, pink) denote separate trajectories with gradient increasing from light to dark with time. Other parameter values in Table 3.1 and $\beta_L = 5, \beta_S = 1$.

frequently encountered one of the boundaries. While trajectories sometimes appeared to be area-constrained, that tendency was mostly an artifact of the initial stochastic direction and reflecting boundaries.

The fully informed memory trajectories (Fig. 3.7), on the other hand, tended to be densely concentrated on one or several patches, leaving the majority of the landscape untraveled. Even with individuals having the exact same memory representation and release site, the stochasticity present in probabilistically picking a direction resulted in different individuals utilizing different patches.

For the uninformed memory trajectories (Fig. 3.8), the low exploration individuals ($M* = 0$) tended to stay in the same location near the release site for both the PRS and GRS. More exploratory individuals ($M* =$ 1e–6) tended to stay near the release site like low exploration individuals for the GRS but move further afield for the PRS. Compared to fully informed foragers, uninformed foragers tended to concentrate their movements in a single area rather than several nearby areas, even when some initial exploration was required to find that area.

Changes in space use through time

Like the individual trajectories, the dispersiveness with time also varies considerably across movement processes and memory state. For both the PRS (Fig. 3.9) and GRS (Fig. 3.10), kinesis displayed a diffusion outwards from the release point at the center with time. Kinesis fully explored/utilized all available habitat, and while it is possible to see some intensity of use of high quality patches, the trajectories in general were not focused there. The initial stages of the trajectories (green) were focused around the center release point, and this initial central space use was actually over a larger area in the high quality GRS scenario. The fully informed memory trajectories also displayed the pattern of initial focus around the center but they were followed by later intensive use (purple/magenta) of high quality patches both proximate to and farther from the initial release point. The patterns did not look markedly different between the PRS and GRS other than the bias towards the lower left in the PRS scenario likely due to the poor quality patch immediately left of the release site.

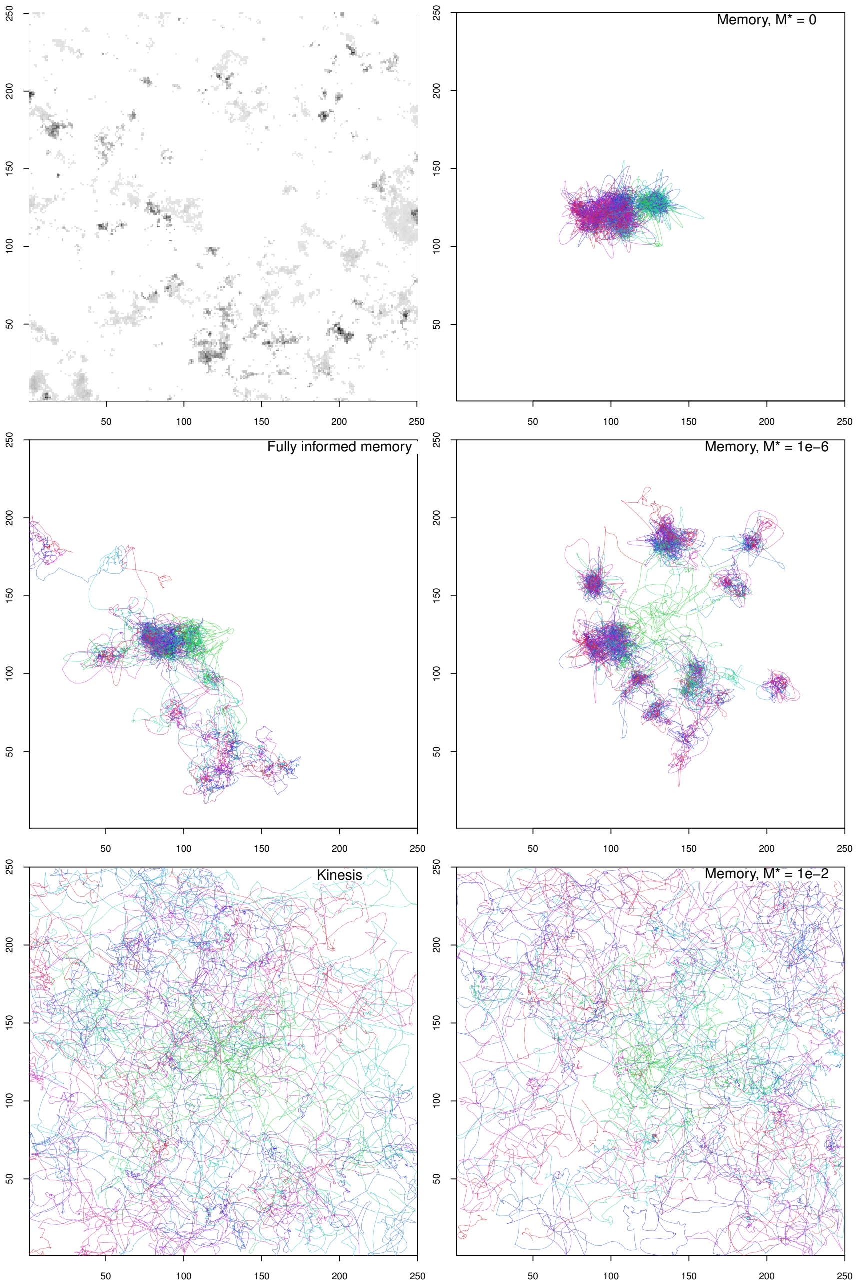

Figure 3.9: Space use for PRS across multiple trajectories with color changing through time (green, blue, purple, magenta). Clockwise from upper left: PRS landscape, uninformed memory ($\alpha = 0.01, \overline{C}(0) = $ 1e–6, $\gamma_Z = 10, M* = 0$), uninformed memory ($\alpha = 0.01, \overline{C}(0) = $ 1e–6, $\gamma_Z = 10, M* = 1e - -6$), uninformed memory ($\alpha = 0.01, \overline{C}(0) = $ 1e–6, $\gamma_Z = 10, M* = $ 1e–2), kinesis ($\alpha = 0.01, \overline{C}(0) = 0.01$, and fully informed memory ($\gamma_Z = 10$). Other parameter values in Table 3.1.

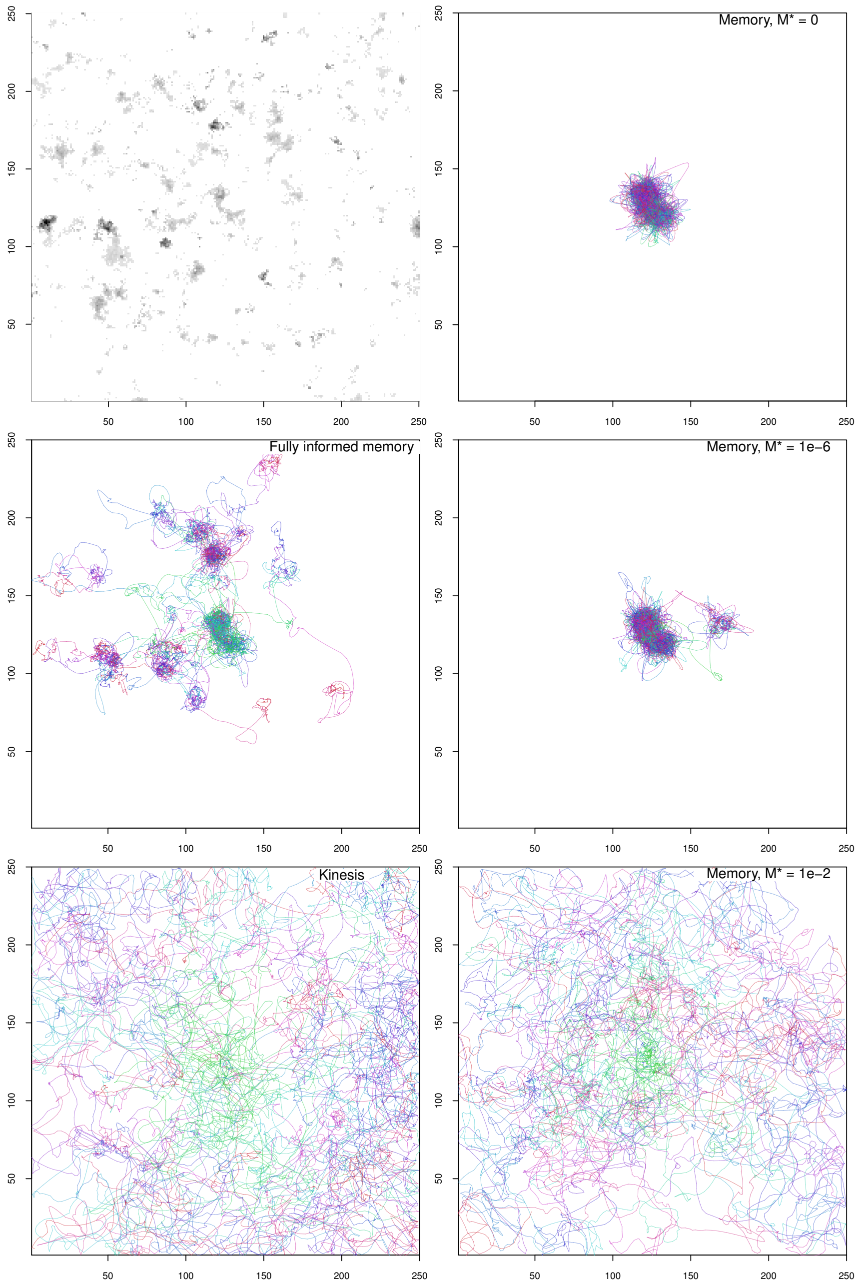

Figure 3.10: Space use for GRS across multiple trajectories with color changing through time (green, blue, purple, magenta). Clockwise from upper left: GRS landscape, uninformed memory ($\alpha = 0.01, \overline{C}(0) =$ 1e–6, $\gamma_Z = 10, M* = 0$), uninformed memory ($\alpha = 0.01, \overline{C}(0) =$ 1e–6, $\gamma_Z = 10, M* =$ 1e–6), uninformed memory ($\alpha = 0.01, \overline{C}(0) =$ 1e–6, $\gamma_Z = 10, M* =$ 1e–2), kinesis ($\alpha = 0.01, \overline{C}(0) = 0.01$), and fully informed memory ($\gamma_Z = 10$). Other parameter values in Table 3.1.

The space use of the uninformed memory trajectories were highly dependent on the forager's position along the exploration–avoidance axis for new habitat. Low exploration foragers stayed in a small area near the release site irrespective of habitat quality in the vicinity. This was also true of moderate exploration with the GRS: the uniformed forager stayed near the release site whereas the fully informed forager exploited other high quality nearby patches. With the PRS, the moderately exploratory uninformed trajectories more closely resembled those of the fully informed foragers in terms of variety of patches used though with more variability due to more stochasticity in initial direction. Finally, as exploration increased, the uninformed trajectories more closely resembled those of kinesis as the forager was quite dispersive with no area restriction.

3.4 Discussion

This chapter evaluates the value of learning compared to movement processes that are either memoryless or already fully informed with respect to habitat quality. This chapter also examines how foragers may update their assessment of the average consumption rate when switching behaviors. An individual's learning ability and tendency to explore are important to the animal's ability to adapt to a new environment. The model provides a chance to explore relocation scenarios with memory that can be hard to manipulate experimentally. Foragers seem relatively insensitive to the consumption rate at their previous location or recent experience negatively impacting their ability to adapt to their new environment. Likewise, most non-extreme learning rates for average consumption are effective at providing the forager with the information it needs to switch between feeding and searching behaviors. Turning to learning rates for memory streams of habitat quality, faster rates are preferred for long-term memory and slower rates for short-term memory. Finally, performance along the exploration–avoidance spectrum was habitat-dependent, with more values performing well at the GRS compared to the PRS, though in general low to moderately exploratory values are successful. These results have implications for how stress may impact relocation success, the importance of the average consumption rate being based on a long-term average in stochastic environments, and issues with selecting animals for relocation based on behavioral type.

Most values for the average consumption learning rate, α, and start value, $\bar{C}(0)$, allowed foragers to adapt to the consumption rate of their new environment. This assumes foragers can learn the quality of new habitat (Brown 1998; Morris 2003), though there has been some suggestion that foragers cannot accurately asses unfamiliar habitat and instead rely on simple cues to evaluate new habitat (Stamps and Swaisgood 2007). Here we used a fairly simplistic learning algorithm (Esposito et al. 2010) that did not take into account the signal given by the transition to a new place from the relocation event. In addition, the start value, i.e., how different the previous environment may have been, did not have a big effect either. Most learning rates had reasonable performance other than values at the extremes of small and large. The exceptions are when no learning takes place, in which case having a well-calibrated start value becomes important, and with very fast learning rates that heavily weight very recent experience.

No learning ($\alpha = 0$) but a good start value still outperforms faster learning rates, showing the importance of having the average consumption value reflect a long-term average. This would suggest that foragers relocated from habitats of very different quality and using a fixed average consumption rate would be at a disadvantage. Indeed, dispersers coming from high quality habitat may experience a strong preference for habitat similar to their natal habitat, resulting in long dispersals from translocation release sites (Stamps and Swaisgood 2007). One difference between the movement processes is that the largest start value (0.01) performs as well as the most accurate start value with memory, even with small/zero learning rate, while it is the worst performing with kinesis. For memory, it is more of an advantage to find the best performing patches, which a large value for behavior switching facilitates, because the forager will be able to return there once found. For kinesis, on the other hand, it is better to exploit any relatively good patch when there, since the forager may never return to that spot again.

The result that animals integrating their experience over a longer time scale (i.e., slower learning rates for average consumption) perform better is in accordance with other model results of patch foraging behavior (McNamara and Houston 1985; Esposito et al. 2010). In particular, Esposito et al. (2010) found that the combination of very fast learning rates (so that behavior is only based on recent experience) combined with heterogenous landscapes led to great variability in consumption and greater risk of death. When discrete resources were patchily distributed, both search time and energy intake were important in patch leaving decisions (Esposito et al. 2010). Here only energy intake is a factor, but it would be interesting to consider some search time criteria for a relocated animal making larger-scale movements. That is, average consumption rate, or energy gain, would affect small-scale switching between searching and feeding behavior, while time searching (as opposed to feeding) would affect larger-scale habitat selection, perhaps through the value of uninformed memory.

For foragers using memory, there are separate learning rates (β_S, β_L) for the short- and long-term streams representing habitat quality. For the long-term attractive memory stream, there is a clear preference for faster learning rates for the GRS and vice versa for the short-term repulsive memory stream. For the PRS, there is also a benefit from faster learning rates, but this is only apparent with moderate levels of exploration–avoidance for new habitat (uninformed memory value). This is likely due to the fact that at the GRS site, it is relatively easy for foragers to find good quality habitat irregardless of the uninformed memory value, thus there is a clear preference with memory values. For the PRS, on the other hand, good patches are more difficult to locate, so the learning rate only matters for those uninformed memory values that actually succeed in locating and remaining long enough in good patches to learn about them and return to them.

There is an asymmetry in the best performing learning rates: faster learning rates yielded higher consumption for the long-term attractive memory stream and slower learning rates yielded higher consumption for the short-term repulsive memory stream. For the short-term memory stream, on the other hand, high learning rates can be a disadvantage depending on the values of other parameters (e.g., short-term decay rate and short memory factor). Like the results in Chapter 1, the short-term memory stream needs to be large enough to initially repulse the animal, but a short-term memory stream that gets too large or decays too slowly is a long-term detriment, preventing the animal from returning to a regenerated area.

It seems self-evident that a faster learning rate would be more successful for long term-memory, and given the structure of the spatial learning kernel, this is likely to increase up to infinity. Even though the learning in the local area quickly saturates at its maximum, larger learning rates still incrementally improve learning about habitat quality farther away due to the bivariate normal kernel (or any kernel with infinite support). Actual learning rates in animals are likely limited by energetic costs or physiological constraints. In fact, stress can impair spatial learning (Hölscher 1999; Zoladz et al. 2012), a concern for relocated animals given that relocations can increase stress (Chipman et al. 2007; Stamps and Swaisgood 2007). In fact, the impact of relocation stress on an animal's ability to learn about its new environment is a particular concern (Teixeira et al. 2007). Relocation stress could effectively lower a forager's long-term learning rate (Fig. 3.3), and thus impair the formation of a spatial map of resources. Teixeira et al. (2007) suggest that this stress-induced resource memory impairment could be an important but unacknowledged factor in the high mortality observed in many animal relocations.

With spatial scale, the same step function-like response observed in Chapter 1, where all but the smallest values perform well, is also apparent here. Spatial scale is important for how differences are integrated across the landscape and how far away habitat quality influences movement decisions. For a fully informed individual, knowing the full extent of resource locations, a larger spatial scale allows access to high quality patches located farther away. This holds true for an uninformed individual as well, though the spatial scale values are less clearly distinguished than the optimal uninformed memory values. This points to the importance of knowing or discovering high quality areas as a precondition to using the appropriate memory spatial scale to relocate them, something that could be impaired by relocation stress (Teixeira et al. 2007).

Indeed, the exploration–avoidance axis is critical for how an animal using memory explores its environment, even more so than the average consumption learning rate. While the average consumption learning rate does affect the total amount consumed, it does not change how the animal uses space or its ultimate location. How precisely the value placed on unexplored habitat changes the resulting habitat use depends on the quality of the release site. With the GRS, little variation was observed across a wide range of exploration–avoidance values, and all but the most exploratory values led to a similar result of exploiting the nearby good patch. It was only extreme exploratory values that resulted in kinesis-like behavior of wide-ranging space use and lower consumption. However, when there was not sufficient quality habitat immediate to the release site, then the precise calibration of the uninformed memory value along the exploration–avoidance axis became more important. Less exploratory and the animal remains in suboptimal habitat near the release site, but too exploratory and the animal moves widely with kinesis-like behavior and never settles into a home range (Fig. 3.9). In fact, with the optimal uninformed memory value, the space use of the uninformed individual most close approximates that for the fully informed individual.

Correlations exist between behavioral types, so individuals scoring high in boldness are also likely to have a high exploratory tendency (Sih and Del Giudice 2012). Behavioral types are also correlated with dispersal behavior. Bolder individuals dispersing more readily and farther away can lead to later species interactions, such as larger impacts on the dispersers prey (Sih et al. 2012). These differences in dispersal tendencies, and the variation in performance for foragers with different exploratory tendencies with release site quality examined here point to additional reasons to be wary about selecting against boldness in relocated individuals (Smith and Blumstein 2008).

It is worth noting that there is no cost in this model associated with ever larger learning rates or even with memory storage itself. A more realistic version could include some debiting of consumption to account for cognitive costs, which could vary by learning rate or other factors. While memory, both of resources and and predation risk in the case of predators, decays in intensity with time, decays in spatial precision could also be included (Fagan et al. 2013). That is, the memory would lose precision of the exact location of resources as time away from the area increased. Decay rates could also have cognitive costs such that maintaining memories more accurately in time and space would be more expensive.

Another limitation of the current model is that animals are considered individually with no competitive effects. Thus, in the case of the GRS, if multiple animals are released at the same location, they might not all be able to take advantage of the nearby good patch. Instead, the PRS might be more representative when competitive interactions come into play. Sociality can also be important, with dispersal distances and mortality both higher in solitary individuals compared to those in groups for introduced elk (Haydon et al. 2008).

While animals may be able to learn average habitat quality, this is just one simplified metric. Other habitat factors may be important (e.g., water sources, nesting/breeding locations, cover) that cannot be encompassed one variable. Another important consideration not covered here is predation. In addition to learning predator locations from encounters (Chapter 2), a forager must have the ability to recognize predators at all and have the appropriate antipredator behavior (Fischer and Lindenmayer 2000). The model also suggests the dispersal period could be critical, especially when resources are unavailable in the immediate release location due to habitat unsuitability there or competition from conspecifics. Animals must be exploratory enough to disperse, but also not too exploratory that they fail to stop at appropriate locations. However, given the differences in optimum values of exploration–avoidance between the GRS and the PRS, habitat differences may be related to maintaining variability in exploration–avoidance within populations.

Spatially-explicit population model that incorporate dispersal and life history traits can be used to predict the distribution of introduced species (Macdonald and Rushton 2003). Animals were assumed to form home ranges in unoccupied habitat of suitable size. However, given the importance of memory to home range formation (Van Moorter et al. 2009; Spencer 2012) and the results here on the effect of memory state on dispersal patterns, incorporating memory into these models could affect the dispersal dynamics of introduced species. Model robustness in predicting dispersal patterns appeared linked to quality of habitat data (Macdonald and Rushton 2003), and lack of finer-scaled habitat quality data could be a barrier to the inclusion of memory to the dispersal process.

Chapter 4

DOES MEMORY STATE MEDIATE THE EFFECT OF PREDATOR INTRODUCTIONS ON FORAGER BEHAVIOR?

Abstract

Predators are important to community structure, and predator reintroductions can serve to protect species and restore ecosystem function. While some observations of prey behavior changes, such as shifts in habitat use, exist, prey response to predator introductions is not well studied. Here a modeling framework is used to examine the impacts of predator reintroduction on foragers and how the forager's habitat memory influences these dynamics. Introduced predators vary in the area threatened and foragers vary in their memory state. Results indicate that area threatened plays a key role in determining how much habitat use changes. The forager's knowledge of alternative habitats and exploratory inclinations affects what types of shifts occur. This finding suggests that habitat shifts by prey can be extreme in some cases, but that prey can make use of refugia in others and are particularly likely to do so when they have less exploratory inclinations. In general, search time increases and consumption decreases after predator introduction. However, spatial memory of the surrounding area can mitigate the effect of introduced predators, as foragers can better access alternate habitat.

4.1 Introduction

Predators can play a key role in ecosystem dynamics, making their reintroduction after extirpation important for both conservation goals and for the complex top-down effects predators can exert (Terborgh et al. 1999; Hayward and Somers 2009; Johnson 2010; Grange et al. 2012). Trophic cascades are widespread and have been documented in a variety of freshwater, marine, and terrestrial ecosystems (Estes et al. 2011). Evidence from aquatic systems shows that both density effects (i.e., changes due to predator-induced changes in prey densities) and behaviorally mediated effects (i.e., changes due to predator-induced changes in prey behavior) are important to trophic cascades triggered by predator declines (Heithaus et al. 2008). Removals of top predators impact ecosystem processes ranging from disease to biodiversity (Prugh et al. 2009; Estes et al. 2011). For example, in a lake system, the removal of the top predator largemouth bass (*Micropterus salmoides*) resulted in dramatic changes to community structure, both in numbers and species composition; critically, after bass were reintroduced, the ecosystem steadily returned to its previous state (Mittelbach et al. 1995). When most carnivores were removed from an area in the northern Serengeti, small ungulate densities increased dramatically compared to a nearby non-removal area while the less-vulnerable larger ungulate did not; again, ungulate densities returned to lower levels with the reintroduction of predators (Sinclair et al. 2003).

Most existing studies in reintroduction biology have been retrospective, however, and Seddon et al. (2007) emphasized the need to shift to more hypothesis-driven research, such as well-designed experiments and modeling approaches. Additionally, topics such as general accounts and population dynamics dominate, with relatively little attention payed to ecosystem effects such as predator–prey interactions (Seddon et al. 2007). This chapter examines predator reintroductions from the perspective of the forager prey and explores how forager memory state can affect habitat shifts by the prey.

First, I survey some examples of predator reintroductions. Perhaps one of the most well-known and well-studied terrestrial predator reintroduction is wolves (*Canis lupus*) in Yellowstone National Park (Fritts et al. 1997). Early studies of plant communities suggested a trophic cascade in which riparian vegetation recruitment ceased when wolves were extirpated from the area in the 1920's, releasing elk (*Cervus elaphus*) from predation risk; with their reintroduction in 1995–1996, wolves were thought to reduce elk densities as well as modify their movement and browsing patterns leading to new recruitment and increased height of woody browse species (Ripple and Larsen 2000; Beschta 2003; Ripple and Beschta 2004, 2006). There is evidence for behavioral changes in elk with the reintroduction of wolves. Elk displayed fine-scale habitat shifts to protective woody areas away from preferred but higher risk open grassland when wolves were present (Creel et al. 2005). Elk preference shifted from aspen stands to conifer forest in high wolf-use areas in winter (Fortin et al. 2005), though comparing elk distribution before and after wolf reintroduction mainly showed habitat selection changes in summer rather than winter (Mao et al. 2005). A winter kill site analysis showed landscape features determine patterns of predation suggesting distinct areas of predation risk and prey refugia independent of wolf distribution (Kauffman et al. 2007). However, further research complicated the initial picture, and recent studies do not support the hypothesis of a behavior-mediated trophic cascade (Vucetich et al. 2005; Kauffman et al. 2010; Winnie 2012; Marshall et al. 2013).

Another example of predator reintroductions is large carnivores, particularly lions (*Panthera leo*), in protected areas of South Africa (Hayward et al. 2007a; Grange et al. 2012). Reintroductions have generally been successful (Hayward et al. 2007a) and, in some cases, negatively impacted prey populations (Hayward et al. 2007b). Predator reintroductions have been used to limit prey populations and restore ecosystem function in reducing forager impacts on vegetation (Brooks and Macdonald 1983). Predators did not necessarily affect prey population trends, even when accounting for most observed prey mortality (Grange et al. 2012). Prey vulnerability can shift with shifting habitat quality (driven by rainfall), which can then affect predator prey preference (Owen-Smith and Mills 2008).

Recolonizations are also examples of predators returning to areas where they have been absent for some time, albeit without direct human involvement. Indirect evidence for the impact of recolonizing lynx (*Lynx lynx*) on their prey in the Swiss Alps comes from observations of smaller home ranges and closely spaced kills at the leading edge of recolonization (Breitenmoser and Haller 1993). For recolonizing lynx in Finland with a four-level food web, habitat productivity alone did not predict species densities (Elmhagen et al. 2010). The relative abundance of the top-predator lynx was important: when lynx controlled mesopredator abundance, lynx and herbivore biomass increased with productivity, while otherwise only mesopredator biomass increased with productivity.

In these studies of predator reintroductions, resulting changes in forager behavior have generally not been considered, with the exception of habitat use changes in Yellowstone elk (Creel et al. 2005; Fortin et al. 2005; Mao et al. 2005). In particular, how foragers might use memory to mediate the effects of predator reintroductions may aid in understanding the behavioral responses of foragers, given the impact of memory on foraging behavior (Chapter 1)) and predator avoidance (Chapter 2). Memory is particularly challenging to study in an ecological context, however, given that it cannot be measured directly, so memory state cannot be inferred even from difficult-to-obtain detailed information on an animal's past experiences. However, experimental evidence exists for the role memory plays in directing foraging behavior (Kamil and Roitblat 1985; Shettleworth 2001; Stephens et al. 2007). Likewise, animals are known to learn from and avoid predator encounters (Huntingford and Wright 1989; Wisenden et al. 1994; Griffin et al. 2000; Nomikou et al. 2003).

Forager state is known to affect risk-taking behavior, particularly in the case of hunger or body condition (McNamara and Houston 1986; Lima 1988; Whitham and Mathis 2000; Olsson et al. 2002; Heithaus et al. 2007). Memory can also be a component of forager state that influences risk-taking. For example, predator-experienced mice (*Mus domesticus*) changed their foraging behavior in response to signals of increased predation risk while predator-naive mice did not, and those differences in foraging behavior correlated with survival (Dickman 1992). These changes in foraging behavior as a result of food–safety trade-offs mean that non-consumptive effects from predators are also possible (Lima and Dill 1990; Preisser et al. 2005; Cresswell 2008). Foragers using memory, as compared to kinesis-driven foraging behavior, have stronger non-consumptive effects from predation (Chapter 2). Given these factors, memory likely plays a role in changing foraging behavior after predator introduction for foragers with those cognitive capabilities. A modeling approach provides a way to gain insight into how memory influences these predator–prey interactions.

This chapter investigates the impact of predator reintroduction on foragers and, indirectly, the resource when foragers are using memory to make movement decisions informed by both habitat quality and predator encounters. Predators are introduced to the areas of highest-quality habitat and vary in how large an area they threaten. Foragers differ in their knowledge of the surrounding habitat and how exploratory they are in the face of new habitat. The movements of the foragers are analyzed before and after predators are introduced to understand how memory influences changes in forager behavior in three areas: (1) consumption, (2) time budget, and (3) space use.

4.2 Methods

Rather than the introduction of naive foragers to a new landscape, as in Chapter 3, this chapter focuses on the before/after experiences of foragers when predators are reintroduced to a landscape. As a framing device, the landscape used for these simulations is the northern range in Yellowstone National Park. Using this landscape provides realistic spatial variation where there are habitat quality data available, not simply habitat type. Note that the model presented here is a generic model of predator reintroduction and is not an attempt to model wolf–elk dynamics there, as wolf hunting mode does not match that of the modeled predators (Preisser et al. 2007), though see Bennett and Tang (2006)for a model that includes memory and learning on the part of the elk. Instead, this chapter seeks to address how memory could impact forager habitat use changes after predator introduction in a general way.

4.2.1 Resource data

The data used for the habitat quality come from the CASA Express NPP dataset, a scaled-down version of the Carnegie Ames Stanford Approach (CASA), which produces estimates of net primary productivity (NPP) in units of g C/m^2/month on a 500m grid (Yellowstone Ecological Research Center and Ecological Forecasting Lab at NASA Ames Research Center 2014). The data used are the 11-year average for 2000–2010 for the month of July when productivity was highest. The spatial extent used in the model was (44.6°, -111°) to (45.02°, -110°) resulting in a 240 x 100 grid, representing the northern park territory.

Because the original data resembled the smoother landscapes of Chapters 1 and 2, a

Table 4.1: Parameters used in the model and values for simulations. Because units are arbitrary in the simulations, L is used for generic length units, T is used for generic time units, and R is used for generic resource biomass units.

	Parameter	Definition	Units	Values
Simulations				
	Δt	model time step	T	1
	T	simulation length (time steps)		4000
	T'	predator introduction (time steps)		2000
Predator environment				
		total predation pressure	T	15000
	δ	predator duration	T	1000
	ρ	predator spatial randomness		0
	ϵ	encounter radius	L	5, 10, 20
Consumption				
	β_R	regeneration rate	1/T	0.01
	β_C	consumption rate	1/T	1
	γ_C	consumption spatial scale	L	1
Memory[a]				
	ψ_M	short-term memory factor		2
	β_L, β_S	learning rates	1/T	5, 1
	ϕ_L, ϕ_S	decay rates	1/T	0, 0.01
	γ_L, γ_S	learning spatial scale	L	1, 1
	γ_Z	memory spatial scale	L	10
	$M*$	uninformed memory	R	0, 1e-4, 1e-3
Predator memory				
	ψ_P	predator memory factor		100
	β_P	predator learning rate	1/T	10
	ϕ_P	predator decay rate	1/T	0.001
	γ_P	predator learning spatial scale	L	ϵ
	γ_R	predator risk spatial scale	L	10

[a] L = long-term memory, S = short-term memory

Table 4.1: (continued)

	Parameter	Definition	Units	Values
Movement[b]				
	τ_S, τ_F	autocorrelation time scale	T	4, 2
	ν_S, ν_F	length of μ	L/T	6, 1
	λ	mean time to update θ	T	1

[b] S = searching, F = feeding

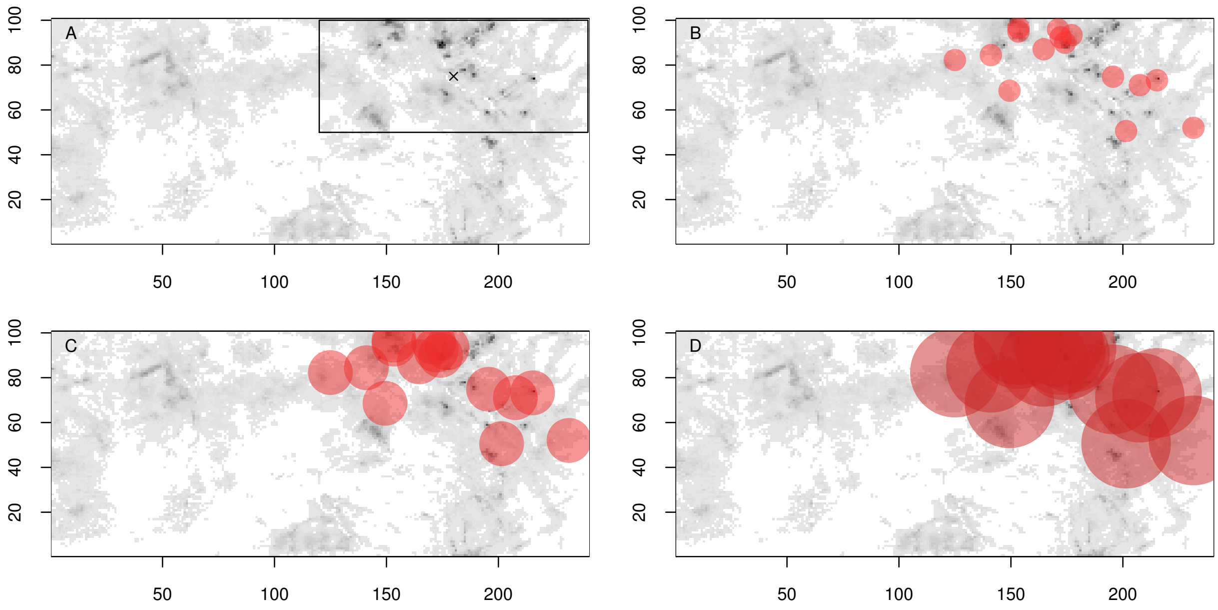

Figure 4.1: Landscape used in the simulation based on transformed NPP in northern Yellowstone National Park (2000–2010) for July showing A) habitat quality and box bounding locations of introduced predators with forager's starting location shown with x, B) Predators with encounter radius of 5, C) Predators with encounter radius of 10, and D) Predators with encounter radius of 20.

transformation was used to more clearly differentiate the poor quality areas from the best quality areas. This transformation can be thought of as a preference function of the forager, expressing a non-linear preference for areas high in NPP compared to areas low in NPP. The transformation used is $f(x) = \exp(0.1x)$ (Fig. 4.1A). In the resulting landscape, the distribution of resources is 42% in the northeast quadrant, 20% in the southeast quadrant, 14% in the southwest quadrant, and 24% in the northwest quadrant.

4.2.2 Simulations

Simulations begin with no predation, then predators appear in the northeast quadrant of the landscape half way through the simulation. Within this quadrant, containing the best quality habitat, predator locations are correlated with landscape quality. That is, the probability of a predator being at a location is proportional to that location's quality relative to the quality in the quadrant. Different predator encounter radii represent the variability in space these could take on, from fairly small to large enough to cover most of the quadrant (Fig. 4.1B-D). A long predator duration is used to represent relatively stable territories for the introduced predators, but still allowing for some variability.

Simulations start with the forager located in the center of the northeast quadrant, the area of highest quality, where predators are eventually released (Fig. 4.1A). All parameters used in the simulation are shown in Table 4.1. Parameters controlling the resource and predation memories that were not varied are set based on the results from Chapter 2 using the optimally performing parameters for the predator environment under high survival.

Foragers vary in their memory initialization, or *memory state*. Some foragers start out *fully informed*, knowing the resource quality for the whole landscape. Other foragers start out *naive* and have a chance to explore the landscape before predators are introduced. It should be emphasized that "naive" refers to the forager being unfamiliar with their surroundings, not the predator (Sih et al. 2010). That is, it is assumed that the foragers display effective antipredator behaviors of escape and remember encounter locations. Memory state is set at the beginning of the simulation by initializing the long-term attractive memory stream, L, and the short-term repulsive memory stream, S (see Eq. 1.4, Chapter 1). For fully informed foragers, S is initialized to zero and L is initialized to the intrinsic resource quality, Q_0. For naive foragers, S is initialized to zero and L is initialized to the uninformed memory parameter $M*$, i.e., how unexplored habitat is valued. In all cases, it is assumed that the foragers know the true average consumption rate of the landscape used to switch between searching and feeding behaviors. Thus foragers differ in their knowledge of the landscape outside their starting region when predators are introduced or how exploratory they are with new habitat.

Half way through the simulation at $t = T'$, predators are introduced. Predators vary in their encounter radii, or how much of the landscape they occupy. This variation affects whether there are refugia within the northeast quadrant once it is occupied by predators.

Each set of parameters is repeated 50 times given the stochastic nature of the results.

4.2.3 Metrics

Foragers' habitat use, consumption, and state are tracked. Several measures permit comparison of forager behavior before and after predator introduction. One key metric is the amount that foragers are consuming, which is a measure of the predator's indirect impact on the resource. The number of predator encounters after predators are introduced is also important to evaluate consumption changes. Another behavior to examine is the forager's time budget, or how it divides its time between searching and feeding. Finally, in order to compare the space use before and after predators are introduced, trajectories are visually examined and the utilization distribution is calculated using `kernelUD` in the `adehabitatHR` package (Calenge 2006) in R (R Core Team 2014).

4.3 Results

4.3.1 Consumption changes

Increasing the predator encounter radius decreased consumption and increased encounters (Table 4.2). Naive foragers with a low exploratory inclination ($M* = 0$) had the highest consumption but also the highest encounters. Fully informed foragers and naive, moderately exploratory foragers ($M* =$ 1e–4) had the next highest consumption and encounters. Naive foragers that were very exploratory ($M* =$ 1e–3) had much lower consumption and slightly lower encounters.

In all scenarios, predator reintroductions depressed the amount consumed relative to the period before predators (Fig. 4.2). The forager's memory state primarily partitioned the pre-predator consumption amounts, although this carried through to the post-predator environment as well, with higher pre-predator consumption associated with higher post-predator consumption. Surprisingly, the least-exploratory forager performed the best, followed by the fully informed forager, the moderately exploratory forager, and then the very exploratory

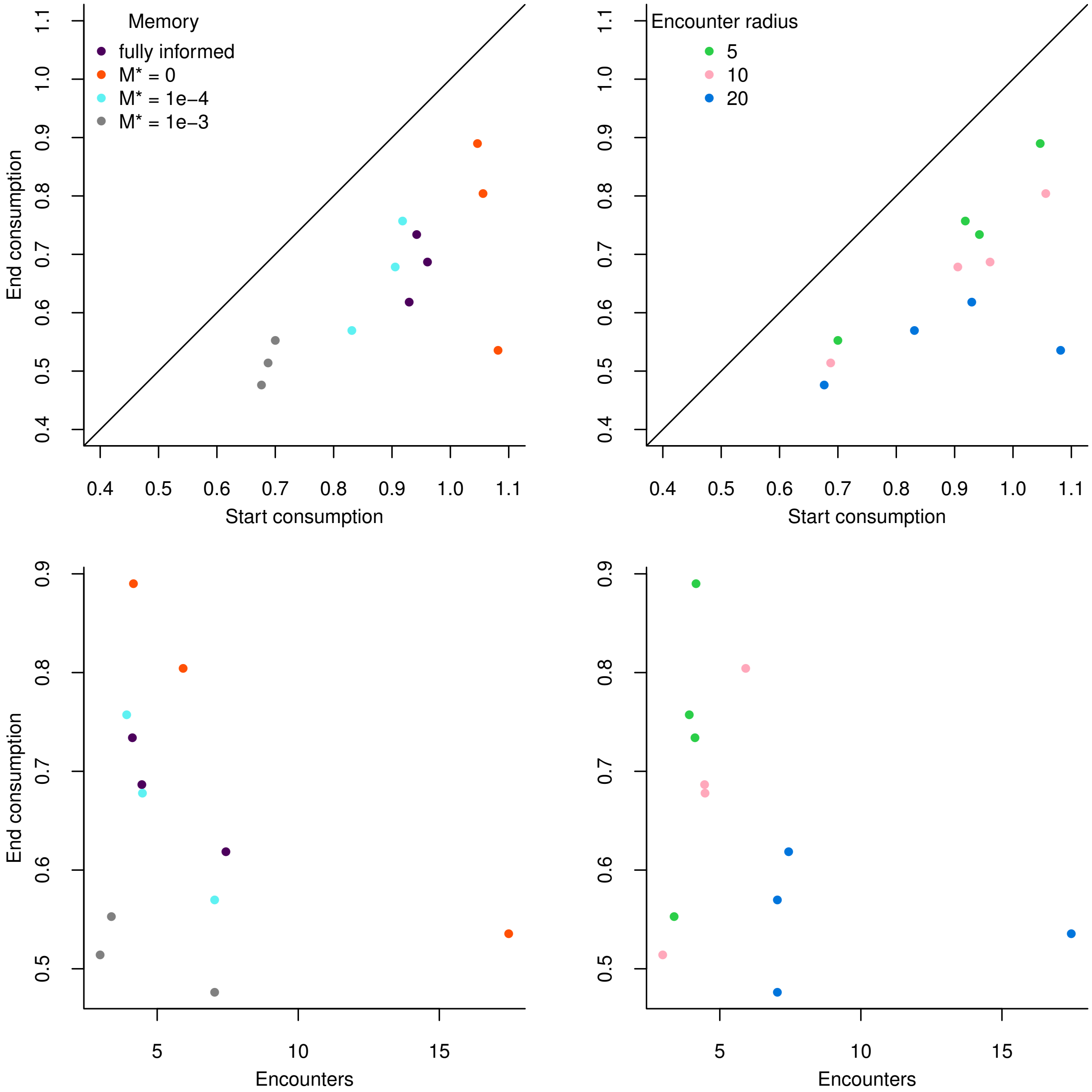

Figure 4.2: Top row: pre-predator consumption vs. post-predator consumption for memory state (left panel) and encounter radii (right panel). Bottom row: encounters vs. consumption in the post-predator environment for memory state (left panel) and encounter radii (right panel).

Table 4.2: Mean total consumption and number of predator encounters for each scenario (memory state and encounter radius) for 50 replicate simulations.

Scenario		Consumption	Encounters
$M*$	ϵ		
full	5	1.68	4.1
full	10	1.65	4.5
full	20	1.55	7.5
0	5	1.94	4.1
0	10	1.86	5.9
0	20	1.62	17.7
1e–4	5	1.68	3.7
1e–4	10	1.58	4.5
1e–4	20	1.40	7.1
1e–3	5	1.25	3.3
1e–3	10	1.20	3.0
1e–3	20	1.15	7.0

forager. For a given memory state, the predator encounter radius controlled how large a decline in consumption occurred after predator introduction, with larger radii associated with larger declines.

The flip side of consumption is predator encounters, and in general higher encounter rates were associated with lower consumption, unlike the food–safety trade-off frequently observed in Chapter 2. Within a memory state, larger encounter radii led to higher encounters and also depressed consumption. While the largest encounter radius of 20 had the highest absolute encounter rate, smaller encounter radii are only ordered with respect to encounters within memory states, not absolutely. The performance of fully informed memory and moderately exploratory ($M* =$ 1e–4) was quite similar for both consumption and encounters.

4.3.2 Time budget changes

The time spent searching increased after predators were introduced, as foragers leave their initial habitat to avoid predators (Fig. 4.3). This occurred even with fully informed memory, where the forager had knowledge of other resource locations (though still had to relocate

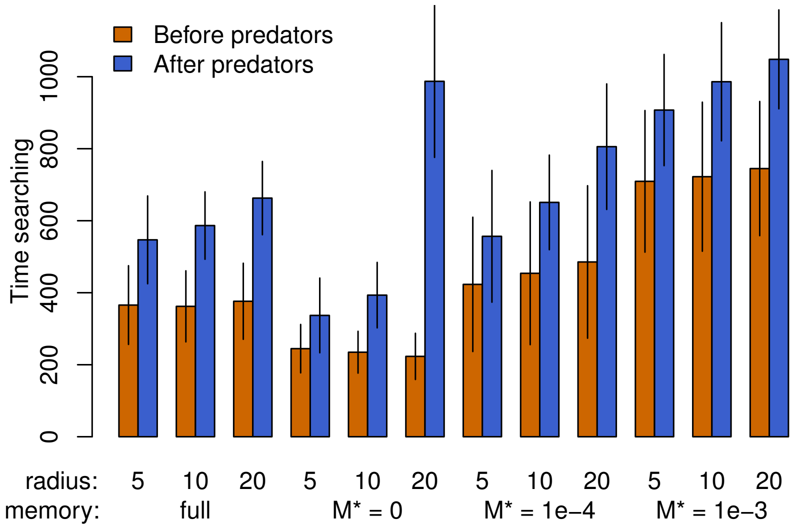

Figure 4.3: Time spent searching before and after the introduction of predators across different values for the encounter radius (top line x-axis) and for memory state (bottom line x-axis, fully informed and different values for uninformed memory) with lines showing the standard deviation. The remainder of the time was spent feeding before predators and split between feeding and escape after predators. A minimal amount of time was spent in the escape behavior (mean 3–17).

there), and uninformed memory, in which case the forager had to initially locate resources. The increase in time spent searching was also larger with increasing encounter radius. This increase could be slight (as in the case of fully informed memory) or dramatic (as with less-exploratory foragers, $M* = 0$). Significantly, the largest increase in search time occurred in the same scenarios with the largest decreases in consumption.

4.3.3 Space use changes

Trajectories

Space use varied dramatically with memory state (Figs. 4.4, 4.5). The least-exploratory forager (Fig. 4.4, right) was the most constrained with large areas of habitat completely unexplored and space use concentrated in the area of release. Fully informed memory (Fig. 4.4, left) exploited the entire landscape but concentrated use in the best quality habitat and minimally traveled through unproductive habitat. The moderately exploratory forager (Fig. 4.5) similarly exploited the entire landscape focusing on high quality areas but spent more time in unproductive habitat as well. Finally, the very exploratory forager (Fig. 4.5) had the most dispersed space use across the entire landscape. The effect of predator radii is also apparent, with all memory states being farther displaced from the best quality northeast quadrant with increasing values of predator encounter radius. The partition of space by time was also clearer with larger encounter radii.

Utilization distribution

The kernel density of space use clearly changed after predators were introduced across encounter radii for fully informed memory (Fig. 4.6) and naive foragers with exploratory inclinations varying from least-exploratory ($M* = 0$, Fig. 4.7) to moderately exploratory ($M* =$ 1e–4, Fig. 4.8) to very exploratory ($M* =$ 1e–3, Fig. 4.9). Examining the space use before predators were introduced, similar patterns in memory state and tendency towards exploration as discussed in Chapter 3 were observed. The least-exploratory forager remained at

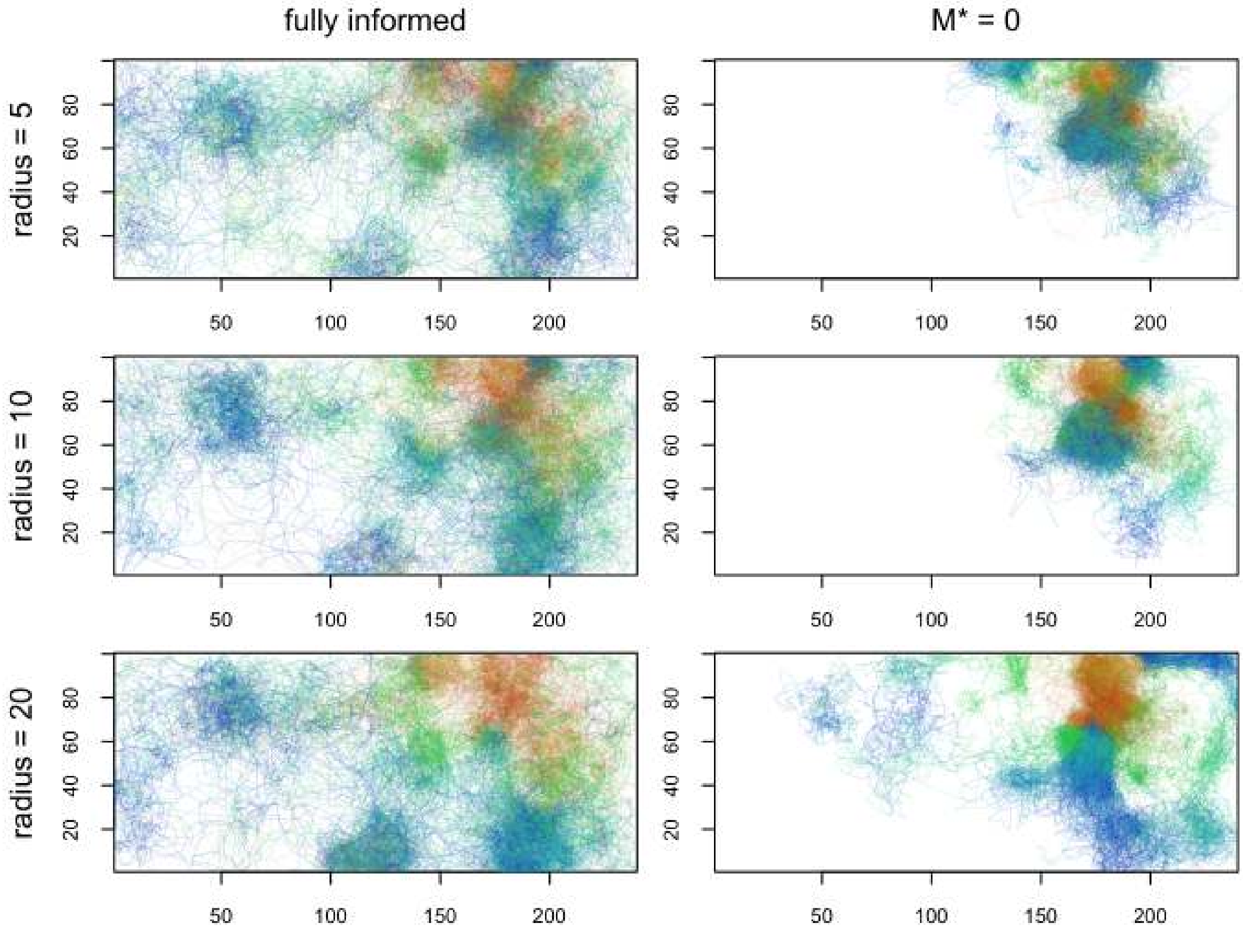

Figure 4.4: Trajectories for all 50 replicate simulations. Color of line indicates time, with color transitioning from red to orange before predators are introduced and green to blue after. Columns show memory state: foragers with fully informed memory (left) and less-exploratory naive foragers, $M* = 0$ (right). Rows show encounter radii: small (top), medium (middle), and large (bottom).

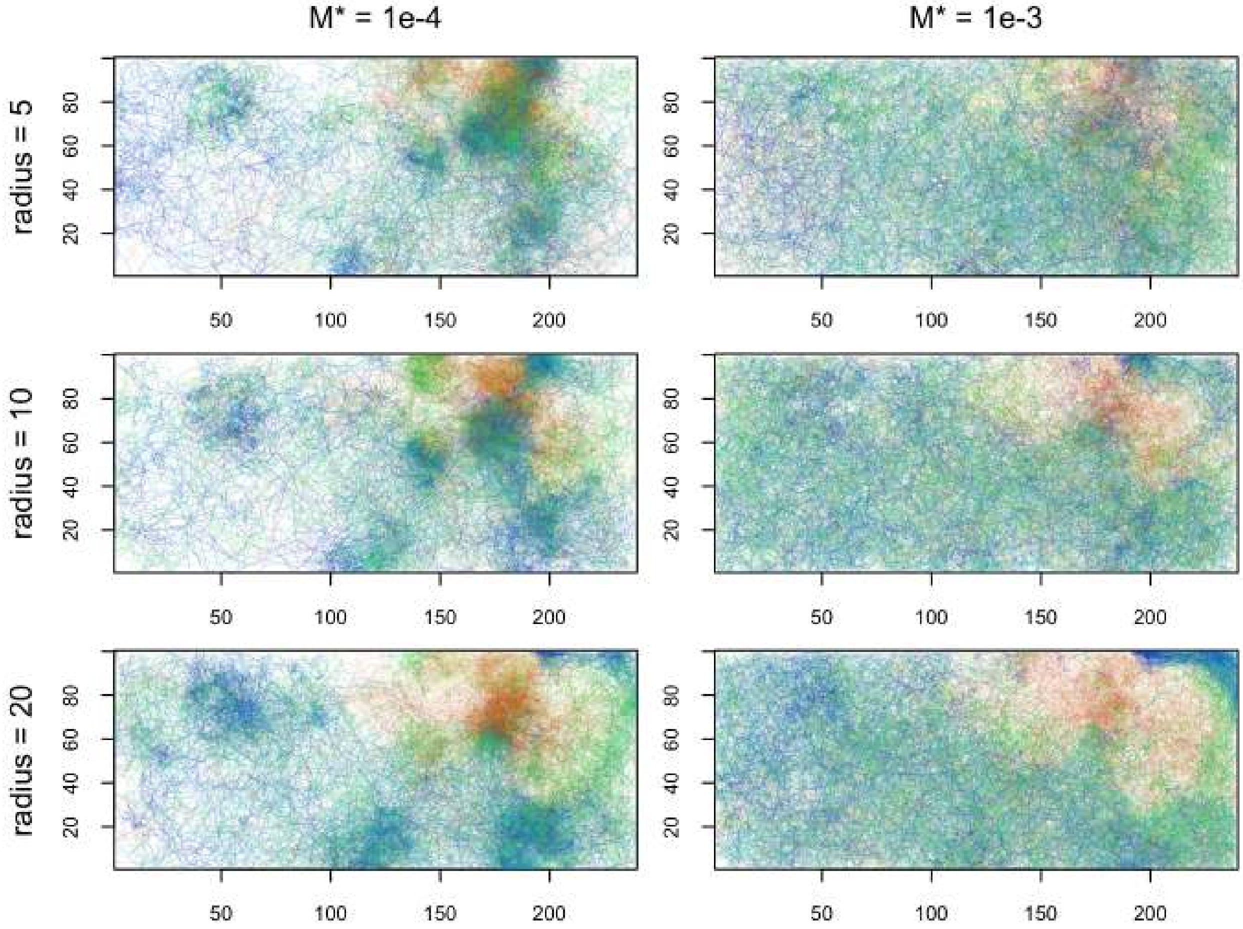

Figure 4.5: Trajectories for all 50 replicate simulations. Color of line indicates time, with color transitioning from red to orange before predators are introduced and green to blue after. Columns show memory state: moderately exploratory naive foragers, $M*$ = 1e–4 (left) and very exploratory naive foragers, $M*$ = 1e–3 (right). Rows show encounter radii: small (top), medium (middle), and large (bottom).

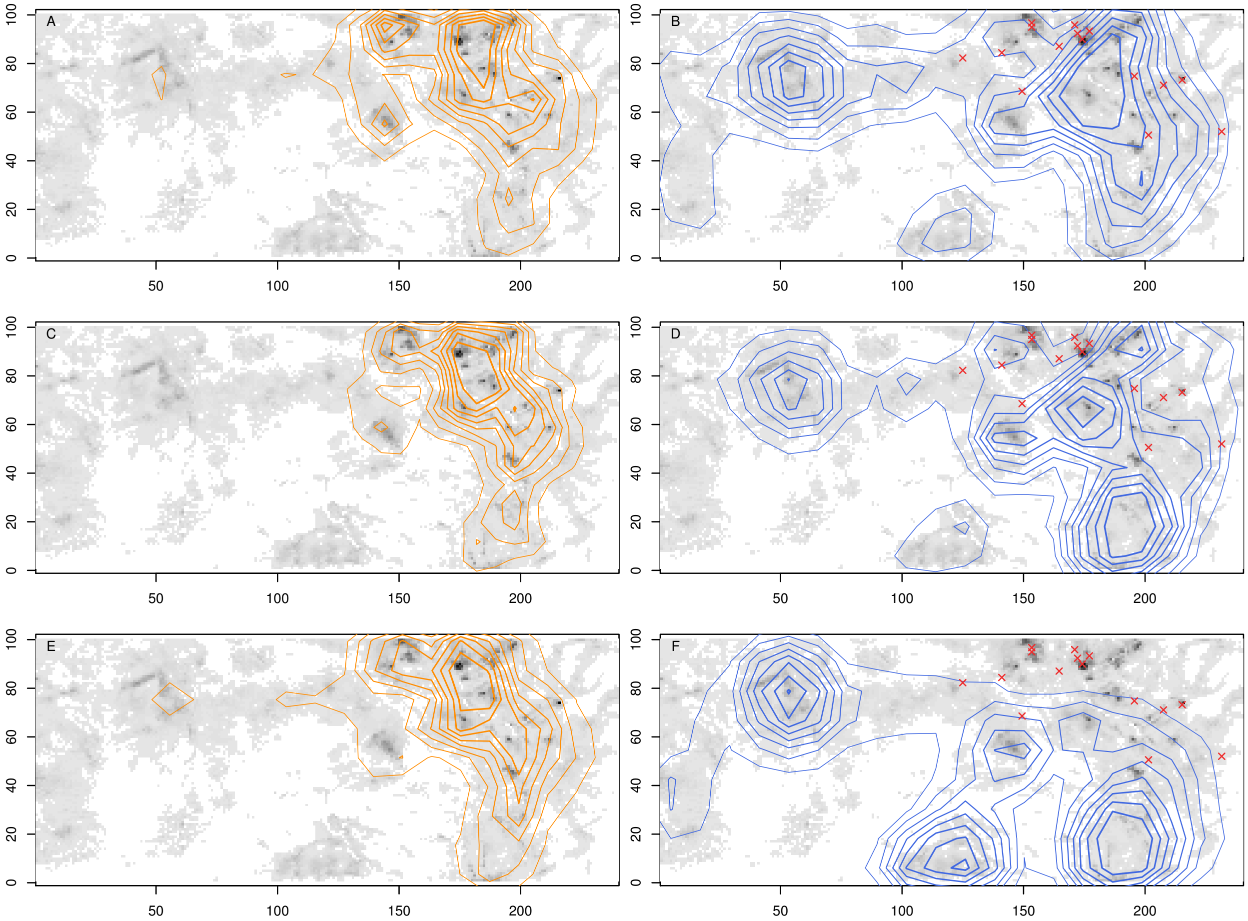

Figure 4.6: Space use for foragers with fully informed memory quantified by kernel utilization distributions comparing before predators (orange, panels A, C, E) to after predators (blue, panels B, D, F). Predator encounter radius varies from small ($\epsilon = 5$, top panels A and B) to medium ($\epsilon = 10$, middle panels C and D) to large ($\epsilon = 20$, bottom panels E and F). Contour lines show 20-90% utilization. Predator center point locations shown with red x's (see Fig. 4.1 for radii). Intrinsic habitat quality shown in grayscale.

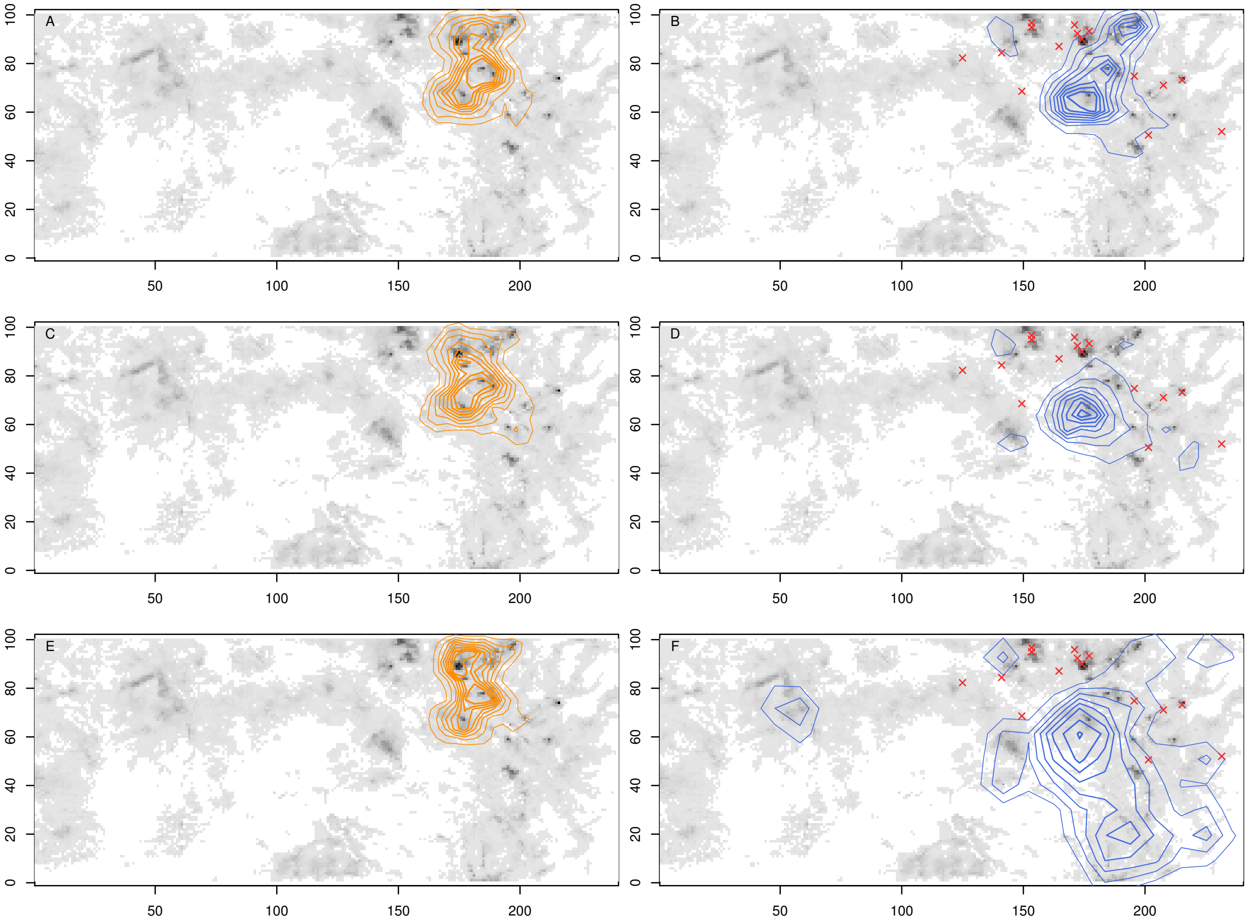

Figure 4.7: Space use for naive less-exploratory foragers ($M* = 0$) quantified by kernel utilization distributions comparing before predators (orange, panels A, C, E) to after predators (blue, panels B, D, F). Predator encounter radius varies from small ($\epsilon = 5$, top panels A and B) to medium ($\epsilon = 10$, middle panels C and D) to large ($\epsilon = 20$, bottom panels E and F). Contour lines show 20-90% utilization. Predator center point locations shown with red x's (see Fig. 4.1 for radii). Intrinsic habitat quality shown in grayscale.

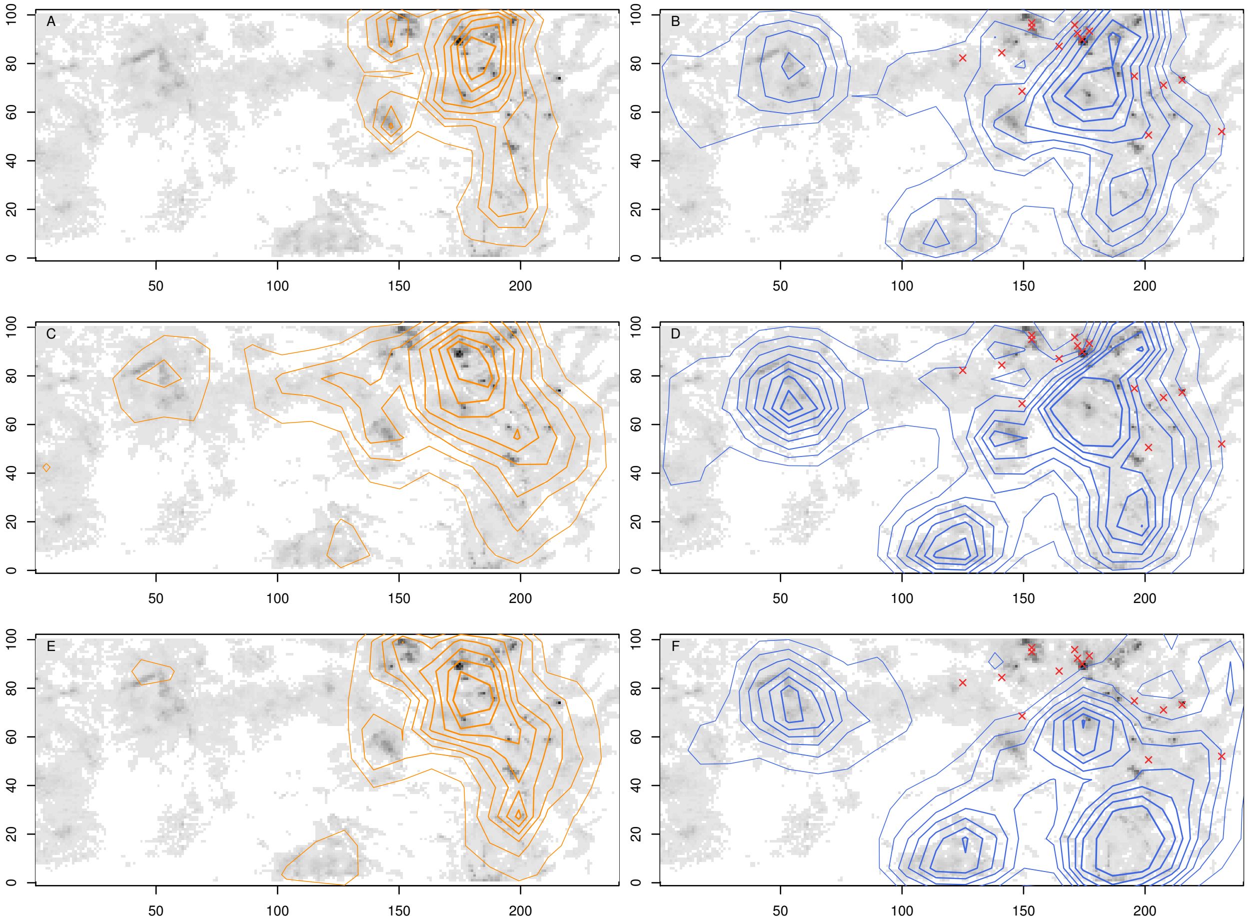

Figure 4.8: Space use for naive moderate exploratory foragers ($M* = 1e\text{–}4$) quantified by kernel utilization distributions comparing before predators (orange, panels A, C, E) to after predators (blue, panels B, D, F). Predator encounter radius varies from small ($\epsilon = 5$, top panels A and B) to medium ($\epsilon = 10$, middle panels C and D) to large ($\epsilon = 20$, bottom panels E and F). Contour lines show 20-90% utilization. Predator center point locations shown with red x's (see Fig. 4.1 for radii). Intrinsic habitat quality shown in grayscale.

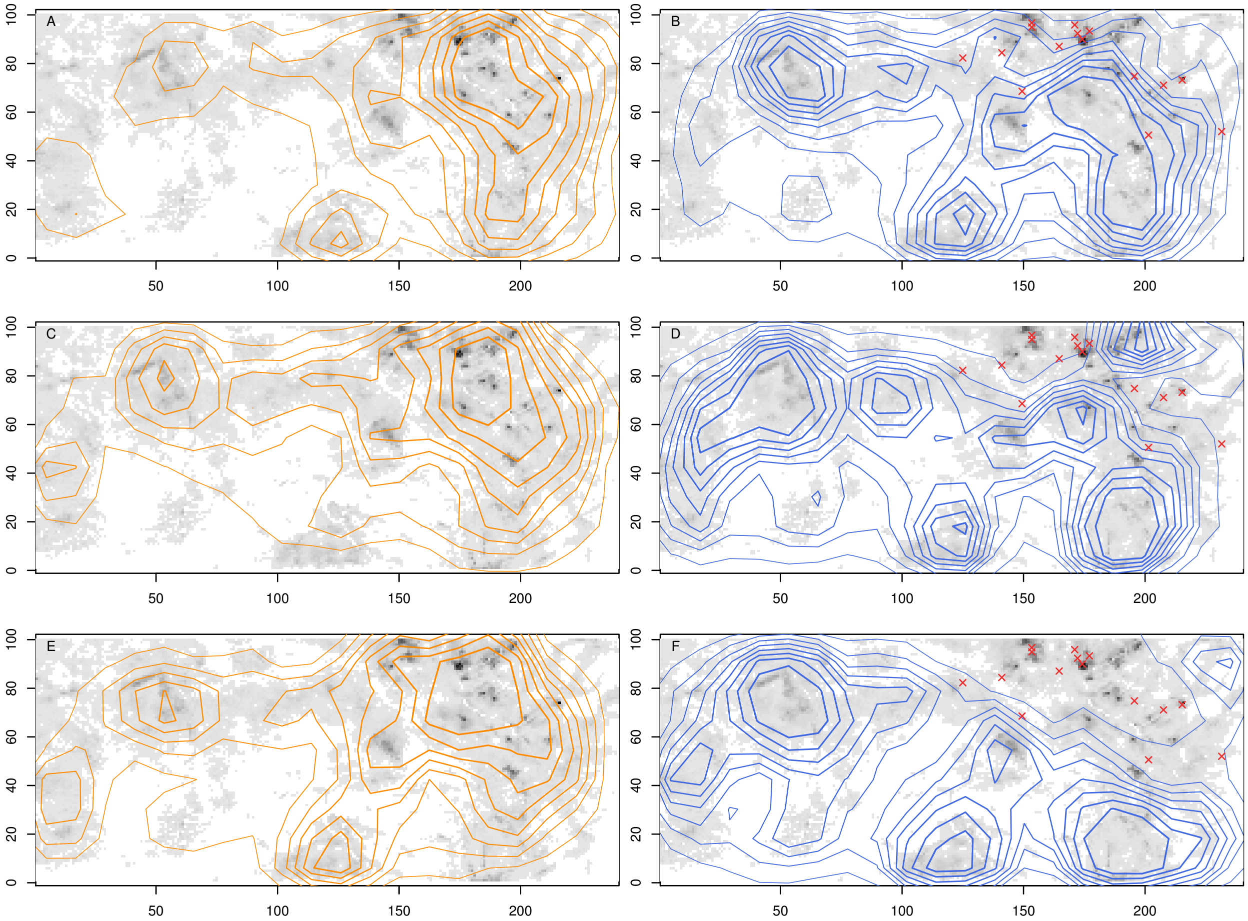

Figure 4.9: Space use for naive very exploratory foragers ($M* = 1e–3$) quantified by kernel utilization distributions comparing before predators (orange, panels A, C, E) to after predators (blue, panels B, D, F). Predator encounter radius varies from small ($\epsilon = 5$, top panels A and B) to medium ($\epsilon = 10$, middle panels C and D) to large ($\epsilon = 20$, bottom panels E and F). Contour lines show 20-90% utilization. Predator center point locations shown with red x's (see Fig. 4.1 for radii). Intrinsic habitat quality shown in grayscale.

the high quality patches closest to the release site, while the moderately exploratory forager exploited the high quality areas of the eastern half of the landscape, and the very exploratory forager was already using the entire landscape. The fully informed memory space use most closely resembled that of the moderately exploratory forager, but was more tightly focused on the best patches. After predators were introduced, the space use changed across all scenarios as foragers were pushed out of the highest-quality areas in the northeast portion of the landscape.

The least-exploratory forager (Fig. 4.7) relocated the least. With the smallest encounter radius, it moved out of the immediate vicinity of the predators but remained in the northeast quadrant exploiting the gaps between predators—the utilization distribution looks remarkable similar, just the upper portion shifted eastward. As the encounter radius increased, the distribution shifted southwards but remained in the northeast quadrant. Finally with the largest encounter radius, the distribution was completely altered moving into the southeastern quadrant. Thus by remaining in the highest-quality quadrant despite predation risk, the least-exploratory forager tended to maintain high consumption but at the cost of higher encounters as well.

The more exploratory foragers showed a stronger shift in habitat use after predatory introduction. The moderately exploratory forager (Fig. 4.8) continued to utilize the better quality habitat in the gaps between predators when the encounter radius was small, but it also expanded into patches to the south and west. This intensified as the encounter radius increased, and the forger shifted to predominately using the patches south and west of the predators. The very exploratory forager (Fig. 4.9), on the other hand, utilized patches across the landscape before predators were introduced, and predators served to move a greater proportion of use to that habitat. With increasing encounter radius, the foragers shifted from using the margins around the predators to being nearly completely excluded from most of the northeast quadrant in the vicinity of the predators.

The space use of fully informed memory (Fig. 4.6) was most similar to the moderately exploratory forager in how the forager relocated in the face of predation. This mirrored the patterns seen with the trajectories (Figs. 4.4, 4.5). The main difference between the fully informed and naive foragers was that the fully informed forager was quicker to exploit more distant patches, even when the encounter radius was small. And while the fully informed forager also continued to exploit habitat close to predators, it did this to a lesser extent that the naive foragers, especially as the encounter radius became large.

4.4 Discussion

How, then, does memory state mediate the effect of predator introductions on forager behavior? Forager behavior, in terms of consumption rates, time budget, and space use, showed clear changes when comparing before and after the introduction of predators. How behavior changed, however, depended on the memory state of the forager as well as the area threatened by the predator. Consumption generally decreased and time spent searching (rather than feeding) increased after predator introduction, with the largest changes seen for larger areas threatened by predators. Foragers with pre-existing knowledge of alternative habitat were quicker to relocated to other areas. Less-exploratory naive foragers exploited refugia between predators while more exploratory naive foragers shifted habitat use farther away from predators. Increases in area threatened by predators led to larger habitat use changes across forager memory state.

One surprising result is that the naive least-exploratory forager has higher consumption than the fully informed forager. This is due to the initial release location being in the highest-quality habitat, a situation where foragers along the low to mildly exploratory spectrum perform well (Chapter 3). Because the northeast quadrant contained nearly half the total resource amount, remaining in that area despite the predation risk led to higher consumption. However, this high consumption is accompanied by high encounters as well, reminiscent of the food–safety trade-off discussed earlier (Chapter 2). Fully informed individuals had pre-existing knowledge of other quality patch locations at the time of predator introduction. This changed their decision-making calculus when evaluating the trade-off between available resources and predation risk compared to naive less-exploratory individuals. When picking a direction, fully informed individuals are attracted to resources in the vicinity of predators and farther away, so when resource directional preferences are scaled by safety from predators, those alternative locations make attractive targets. It is also worth noting that when the encounter radius is increased enough that the foragers are pushed out and must seek new habitat, the naive least-exploratory forager is the among the worst performing, with low consumption and extremely high encounters (the naive highly exploratory forager had slightly lower consumption but much lower encounters).

Habitat shifts due to changing predation threat have been observed in a wide variety of both terrestrial and aquatic systems (Sih 1980; Heithaus and Dill 2002; Creel et al. 2005; Mao et al. 2005; Wirsing et al. 2007; Belovsky et al. 2011) as animals seek to manage the food–safety trade-off. A forager's internal state may also be a factor, with animals in poor condition being more likely to risk foraging in high-quality, high-risk locations (Olsson et al. 2002; Heithaus et al. 2007). Additionally, the optimal predator memory parameterization that best manages this food–safety trade-off depends on the survivability of encounters (Chapter 2), here assumed to be high. That is, remaining in the vicinity of predators to continue to exploit the best resources makes sense when encounters are likely to be survived, but does not when the risk of death is higher. Thus the degree of habitat shift observed with predator reintroductions will likely depend on both the encounter survival rate as well as alternative antipredator behavior that foragers could employ in the presence of predators such as increased vigilance.

The non-consumptive effects of predation across all scenarios are clear with the reduced consumption before and after predator introduction. Here, there were no forager removals, so all of the decline in resources consumed was due to non-consumptive effects (i.e., habitat shifts) rather than consumptive effects, which would be an additional effect. Increasing encounter radius led to more encounters but also larger drops in consumption as foragers were effectively excluded from a larger area where the highest-quality habitat was located. There was less influence of encounter radius on the most exploratory foragers, as they tended to have the most kinesis-like wide ranging movements and were less likely to still remain in the initial release location when the predators were introduced.

An increase in search time is another underlying reason for the decrease in consumption. All memory states spent more time searching compared to feeding after predator introduction, and the largest increases in search time correspond with the largest drops in consumption. The pattern of the naive less-exploratory forager is interesting with the switch from the smallest to largest search time between small to medium and large encounter radii mirroring the large drop in consumption. With the smaller encounter radii, the main space use is similar between the less-exploratory forager and the fully informed forager though more constrained (see Figs. 4.6BD and 4.7BD). Once the less-exploratory forager is forced out more completely by the larger encounter radius, it primarily moved just south to lesser quality habitat rather than the better patches farther south or west used by other memory states (Fig. 4.7F).

For foragers with fully informed memory, the increase in search time after predator introduction were relatively modest, reflecting the advantage of knowing alternate resource locations. This suggests that animals with knowledge of habitat beyond the immediate area threatened by the introduced predators might better adapt to that predator, or conversely that the introduced predator in this scenario might struggle to find prey. While differentiating between searching and feeding behavior is more challenging in field situations, this is an active area of research (Morales et al. 2004; Gurarie et al. 2009; McClintock et al. 2012). Changes in time allocation pre- and post-predator introduction could provide important information on prey response, either in addition to or as an alternative to habitat changes, especially if vigilance levels could be quantified.

In a larger context, these results suggest that how large an area predators threaten and potentially exclude foragers from mediates the impact of predation risk on foragers. An animal's habitat domain is the part of the available microhabitat it uses, with broad-domain species that range throughout the available microhabitat contrasted with narrow-domain species using only some subset of the available microhabitat (Preisser et al. 2007). Applying this paradigm to the model results, predators switch from narrow-domain to broad-domain as encounter radius increases and removes potential refugia in the high-quality northeast quadrant. The broad-domain foragers also retain an additional refuge in the lower-quality habitat spatially removed from the predators. Predator hunting mode affects the strength of non-consumptive effects (stronger effects for sit-and-wait and sit-and-pursue versus active predators). Within a hunting mode, habitat domain may also affect non-consumptive effect strength, with evidence for stronger effects from broad domain predators than narrow domain predators (Preisser et al. 2007). That agrees with the reduced consumption and increased time searching seen with increasing area threatened. Finally, multiple predators sharing a habitat domain can reduce the predation risk experienced by the prey, an important consideration for multi-predator systems (Woodcock and Heard 2011).

Spatial memory of the surrounding area can mitigate the effect of introduced predators, as foragers can better access alternate habitat. Empirical field studies do not usually consider memory directly since it cannot be measured, but the potential implications for some example systems can be examined. The tiger sharks (*Galeocerdo cuvier*) that threaten dolphins (*Tursiops aduncus*) (Heithaus and Dill 2002) and dugongs (*Dugong dugon*) (Wirsing et al. 2007) are not introduced predators, but their seasonal presence and absence work like a small-scale repeated predator introduction scenario. Tiger shark densities were highest in shallow productive habitat, and dolphins and dugongs shifted their habitat use towards deeper less-productive areas when sharks were present. If we assume dolphins and dugongs are familiar with the entire habitat area, the best-matching model scenario would be that of the forager with fully informed memory that can shift quickly to alternative habitats. It is also important to consider changing levels of vigilance, as the degree of the shift can depend on the background level of predation risk (Creel et al. 2008). Thus it is not just the absolute level of risk that is important, but the changing pattern of risk.

For foragers pushed out of their existing habitat, the simulations with naive foragers suggest that the level of exploration strongly influences their ultimate location. Additionally, the survivability of encounters affects the optimal predator memory parameterization (Chapter 2), and thus how willing foragers are to risk increased encounters in order to access high-quality foraging areas. Here, we can see memory state, in terms of knowledge of alternative habitat and exploratory tendency, also affects risk-taking behavior by the forager in the willingness to remain in the area after predators are introduced. How foragers weigh this food–safety trade-off could also depend on energy reserves or other antipredator behaviors (e.g., vigilance) to mitigate risk. An interesting extension of the model would be to contrast large-scale habitat-use changes (like those explored here) with small-scale habitat-use changes and other antipredator behavior like vigilance. Another interesting direction would be to change encounters from static certainties to instead be based on a predation risk map (such as the one developed by Kauffman et al. (2007) based on kill sites) that would modify encounter probability and encounter riskiness. The predator memory would then have two spatial layers for predator location and predation riskiness that could modify the directional decision-making of the forager.

In conclusion, predator introductions can change habitat usage and consumption rates of foragers to a large or small degree depending on area threatened and how critical it is to avoid encounters. When foragers do shift habitat use in response to predator introductions, memory state (habitat knowledge and degree of exploratory inclination) mediates how foragers use alternative habitats. Search time increased and consumption decreased after predator introduction across all memory states. For foragers with full knowledge of the habitat, the increase in search time was relatively modest, reflecting the advantage of knowing alternate resource locations. Thus, spatial memory of the surrounding area can mitigate the effect of introduced predators, as foragers can better access alternate habitat. Potential changes in foraging behavior are an important, though often neglected, component of predator reintroductions, given the far-reaching ecological consequences of top-predator losses (Estes et al. 2011). While memory is challenging to consider in experimental studies of reintroduction, evidence from modeling here suggests that memory is a important component of how forager behavior changes.

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Appendix A

APPENDIX A

Comparisons of space use using the utilization distribution calculated with `kernelUD` in the `adehabitatHR` package (Calenge 2006) in R (R Core Team 2014). The three movement processes were simulated on a limited number of landscapes representing the four extremes ($\mu_Q = -1.5, \gamma_Q = 2$; $\mu_Q = -1.5, \gamma_Q = 10$; $\mu_Q = 1, \gamma_Q = 2$; $\mu_Q = 1, \gamma_Q = 10$), with one memory parameterization ($\phi_L = 0.001$, $\phi_S = 0.01$, $\psi_M = 2$, $\gamma_Z = 10$). For values of Δt (0.1, 0.5, 1, 2) were compared with three values of λ (0.5, 1, 2). Space use was similar though variable across combinations of Δt and λ for each combination of landscape and movement process

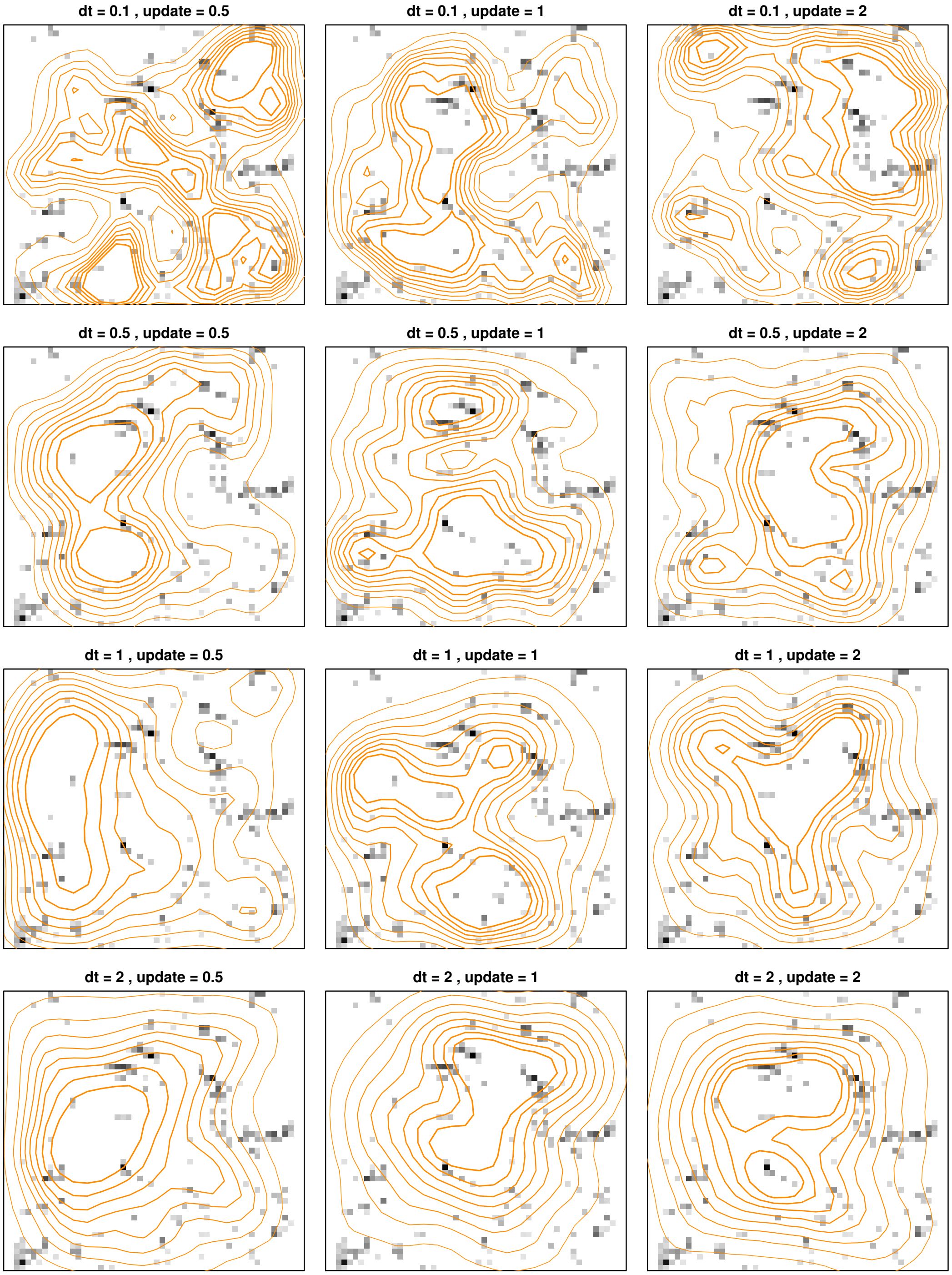

Figure A.1: Space use for random walk on a small-patch, concentrated landscape ($\mu_Q = -1.5, \gamma_Q = 2$) across a range of values for Δt and λ.

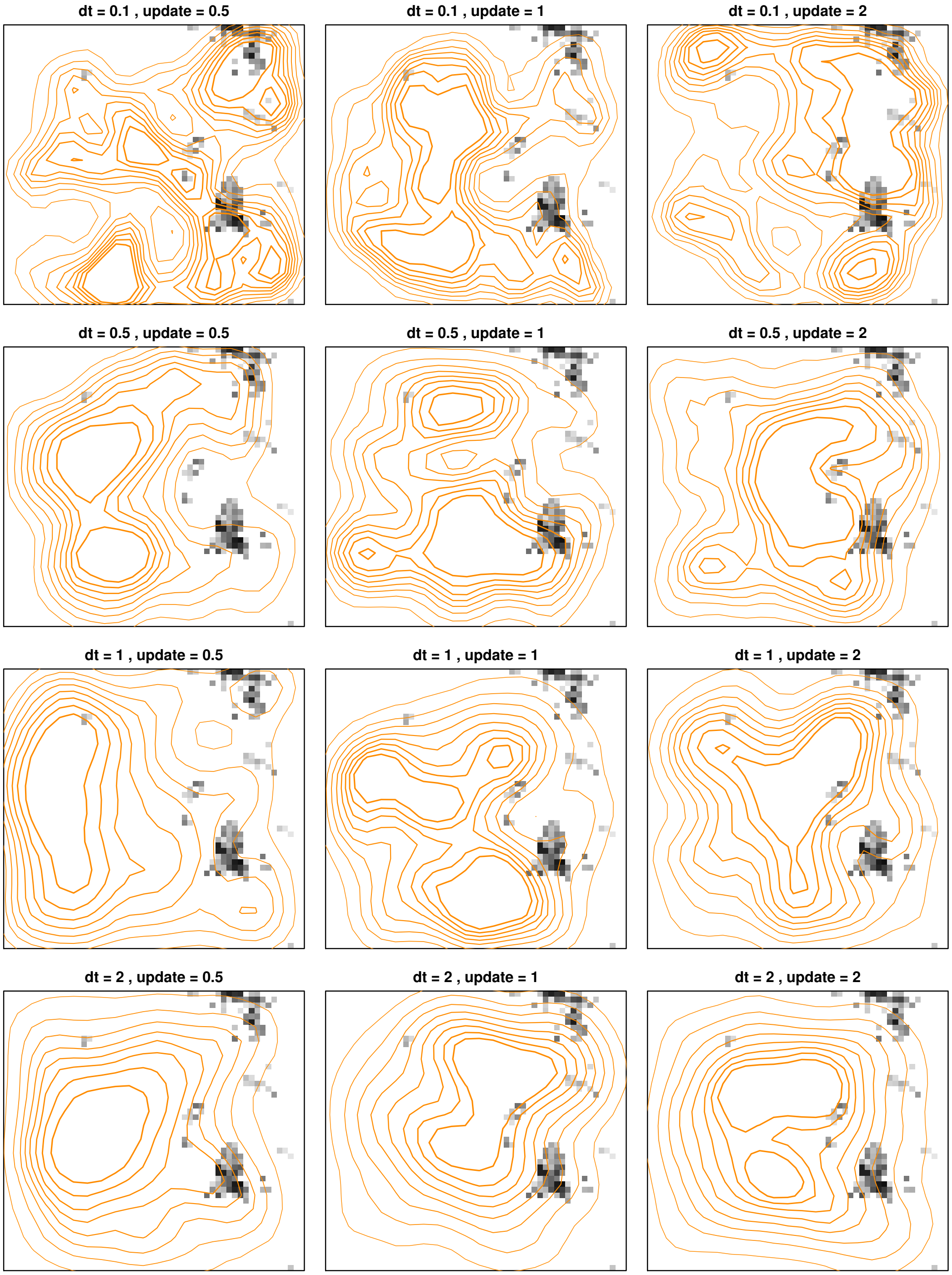

Figure A.2: Space use for random walk on a large-patch, concentrated landscape ($\mu_Q = -1.5, \gamma_Q = 10$) across a range of values for Δt and λ.

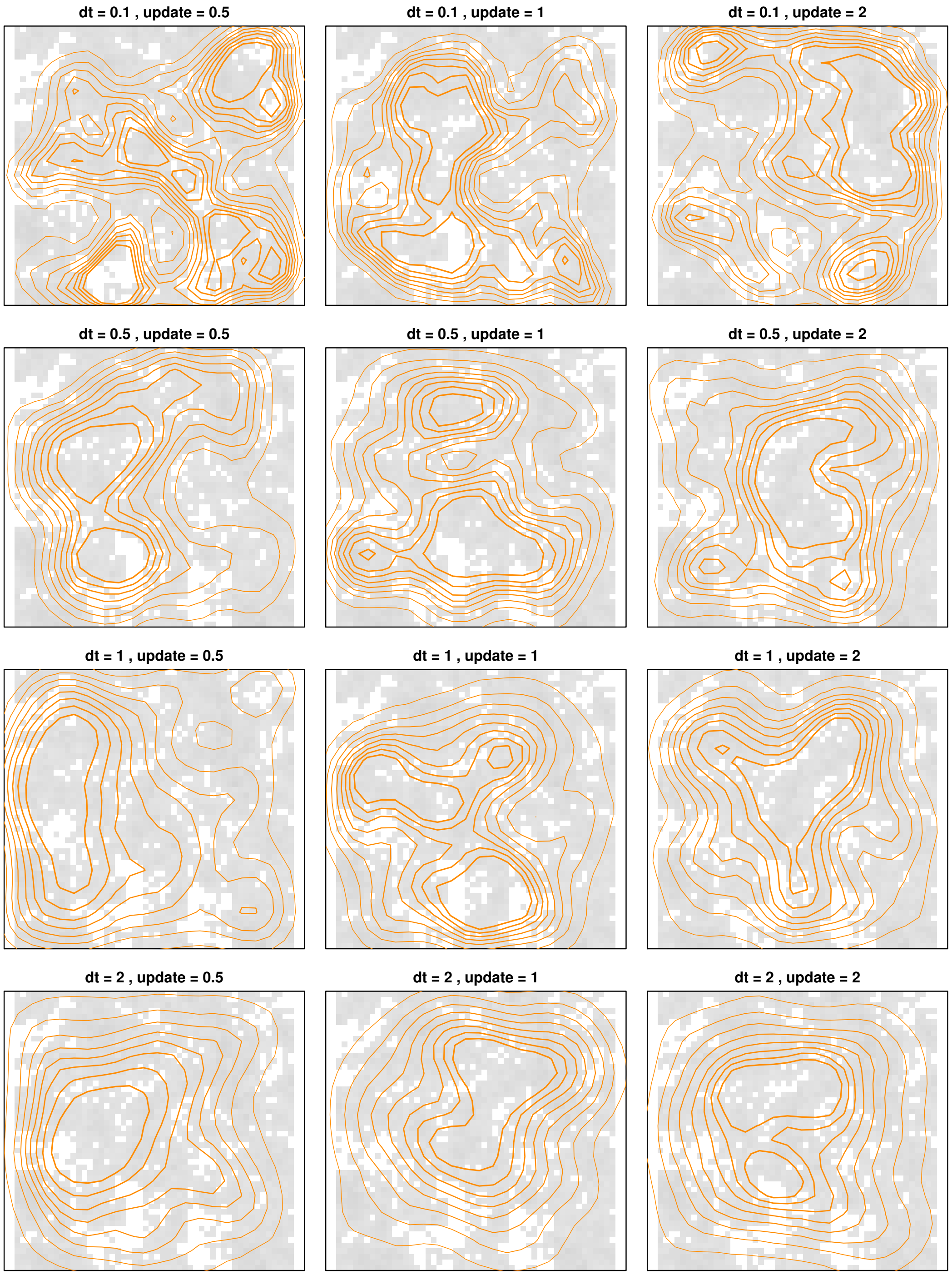

Figure A.3: Space use for random walk on a small-patch, smooth landscape ($\mu_Q = 1, \gamma_Q = 2$) across a range of values for Δt and λ.

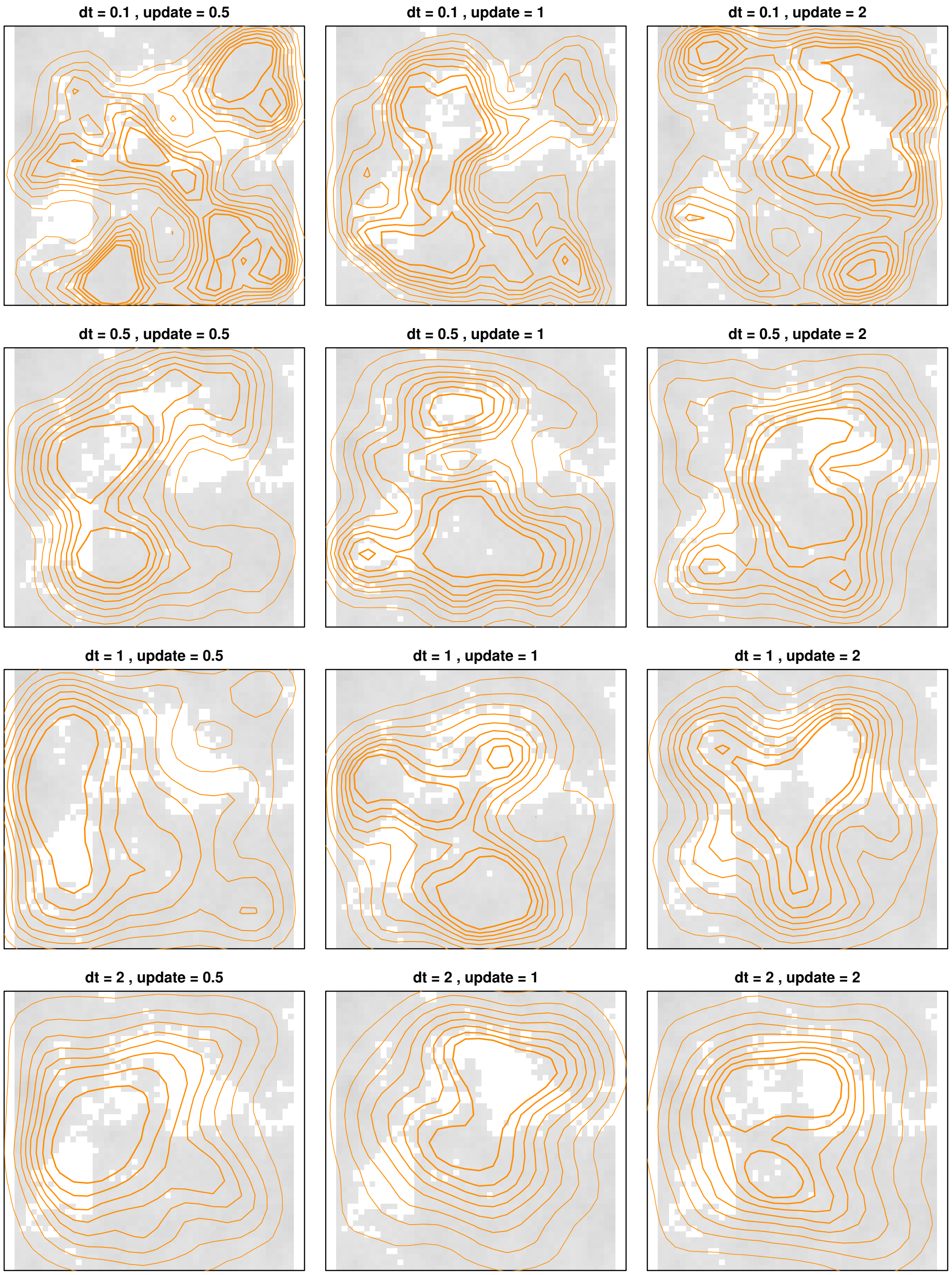

Figure A.4: Space use for random walk on a large-patch, smooth landscape ($\mu_Q = 1, \gamma_Q = 10$) across a range of values for Δt and λ.

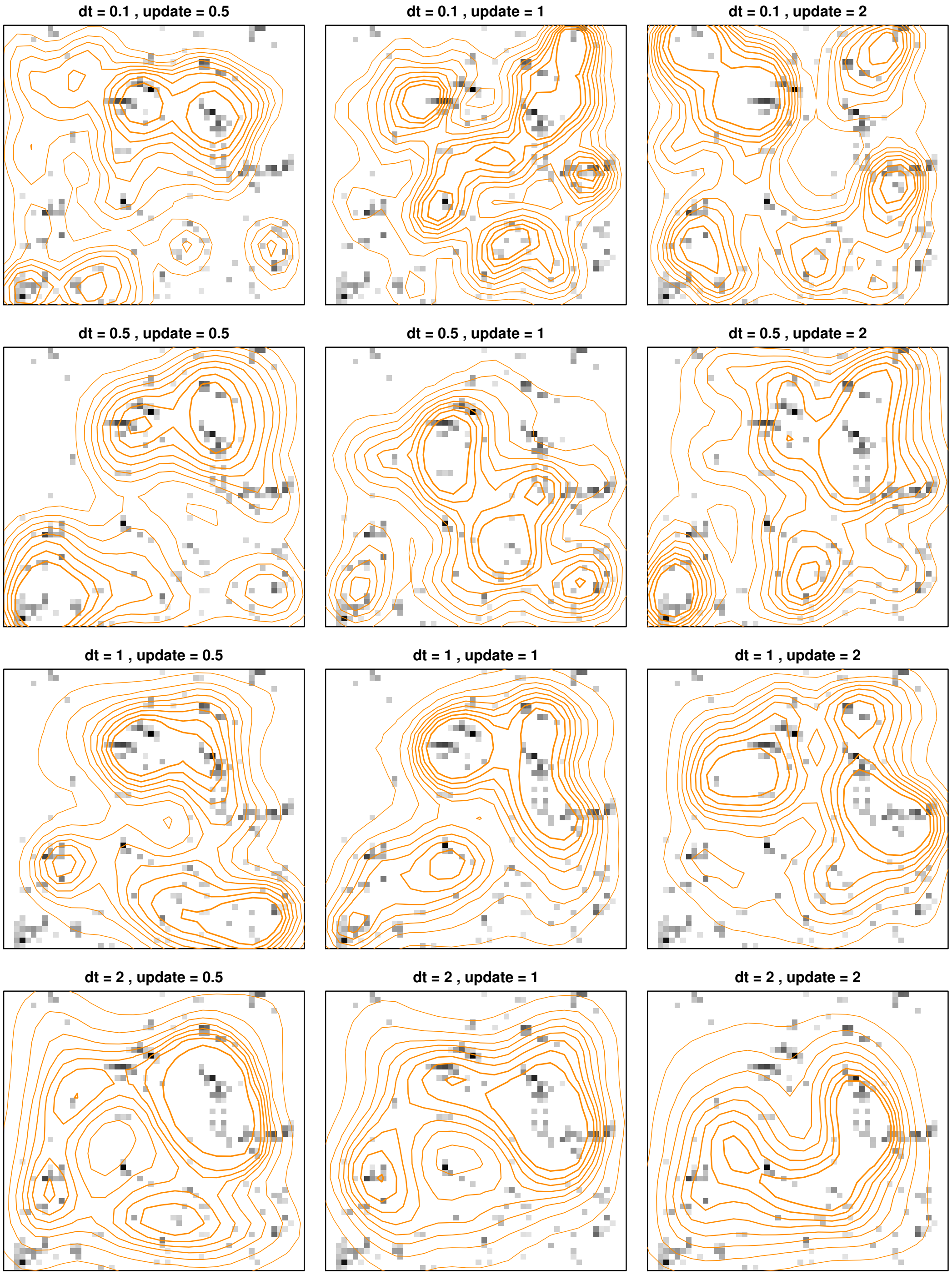

Figure A.5: Space use for kinesis on a small-patch, concentrated landscape ($\mu_Q = -1.5, \gamma_Q = 2$) across a range of values for Δt and λ.

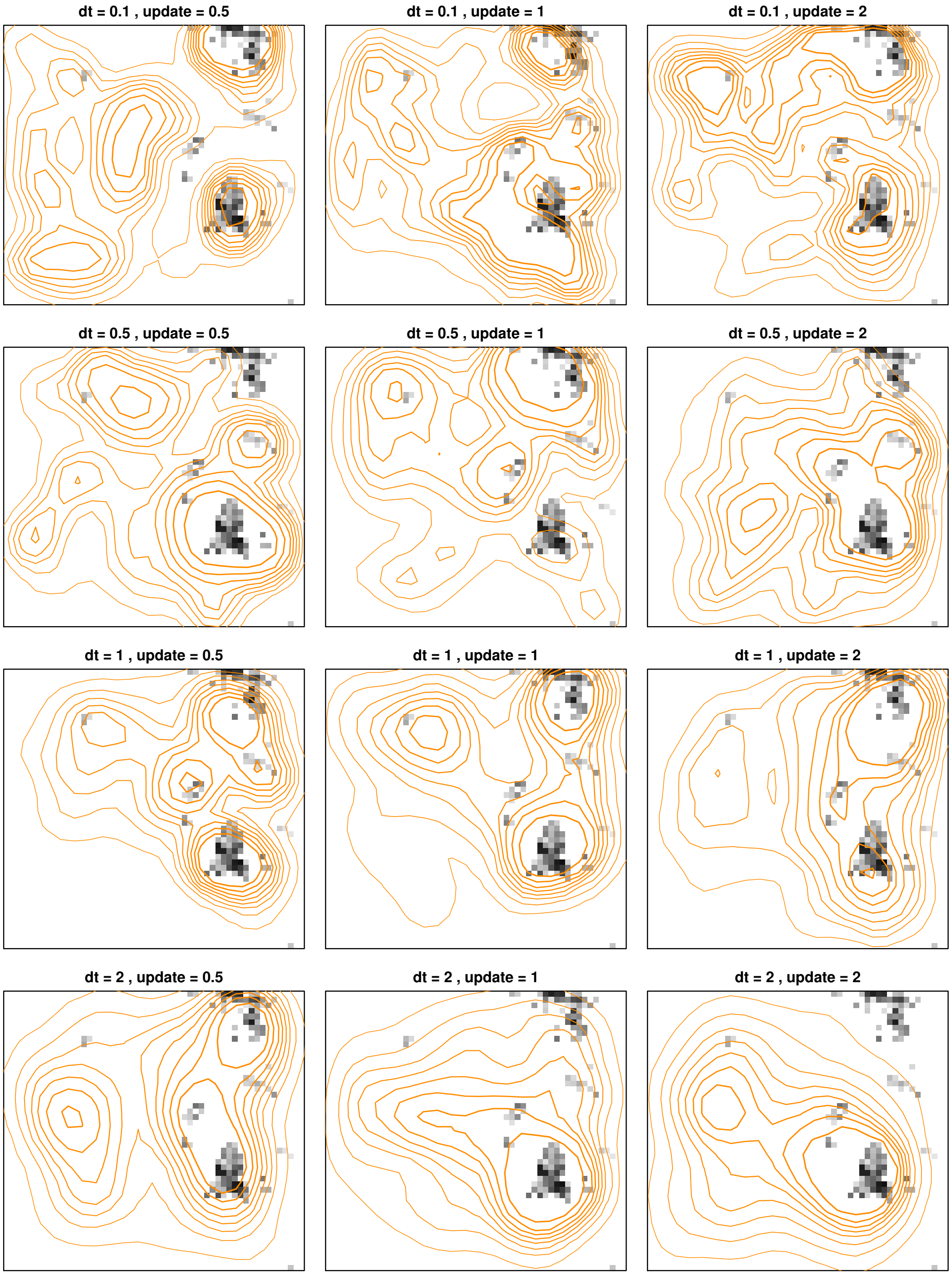

Figure A.6: Space use for kinesis on a large-patch, concentrated landscape ($\mu_Q = -1.5, \gamma_Q = 10$) across a range of values for Δt and λ.

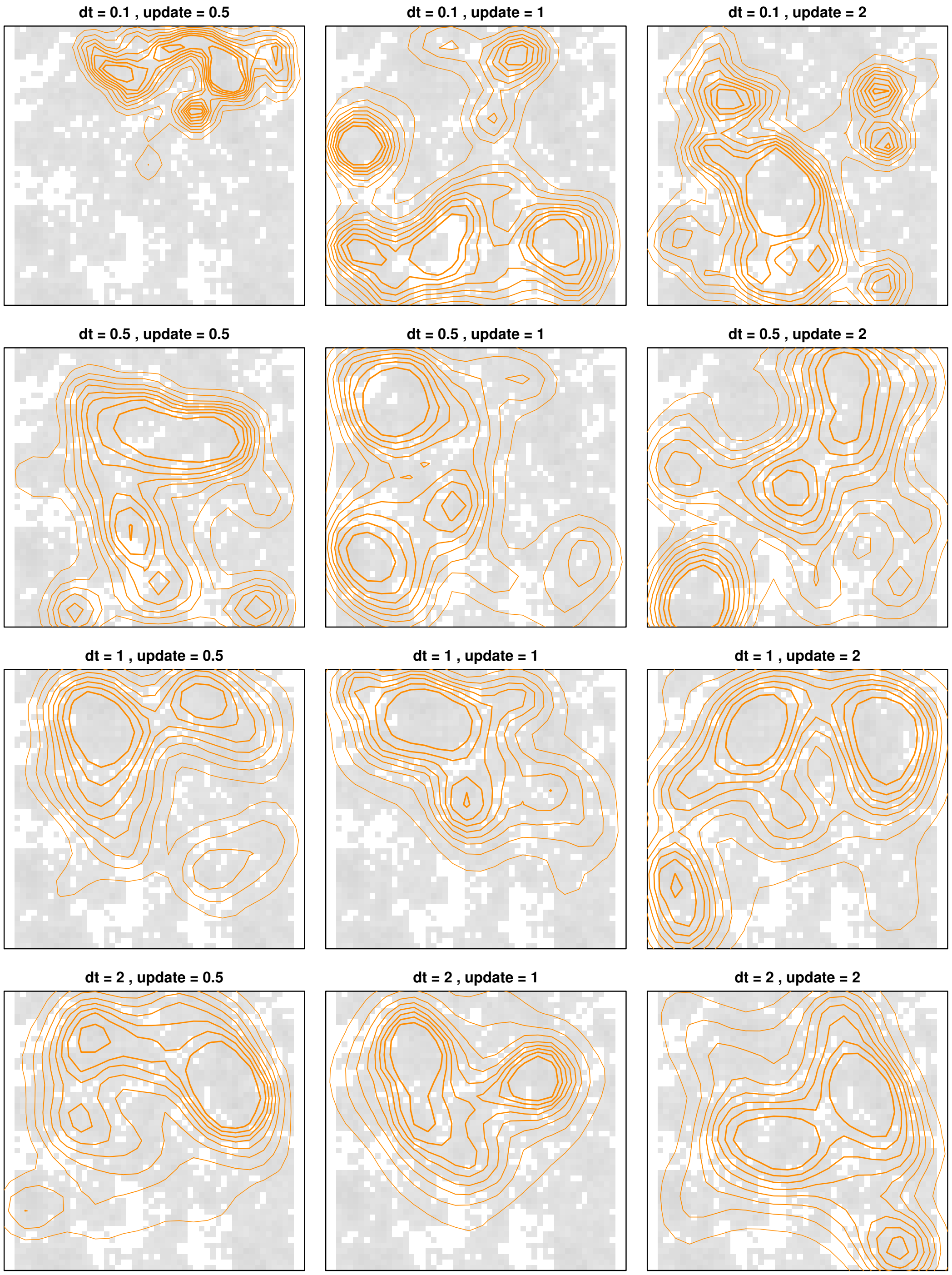

Figure A.7: Space use for kinesis on a small-patch, smooth landscape ($\mu_Q = 1, \gamma_Q = 2$) across a range of values for Δt and λ.

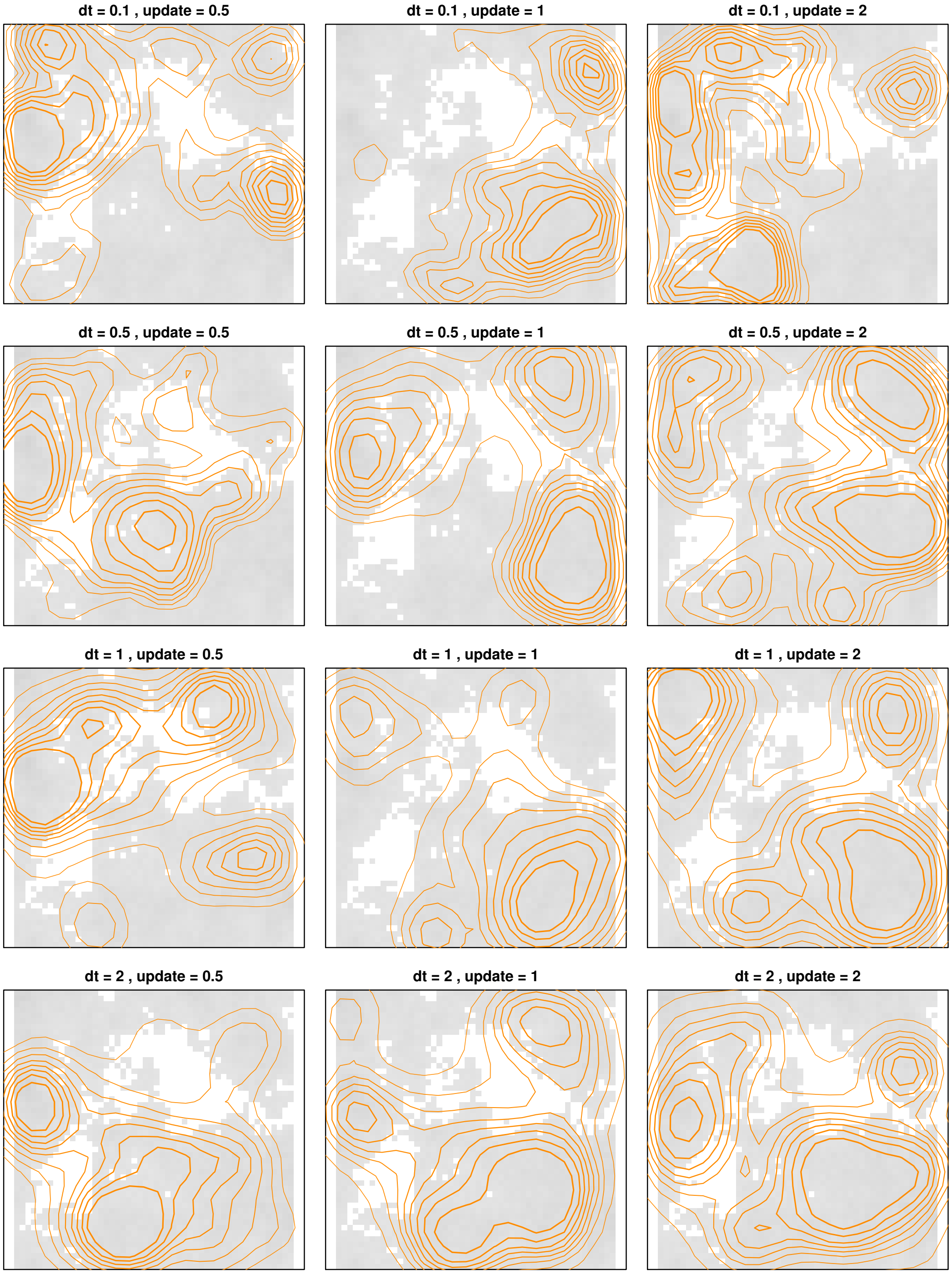

Figure A.8: Space use for kinesis on a large-patch, smooth landscape ($\mu_Q = 1, \gamma_Q = 10$) across a range of values for Δt and λ.

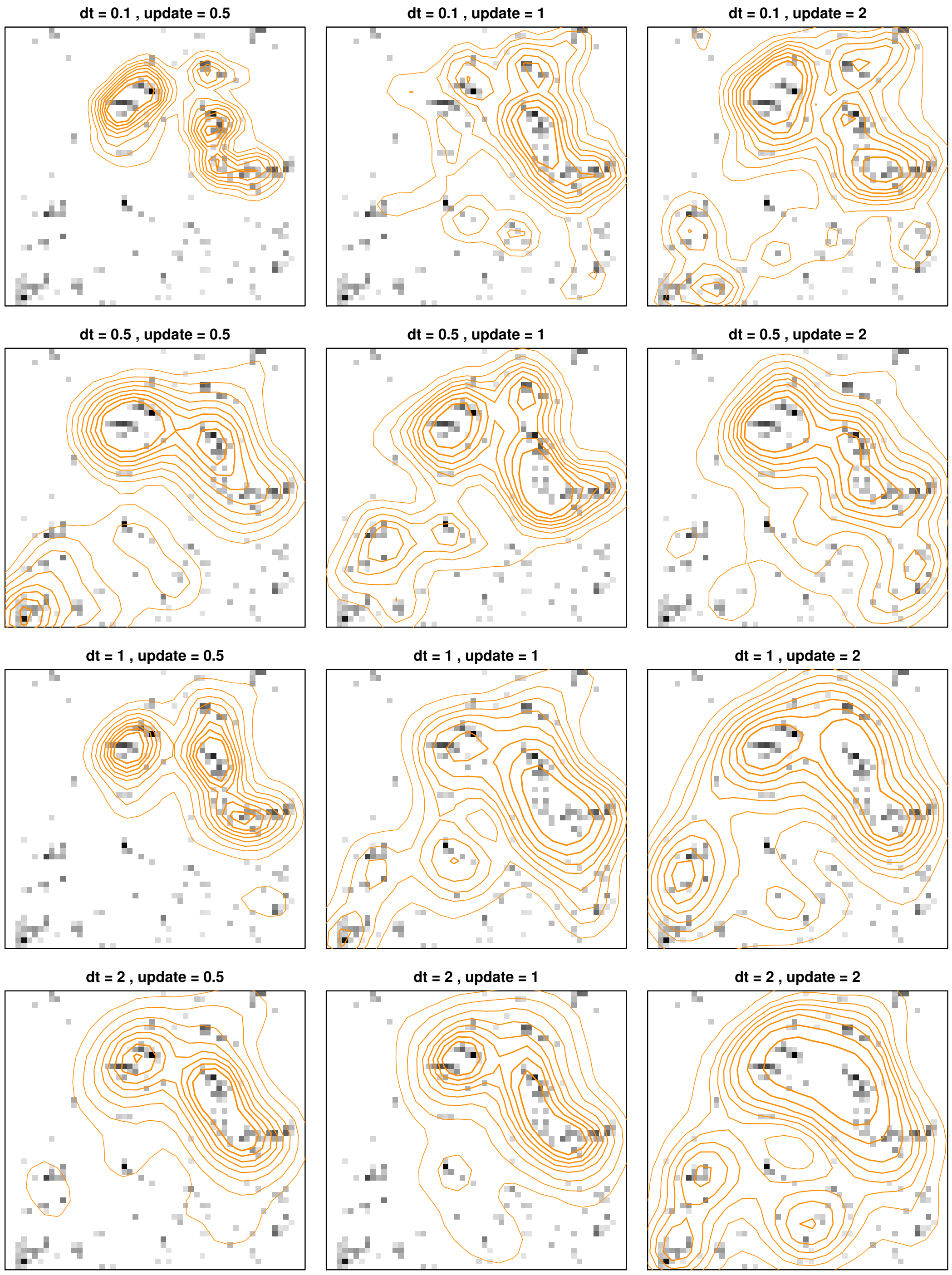

Figure A.9: Space use for memory on a small-patch, concentrated landscape ($\mu_Q = -1.5, \gamma_Q = 2$) across a range of values for Δt and λ.

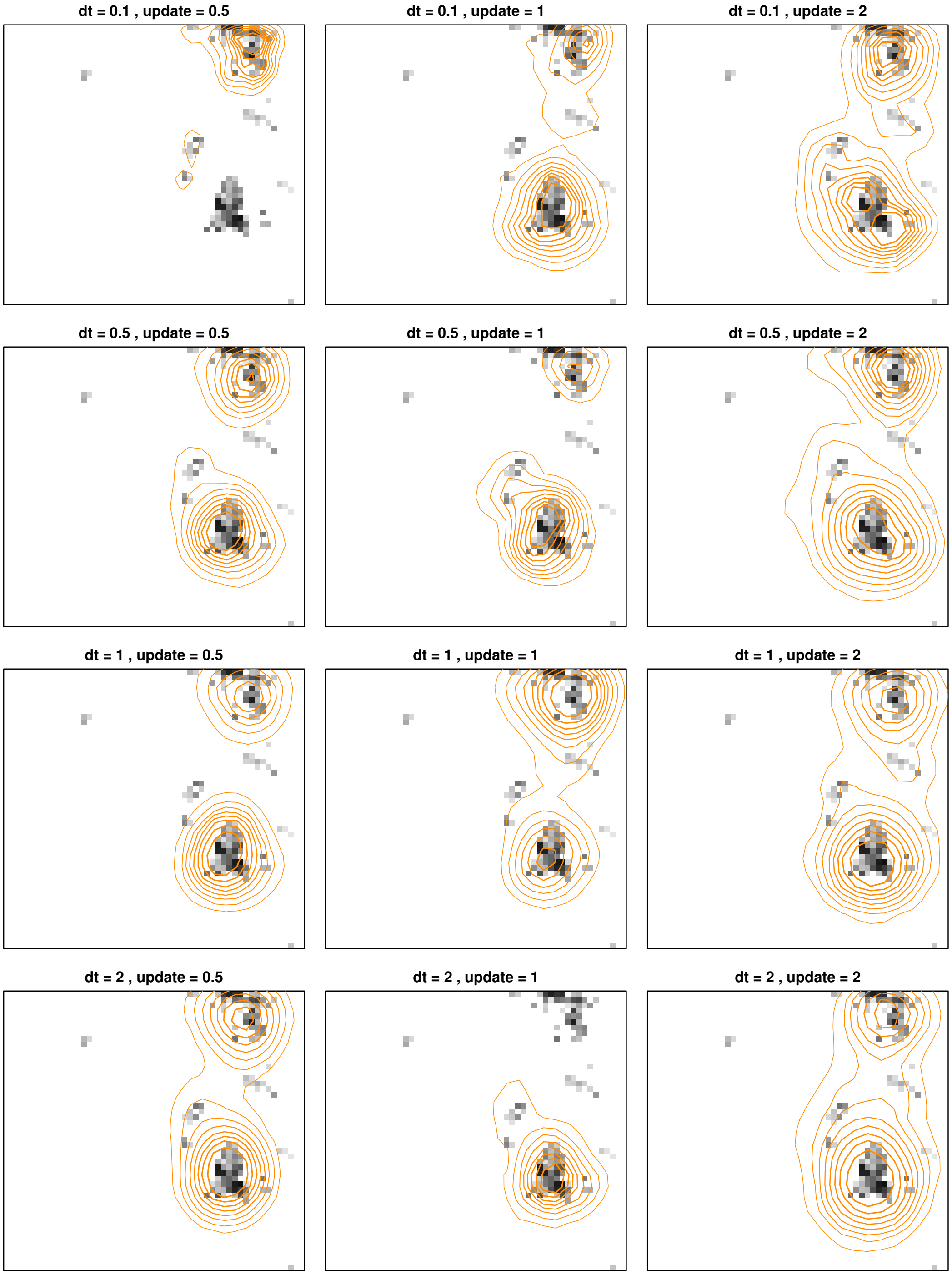

Figure A.10: Space use for memory on a large-patch, concentrated landscape ($\mu_Q = -1.5, \gamma_Q = 10$) across a range of values for Δt and λ.

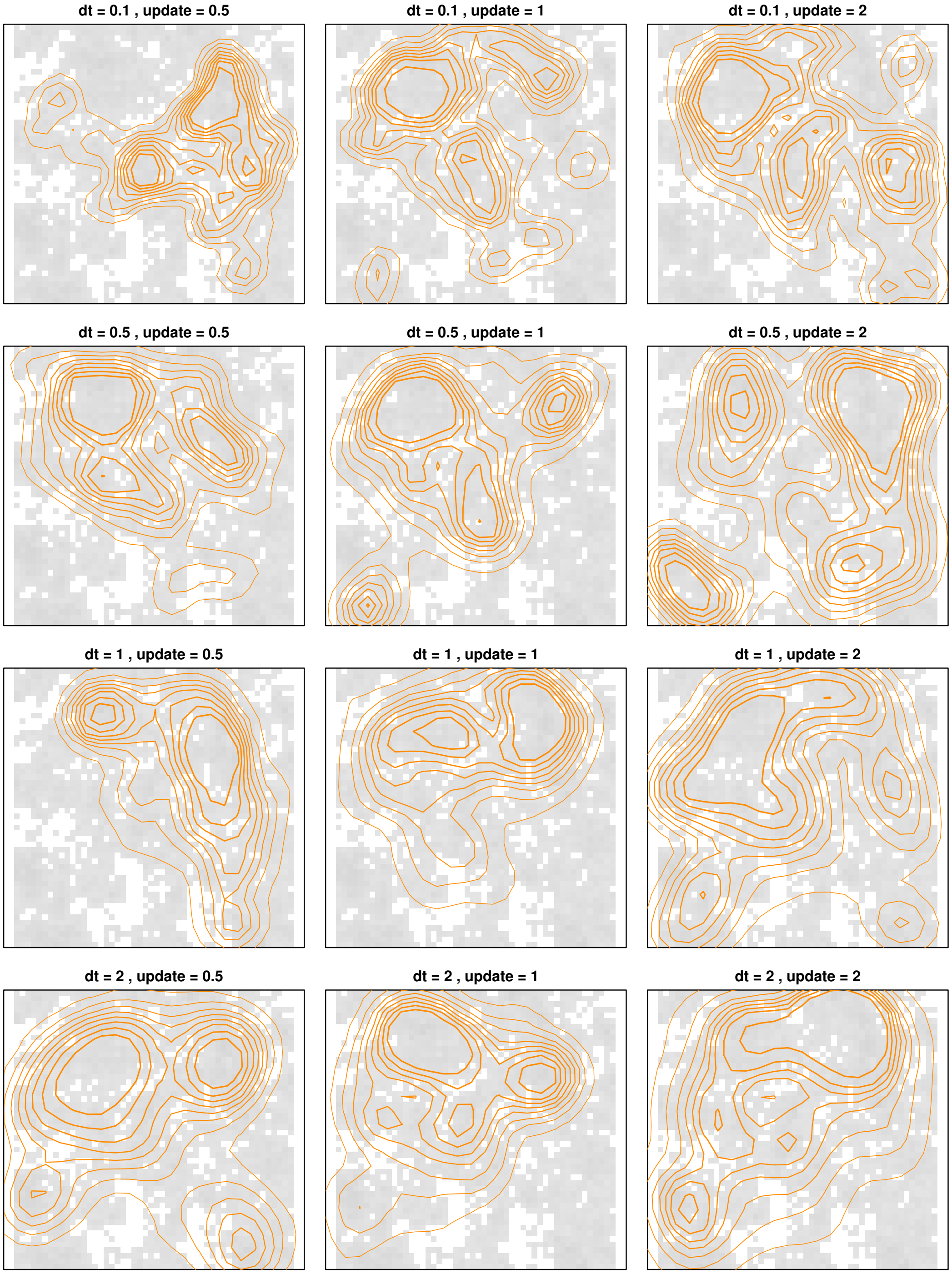

Figure A.11: Space use for memory on a small-patch, smooth landscape ($\mu_Q = 1, \gamma_Q = 2$) across a range of values for Δt and λ.

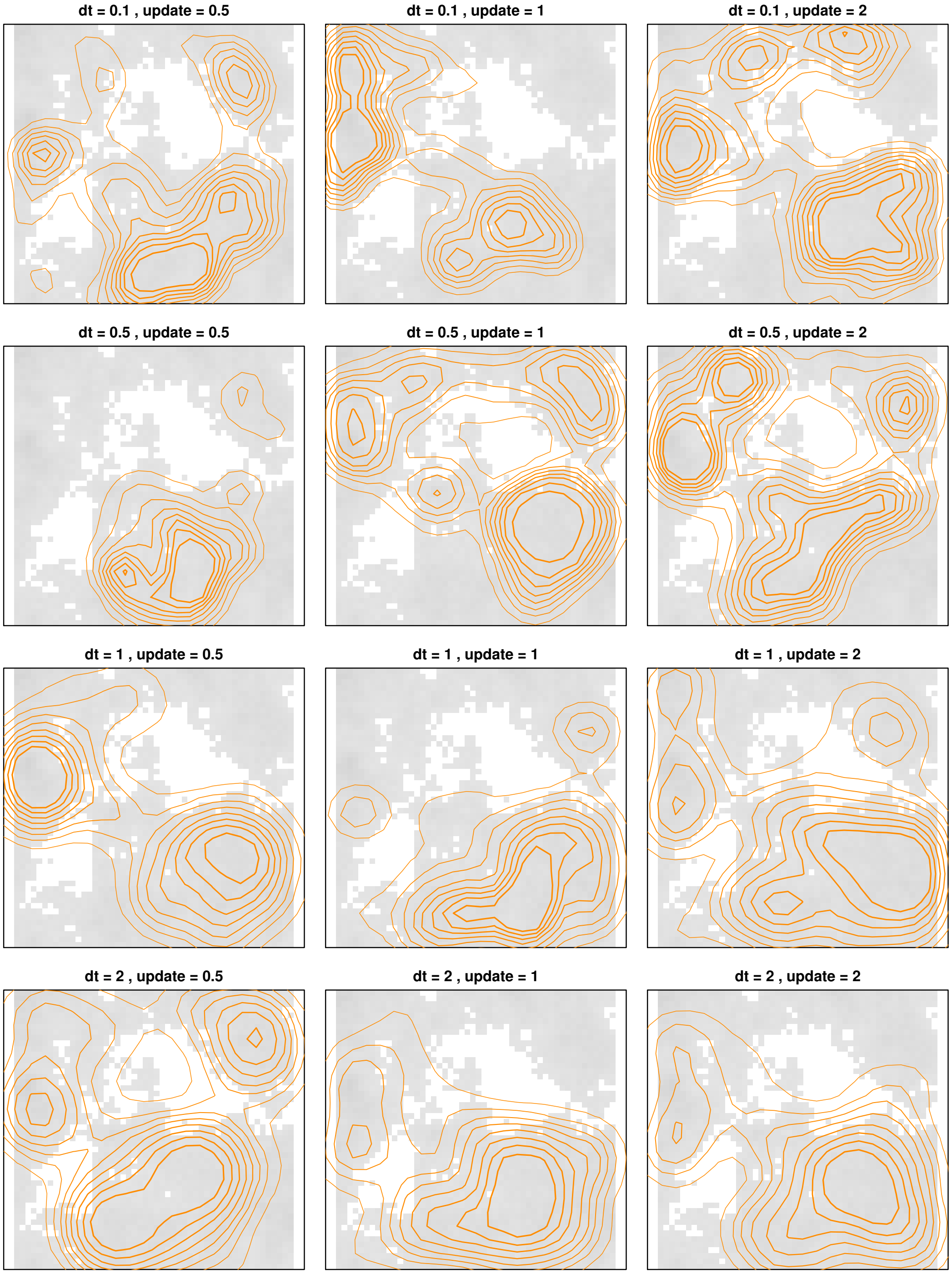

Figure A.12: Space use for memory on a large-patch, smooth landscape ($\mu_Q = 1, \gamma_Q = 10$) across a range of values for Δt and λ.