The effect of spatial environmental heterogeneity on hominin dispersal events and the evolution of complex cognition

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DEDICATION

This dissertation is dedicated to my daughter, Fiya, and my son, Ash. You have filled me with purpose in a way I didn't know was possible.

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ABSTRACT

Modern humans are unique in the vast geographic range we inhabit. However, how, why, and under what conditions humans and our hominin ancestors successfully dispersed and settled throughout the world is still poorly understood, and presents one of the biggest challenges to understanding our evolutionary history. Increasingly sophisticated hominin cognition is assumed to play an important role in major dispersal events but it is unclear what that role is. This dissertation uses a series of agent-based models to explore the close relationship between cognitive complexity, the spatial heterogeneity of the landscape, and dispersal potential and velocity. Since dispersal is the global scale product of local scale mobility, the first agent-based model evaluates the role of cognitive complexity in the foraging related mobility of small foraging groups. As a proxy for cognition, model foraging groups, or agents, possess a variable accuracy of assessing the quality of their local environment as they decide where to move to maximize resources. The model results show that the spatial heterogeneity of the resource landscape exerts a selective pressure such that lower cognition is adaptive in low heterogeneity landscapes, and higher cognition is adaptive in high heterogeneity landscapes. In the models, cognition preferentially directs movement towards known resources, and indirectly inhibits dispersal outwards into unknown landscapes. This suggests that increased cognition could have inhibited hominin dispersal, and that the dispersal events that did occur likely came from low heterogeneity environments. The second section of this dissertation evaluates the robustness of these findings in two new models by extending how foraging groups acquire knowledge of their environment before making mobility decisions. The first varies the size of

the agent's resource assessment area, and the second allows agents to learn about the resource landscape through social interactions instead of direct observation. In each case, low levels of environmental knowledge are advantageous, particularly in low heterogeneity environments. This adds further support to the hypothesis that hominin dispersals likely originated from a low heterogeneity environment, as this would have favoured the evolution of the low cognition hominins that had the highest dispersal potential. The final section of the dissertation combines the model of cognitive dispersal with the wave of advance model. The model quantifies the impact of cognition on dispersal velocity and wave pattern. The results show that the greater the level of cognitive complexity, the slower the wave of advance. Increased heterogeneity of the environment further decreases wave velocity when cognition is involved in mobility. Random movement, i.e. non-cognitive mobility, provides the highest velocity across almost all landscapes. This suggests that previous research has either overestimated the importance of cognition in facilitating dispersal events, or has grossly underestimated the rate of population growth and per generation dispersal distance of hominin populations. A large body of archaeological and palaeoanthropological research is focused on the assumed advantages of cognitive sophistication for dispersal. However, the results of this dissertation suggest that the spatial characteristics of the environment played an important inhibitory role in the natural selection of hominin cognition and dispersal potential, and in reducing dispersal velocity. Surprisingly, hominin dispersal events may have originated from low spatial heterogeneity environments since these landscapes preferentially gave an advantage to populations with lower cognitive complexity.

ABRÉGÉ

Les humains modernes sont uniques de par la diversité écologique et la vaste étendue de nos habitats. L'histoire de la dispersion des nos ancêtres hominidés et ses raisons et mécanismes sont peu compris et présentent l'un des principaux mystères de l'évolution humaine. On suppose souvent que l'accroissement des capacités cognitives des hominidés y est pour quelque chose, mais son rôle n'est pas clairement identifié. Cette thèse utilise la modélisation basée agent pour explorer l'interaction entre la complexité cognitive, l'hétérogénéité spatiale des environnements et la dispersion des hominidés. Étant donné que la dispersion globale est le produit de processus locaux de mobilité, le premier modèle présenté évalue le rôle de la complexité cognitive dans la mobilité reliée à la subsistance pour de petits groupes d'agents. Les agents de ce premier modèle varient dans leur capacité à évaluer la qualité de leur environnement immédiat, ce qui a une influence sur leurs décisions reliées à la mobilité et à la subsistance. Les résultats de ce modèle démontrent que l'hétérogénéité spatiale des environnements crée une pression sélective sur la capacité cognitive. Les environnements plus homogènes favorisent une complexité cognitive réduite, tandis que les environnements plus hétérogènes favorisent une plus grande complexité cognitive. De plus, une complexité cognitive accrue favorise les mouvements des agents vers des ressources déjà connues et tend à ralentir la dispersion des groupes vers de nouveaux environnements. Ce résultat suggère que l'accroissement de la complexité cognitive des hominidés pourrait ne pas avoir favorisé la dispersion de l'espèce et que cette dispersion aurait pu être favorisée par des périodes de stabilité environnementale. Les deux modèles suivants évaluent la solidité de ces premiers résultats

en donnant aux agents plus de connaissances de leur environnement. Un des deux modèles varie l'étendue de la zone dans laquelle l'agent a accès à de l'information pouvant affecter ses décisions de mobilité. L'autre donne aux agents la capacité d'acquérir de l'information d'autres agents plutôt que par observation directe. Dans chacun des cas, les agents sont avantagés quand ils ont accès à une quantité d'informations plus limitée sur leur environnement, surtout dans les environnements plutôt homogènes. Ces seconds résultats renforcent l'hypothèse que les grands épisodes de dispersion des hominidés auraient eu leur origine dans des environnements relativement homogènes qui favorisent l'évolution d'une complexité cognitive limitée, créant ainsi un fort potentiel pour la dispersion spatiale. Un dernier modèle combine ces modèles de complexité cognitive variable et de mobilité locale avec un modèle de diffusion démique. Ceci permet de quantifier l'influence de la complexité cognitive sur la vitesse et la distribution des vague de dispersion. Le modèle démontre qu'il y a une relation inverse entre la complexité cognitive et la vitesse des vagues de dispersion. L'hétérogénéité environnementale réduit encore plus la vitesse de ces vagues. Le mouvement aléatoire, qui n'est donc pas guidé par un l'appareil cognitif de l'agent, produit les vagues de dispersion les plus rapides dans la plupart des types environnement. Ensemble, ces résultats suggèrent que les approches existantes surestiment l'importance de la complexité cognitives comme outils permettant la dispersion des hominidés, ou qu'elles sous-estiment fortement les taux de croissance des populations hominidés et leur distance de mouvement intergénérationnel pendant les grands épisodes de dispersion. Or, la complexité cognitive de nos ancêtre occupe un rôle important dans la pensée archéologique et anthropologique sur les causes et le mécanismes de la dispersion des hominidés. Par contre, les résultats des modèles présentés ici suggèrent que l'environnement a pu avoir un rôle modérateur sur l'accroissement de la complexité cognitive humaine et sur le potentiel de dispersion de l'espèce. Contre les attentes, ils suggèrent aussi que les grands épisodes de dispersion auraient eu leur origine dans les environnements homogènes qui favorisaient l'évolution de population à complexité cognitive limitée.

PREFACE

My interest in patterns of movement in archaeology began when I started taking Geographic Information Science courses during my undergraduate degree. Over time I realised that the spatial-temporal distribution of the archaeological record is as much an artefact of human behaviour as lithics, fauna, ceramics, and architecture. As an object of study, the space and time between things presents an interpretive challenge that I try to tackle with innovative methodological approaches. I greatly expanded my repertoire with a M.Sc. in GIS and Spatial Analysis from University College London. My supervisor, Dr. Mark Lake taught my first course in agent-based modelling and threw me in the deep end of programming with Java, C, bash, GRASS, and R all at the same time. I was well into the models of this dissertation before I realised how instrumental Dr. Lake's hungry rabbit training model was in my thinking of hominin dispersal.

I entered McGill's Ph.D. program intending to use agent-based modelling to study diffusion and dispersal but for a slightly different purpose. My original question asked if it was possible to use models to distinguish between people, cultural traits, and trade goods moving around in the past. I identified migration, demic diffusion, cultural diffusion, trade, and independent innovation as different mechanisms used to interpret changes in the spatial and temporal patterning of the static archaeological record. I systematically identified the variety of models used to describe these mechanisms (e.g. wave of advance and GIS models) and the factors archaeologists use to determine which mechanism was responsible (e.g. rate and extent of change, single vs. multi-trait complexes).

I selected the spread of farming through Europe as a test case, as it is a well documented case study where there is some debate about the relative importance of demic diffusion (i.e. population replacement) versus cultural diffusion (i.e. acculturation). Within a month of my proposal defence I had working computational models of demic and cultural diffusion, as well as a model using imported GIS layers of European topography. At this point a colleague sent me a paper by Lemmen et al. (2011), who used a simulation to evaluate the relative roles of demic and cultural diffusion in the spread of farming through Europe. The study was very well done and came to the same conclusion that even my preliminary models were suggesting: since the vector of cultural diffusion is still the movement of people, it may not be possible to differentiate between cultural and demic diffusion from the resulting spatial and temporal pattern in the archaeological record. Lemmen et al.'s (2011) study had already answered my research question in approximately the same way I had intended to, and in some ways, more thoroughly than I had planned.

A few months later, Dr. Ariane Burke ask if I would create a model of anatomically modern human dispersal into Iberia using global climate simulation data calibrated to the palaeoenvironmental context. This dissertation is the product of that investigation. In developing this model I quickly discovered the fundamental limitation of the wave of advance model, namely that the rate and pattern of the wave is unaffected by the underlying environmental landscape. Further, the random walk did not seem like a reasonable mechanism for mobility given the importance ascribed to complex cognition and human-environment interaction. I borrowed the concept of foresight, which Julian Z. Xue and Dr. Andre Costopoulos were developing (in the same room), adapted it for a spatial context, and set about incorporating cognition into a general model of human dispersal.

CONTRIBUTION OF AUTHORS

This articles-based dissertation includes two co-authored chapters. However, I conducted all the research, data analysis, figure design, and writing in these chapters. The co-authors contributed only through guidance and editing.

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The published version of chapter 2 lists Julian Z. Xue, Andre Costopoulos, and Ariane Burke as co-authors. Julian Z. Xue and I presented a co-authored poster at a conference titled the, "Royal Society Theo Murphy international scientific meeting on Early anatomically modern humans in Eurasia: coping with climatic complexity" (Wren et al., 2011). After a positive response from the conference organizers, we were invited to submit an article to a proposed special issue of the Journal of Human Evolution. Xue's component of the poster had already been published elsewhere (Xue et al., 2011), so the article we submitted presents my work alone. The concept of spatial foresight, and the natural selection of intermediate levels of foresight, were inspired by Xue's work with temporal variability and his continued role as a sounding board as I developed the theoretical, and then the computational, model of spatial foresight. Andre Costopoulos provided guidance during all stages of the project and edited the initial and revised drafts. Ariane Burke provided financial support to attend the initial conference and edited both drafts.

Wren, C.D., Costopoulos, A., submitted. Putting (hominin) thought into hominin dispersal. Journal of Human Evolution.

I submitted chapter 4 to a special issue of the Journal of Human Evolution stemming from a session at the Society for American Archaeology meetings, titled “Modelling the impact of environmental variability on hominin dispersals”. Andre Costopoulos provided guidance during all stages of the project and edited the submitted draft.

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CHAPTER 1
Introduction

1.1 Research question and approach

Modern humans are unique in the vast geographic range we inhabit. However, how, why, and under what conditions humans and our hominin ancestors successfully dispersed and settled throughout the world is still poorly understood, and presents one of the biggest challenges to understanding our evolutionary history.

Our geographic expansion beyond Africa began approximately 1.8 million years ago, surprisingly early in our evolutionary history. Subsequent major dispersal events occurred approximately 130, 60 and 10 thousand years ago. Each dispersal represents a fundamental shift in human history, as our ancestors diversified and adapted to new habitats (Gamble et al., 2004; Banks et al., 2008; Bar-Yosef and Belmaker, 2011). It is assumed that both environmental change and increasing cognitive sophistication played important roles in facilitating dispersal events, but the specific mechanisms of their interaction and how they generate dispersal is still under debate (Bar-Yosef and Belfer-Cohen, 2013). This is perhaps because comparatively little attention has been paid to the local scale drivers of mobility that enable dispersal events, and particularly to the long term climate conditions that shaped the evolution of mobility behaviour.

In investigating the factors influencing dispersal I formed two specific questions: how do the characteristics of the environment influence the natural selection of cognitive complexity, and what is the relationship between cognitive complexity and dispersal? These questions arose as I realised that dispersal is not necessarily a fundamental human characteristic, akin to a drive, for example, but rather the product of individual decisions made about daily movement. Research into the evolution of dispersal mechanisms should therefore focus on the cognitive development that enables mobility behaviour. Understanding the selective pressures for mobility will help answer if this behavioural pattern would increase or decrease the dispersal potential of populations. Finally, what effect will cognition have on the velocity and pattern of dispersal waves across different types of landscapes?

Before I come to these specific questions and how they developed, it is worth defining dispersal and asking why it is important that we study it. Dispersal, also known as demic diffusion, occurs as a population increases in size and expands their geographic range in relatively small steps per generation. This distinguishes it from migration or colonisation, where a group intentionally moves a long distance within a generation, not necessarily with population increase (Ammerman and Cavalli-Sforza, 1971), and cultural diffusion where cultural traits spread between groups without significant displacement of people (Lemmen et al., 2011). Explaining the broad scale patterns of human movement is a key goal of archaeological research as it gives context to the spatial and temporal distribution of the archaeological record.

Major dispersal events are often assumed to be triggered by a change in the biological and cultural evolution of the dispersing population, and are therefore looked at as turning points in evolutionary history. Dispersal also tends to result in a wider range of environments being occupied, or at least new challenges to adapt to, and thus contributes to our understanding of hominin creativity and adaptability. Finally, dispersal speaks to our romantic ideas of exploration and voyages into the unknown (Semple and Ratzel, 1968), although this bears little resemblance to how the process of dispersal generally occurred.

Dispersal events are a common topic in archaeology and palaeoanthropology and as such, the data is extensive and the overall spatial and temporal pattern is fairly clear. However, the narratives describing how and why each dispersal occurred are highly debated and are frequently invalidated as even earlier sites are located, and the chronologies of key sites are refined with more accurate dating methods. For example, a beach in Happisburgh, UK, marked by hominin footprints recently pushed back the date of the earliest occupation of Northern Europe by 350 000 years (Ashton et al., 2014). Rather than focus on the reconstruction of a particular dispersal event, this dissertation sees dispersals as expressions of general mechanisms underlying human-environment interaction.

1.2 Dispersal mechanisms

Population growth is an important requirement for dispersal, since geographic expansions also require large increases in total population to maintain a viable population density (Mellars, 2006b). A complete list of factors influencing dispersal must include a mechanism for population growth, as well as explaining why humans moved from one location in favour of another.

Dispersal mechanisms may either make the current location worse, providing a push outwards, or improve the attractiveness of another location, pulling towards somewhere new. The source of the mechanism may be from external (i.e. environmental) or internal processes of change (i.e. behavioural) (Table 1–1).

Change	Push	Pull
Environmental	Niche degradation	Niche expansion
Behavioural	Population growth	Niche broadening*

Table 1–1. Typology of dispersal mechanisms. *after Shea and Sisk (2010)

Environmental change may either reduce the suitability of the current location or expand the geographic range of the currently occupied ecological niche. Behavioural changes expand the geographic extent of potential habitat by redefining the ecological niche to include a new range of exploitable resources (e.g. with new tool technology) or by improving tolerance to previously marginal environments (e.g. with clothing or social networks).

1.3 Cognition in dispersal

Increases in cognitive complexity, through increases in brain size (Aiello and Dunbar, 1993) or inferred reorganizations of the brain (Klein, 2003), are often implicitly or explicitly implicated in these behavioural changes. The development of tools with complex lithic reduction sequences is an explicit example. Haidle (2010) argues that complex tool forms require a capacity for forethought not seen outside of the hominin lineage (also see Belfer-Cohen and Goren-Inbar, 1994). Shea and Sisk (2010) links this increased capacity, and the development of bow and arrow technology in particular, to an increase in the range of environments that are inhabitable and the probability of survival in others. Implicit examples include the hypotheses that symbolism enabled human dispersal by expanding social networks over larger areas (Gamble, 1998), and by giving modern humans an adaptive advantage over Neanderthals (Mellars, 2004).

These studies are a part of the broader focus on the evolution of a modern the level of cognitive complexity. Borrowing from cognitive science, in particular the concepts of working memory and executive functioning, they evaluate when the impact of modern cognition is first reflected in the archaeological record (Coolidge and Wynn, 2005; Wynn and Coolidge, 2010).

Some of the hypotheses purporting to explain the dispersal success of anatomically modern humans (e.g., language and the bow and arrow) can sound like special-pleading as *Homo erectus sensu lato* had dispersed through the same landscape much earlier with a smaller brain, simpler technology, and perhaps without language capability (Coqueugniot et al., 2004). This highlights a significant disciplinary divide between those studying the dispersals of *H. sapiens* versus *H. erectus s.l.*, and emphasises that the approach to studying hominin dispersal has been somewhat post-hoc.

Instead of looking for justifications in the observable archaeological record, this dissertation takes a more bottom-up approach to dispersal. Several assumptions guided the models developed here. The primary one was that dispersal is an emergent phenomenon resulting from individual, or group, movements aggregating over time. The identification of dispersal mechanisms should not stem from the characterisation of the dispersal pattern at the broad scale, but the factors driving individual or group movement at the local scale. Previous computational dispersal models generally assume that individual decision making would have a negligible effect over long time scales and that mobility should approximate a random process (Mithen and Reed, 2002; Hazelwood and Steele, 2004; Hughes et al., 2007). In other words, this assumes that there was no systemic behavioural bias influencing local scale mobility decisions.

So what drives the mobility patterns of individuals or small groups? Resource acquisition, particularly food and water, seems to be the most plausible and plays a major role in mobility decisions. This mechanism also has the advantage of being relatively easy to model.

Subsistence resource related mobility makes an explicit connection to the other major branch of dispersal research, palaeoenvironmental reconstruction. Palaeoenvironmental research uses a combination of marine and lacustrine cores, ecological preferences of other identified flora and fauna, and global climate simulations to determine the changing ecological conditions of various regions (Kingston, 2007; Bar-Yosef and Belfer-Cohen, 2013; Palombo, 2013; Potts, 2013). As I discuss in chapter 4, this branch forms a passive narrative of dispersal, in which humans don't select locations for occupation, but rather diffuse into them when environmental change opens them up.

The language of these studies may characterise a region as closed if it is assumed that hominins could not survive there in significant numbers (e.g. deserts, high altitude, or tundra). Later, doors could open when climate conditions became more permissive (Bar-Yosef and Belfer-Cohen, 2013). The search for key dispersal corridors is a common theme in this research (Goren-Inbar et al., 2000; Petraglia and Alsharekh, 2003; Rohling et al., 2013), perhaps because of the long-term research program into the ice-free corridor model of New World colonization. In the Old World, coastlines and river valleys are more commonly hypothesised as corridors (e.g., Davison et al., 2006; Rohling et al., 2013). In another approach, Banks et al. (2008) models the characteristics of a human eco-cultural niche. However, each of these approaches divides up the environment into a simplistic binary classification system of open or closed. In contrast, the few published computational dispersal models use a landscape with more gradations to the environment, typically representing carrying capacity (e.g., Steele et al., 1998; Hughes et al., 2007).

The variety of dispersal mechanisms, both behavioural and environmental, calls out for a way to test the implications of each. We need a framework for investigating the sphere of hominin-environment interaction and how it changes over time, and the emergence of dispersal patterning from that interaction. How does the environmental pattern interact with natural selection to create, indirectly, a dispersible population?

In the first and third chapters, I describe published modelling approaches that have attempted to evaluate different dispersal mechanisms in some detail. As I point out, most archaeological dispersal models have relied on only one model, the wave of advance. The dispersal mechanism of this model is a combination of population growth and even spread in all directions, sometimes modelled as small, randomly directed movements known as a random walk. In other words, the model assumes that human cognition will have no impact on the velocity, direction, or pattern of the dispersal.

In evaluating the relationship between cognitive complexity and dispersal, this dissertation employs a much less specific model of cognitive complexity than is discussed above. However, it is an abstraction that is tied to the cognitive abilities to develop and remember an accurate representation of the surrounding landscape, and to strategize and plan complex actions based on that mental model (Belfer-Cohen and Hovers, 2010; Davidson, 2010; Wynn and Coolidge, 2010).

1.4 Dissertation outline

Chapter 2 introduces the concept of spatial foresight, an accuracy at which foraging groups identify suitable habitat within their local area. As a proxy for cognitive complexity, foresight is the imperfect ability to make mobility decisions to locate the best resources in a landscape. As foresight concentrates mobility towards resources, the inverse is effectively an index for the dispersal potential, or dispersibility, of the population.

The chapter describes an agent-based model where a population of agents, representing foraging groups, evolve towards an optimal accuracy level. The spatial heterogeneity of the environment exerts a strong selective pressure on this optimal level of foresight such that low accuracy evolves in low heterogeneity landscapes, and an intermediate accuracy evolves in high heterogeneity landscapes. This has several implications for hominin dispersal. First, it re-directs the focus of dispersal mechanisms to behaviour at the local scale and sees dispersal itself as an emergent phenomenon. Second, it suggests hominin dispersal research should look towards the long-term environmental trends that resulted in high dispersibility, rather than just at the moment the dispersal occurred. Finally, the model predicts that a period of low spatial heterogeneity would be needed to evolve the dispersibility needed to expand into Eurasia.

A version of this chapter is published in the Journal of Human Evolution (Wren et al., 2014), and is featured as a Research Highlight in Nature (Callaway, 2014).

Chapter 3 expands the way agents acquire information about their environment in two distinct ways, one individual and one social. In each case, the trait evolves towards a value that optimizes the fitness of the population. In model one, agents can evolve increased or decreased assessment radius, the amount of the landscape that is visible to them when they make their foraging-biased mobility decisions (I changed the term spatial foresight to foraging-biased mobility as it was a more descriptive term). In model two, agents randomly select another agent from the population, receive information about the location and value of their resources, and then make a mobility decision based on that information. Agents can either evolve an increased or decreased probability of copying, which also determines the amount of environmental knowledge available to them. In both models, knowing little (but more than nothing) about the environment is the most adaptive, especially for low heterogeneity landscapes.

In chapter 4, I incorporate foraging-biased mobility into the most commonly used dispersal model in archaeology, Fisher's (1937) wave of advance. This effectively quantifies the impact of cognition on the two aspects of human dispersal events that are directly measurable with archaeological data, rate and pattern. The model suggests that the level of cognitive complexity, through the proxy of resource assessment accuracy, the slower the dispersal wave's velocity and the more sinuous the wave front. The other variables in the equation, population growth rate and inter-generational movement distance, must be increased considerably to account for the discrepancy in modelled and archaeological observed dispersal velocity. The spatial heterogeneity of the environment did have a small impact on wave velocity, but not as much as dispersal corridors or increasing gradients.

CHAPTER 2
The role of spatial foresight in models of hominin dispersal

Wren, C. D., Xue, J. Z., Costopoulos, A., Burke, A., 2014. The role of spatial foresight in models of hominin dispersal. Journal of Human Evolution

2.1 Abstract

Increasingly sophisticated hominin cognition is assumed to play an important role in major dispersal events but it is unclear what that role is. We present an agent-based model showing that there is a close relationship between level of foresight, environmental heterogeneity, and population dispersibility. We explore the dynamics between these three factors and discuss how they may affect the capacity of a hominin population to disperse. Generally, we find that high levels of environmental heterogeneity select for increased foresight and that high levels of foresight tend to reduce dispersibility. This suggests that cognitively complex hominins in heterogeneous environments have low dispersibility relative to cognitively less complex organisms in more homogeneous environments. The model predicts that the environments leading up to major episodes of dispersal, such as the initial hominin dispersal into Eurasia, were likely relatively low in spatial heterogeneity and that the dispersing hominins had relatively low foresight.

2.2 Introduction

The relationship between increasing cognitive complexity of hominins and their ability to adapt to complex and heterogeneous environments has been a focus of palaeoanthropological research in general (Dunbar, 1998;

Potts, 2002; Grove et al., 2012), and, more specifically, in the study of the initial hominin dispersal into Eurasia (Kingston, 2007; Bar-Yosef and Belfer-Cohen, 2013; Palombo, 2013). The issue has also been central to debates concerning the replacement of Neanderthals by anatomically modern humans (Müller et al., 2011; Barton and Riel-Salvatore, 2012; Stewart and Stringer, 2012). Increasingly detailed palaeoenvironmental reconstructions and better chronological control of both environmental and human fossil data are helping to identify where and when particular regions were suitable for dispersing populations (for a recent review see Palombo, 2013). Kingston (2007) has argued that increases in the quantity and quality of data alone are not likely to help us gain a detailed understanding of hominin adaptive landscapes and of the emergence of global scale evolutionary phenomena. Modelling of dynamic hominin-environment interactions at spatial and temporal scales relevant for both hominin behaviour and evolution can help us make sense of this increasingly abundant and detailed information. Specifically, we have yet to fully investigate the factors that would push or pull hominins into unknown but potentially suitable regions. The explicit connection between mobility decisions made by hominins at the local scale, enabled by increased cognitive complexity, and the emergent pattern of dispersal and replacement at the global scale, has not been explored. Modelling and simulation allow us to study the ways in which global long-term scale phenomena, such as dispersal, emerge from local short-term scale phenomena, such as daily mobility decisions related to foraging.

We seek to address three specific questions in this study. First, how does advanced cognition help hominins navigate and exploit resource landscapes? Second, what effect does environmental heterogeneity have on the natural selection of increased cognition in hominins? Third, how is the dispersibility of a population linked to their cognitive ability? We develop an agent-based model to evaluate the relationship between cognitive complexity, environmental heterogeneity, and hominin dispersal. An agent-based model is a computational simulation of autonomous 'agents' that allows us to study the broader scale effects of a large number of local scale individual actions. Agents, which may represent individuals or groups, are programmed to have simple traits and behaviours that may change over time in response to their interaction with the social and physical environment (Rouse and Weeks, 2011). We argue that global scale patterns of dispersal emerge from local scale foraging-based mobility decisions rather than some innate or vitalist drive to explore. Specifically, the model tests the effect of foresight on patterns of mobility through heterogeneous resource landscapes. We define foresight as the ability of agents to deliberately and accurately assess and select a preferred environment. The model tests whether this ability could result in increased fitness, whether there is selection for maximum or perfect foresight, and how this selection is affected by environmental heterogeneity. We also discuss how various levels of foresight affect the net directional mobility, or dispersibility, of a population with that ability.

In previous work, we have shown that in some specific types of rapidly changing environments, intermediate rather than maximum levels of foresight are optimal (Xue et al., 2011). In that paper, which used reconstructed temperatures from the Vostok ice core for the last 400 000 years as a proxy for environmental change, but did not deal with a spatial environment, the model found that agents who tracked environmental change too closely during periods of slow change were at a disadvantage during rapid reversals. Agents who were slightly worse at evaluating and tracking the environment were fitter in the long-term and were less adversely affected by climate reversals (Xue et al., 2011). The current paper explores the role of foresight in a spatially complex, or heterogeneous, resource landscape using an agent-based model and demonstrates that intermediate rather than perfect foresight is also optimal in a spatial context. If we assume that high levels of foresight have an associated energetic cost, from increased demands on cognition, our results suggests that the cost would only be paid when specific environments require it.

Palaeoenvironmental reconstructions tell us where and when the doors to dispersal were open and hominin fossils and artefacts provide 'road-signs' telling us where and when hominins arrived (Bar-Yosef and Belfer-Cohen, 2013). In this research, we explore how increased cognitive capacity in the form of spatial foresight could have enabled or inhibited hominins from dispersing. Over the course of human evolution, resource availability could have functioned as a powerful but variable 'pull' mechanism, shaping dispersal patterns into novel environments, but its impact will have been mitigated by the level of foresight (cognitive ability) that hominins had developed.
In short, high levels of environmental heterogeneity might have selected for increased foresight and high levels of foresight might have effectively reduced dispersibility. This suggests that cognitively complex hominins in heterogeneous environments might have had low dispersibility relative to cognitively less complex organisms in more homogeneous environments. Taking this one step further, the model predicts that the environments leading up to major episodes of dispersal, such as the initial hominin dispersal into Eurasia, were likely relatively low in spatial heterogeneity and that the dispersing hominins had relatively low foresight.

2.3 Modelling dispersal

In order to study the role of foresight as hominin populations move through landscapes, we must understand how populations disperse through space. Population dispersal is an enigmatic phenomenon. Despite the fact that population dispersal is responsible for broad-scale spatial patterning in the archaeological record, there is little direct evidence of how it occurs. The instances of human populations dispersing into unoccupied territory within recorded history are essentially zero, and documented instances of populations moving into sparsely or variably occupied territory are very few (Kelly, 2003). We are left trying to predict the types of behavioural patterns that would result in dispersal, and then characterizing the spatial patterns this would create in the archaeological and genetic records.

The prevalent strategies for modelling dispersal discussed below rely on different assumptions about the importance of demographics, environment, social networks, and especially the importance and scale of environmental knowledge. We discuss approaches from archaeology when available, and introduce useful approaches from other disciplines, particularly ecology, where needed. A brief survey of the main approaches to modelling mobility, environments, and agents and their application to hominin dispersals will help set the stage for the description of our model.

2.3.1 Wave of advance

Ammerman and Cavalli-Sforza (1971) introduced the wave of advance approach in their study of the spread of Neolithic agriculture across Europe. It has since been applied to the Middle to Upper Palaeolithic transition (Bocquet-Appel and Demars, 2000; Davies, 2001; Mellars, 2006a), and the colonization of the New World (Steele et al., 1998; Hamilton and Buchanan, 2007). These studies estimate how fast populations can grow and spread, and how early we could expect the wave to arrive in a given location. Several studies based on Fisher's (1937) wave of advance equation (Ammerman and Cavalli-Sforza, 1973) or Reaction-Diffusion models (Steele, 2009) focused on the parameter values for the following equations:

$$\frac{\partial n}{\partial t} = \alpha n \left(1 - \frac{n}{K}\right) + D\nabla^2 n \tag{2.1}$$

and

$$v = 2\sqrt{D\alpha} \tag{2.2}$$

where K is carrying capacity, α is intrinsic maximum population growth, D is a diffusion distance constant, n denotes population size at a given time, t, and spatial location, and v is wave speed (Steele, 2009). Equation 2.1 consists of two terms, the first a logistic population growth, and the second a diffusion of that population evenly into the surrounding two-dimensional space. Steele et al. (1998) used values obtained from ethnographic and archaeological literature. These were applied to the Palaeoindian colonization of North American by looking at both the speed of the colonizing wave front and the spatial distribution of resulting populations assuming different rates of population growth, α, and intergenerational movement distance, D.

Wave of advance models generally assume that population growth fills the landscape to carrying capacity and that the movement from dense population centres is random in direction. Neither assumption is necessarily warranted (Meltzer, 2003; Rockman, 2003). For example, Hayden (1972) discusses the self-regulation of human populations well below carrying capacity via a variety of social mechanisms. Moreover, it is unlikely that mobility decisions were made by agents who were blind to the resource potential of the surrounding landscape. Hazelwood and Steele (2004) correctly acknowledge that this is a necessary assumption as a first step to examining dispersal, however, it is unclear how this assumption affects the modeled dispersal pattern.

2.3.2 Least-cost path modelling

Anderson and Gillam (2000) first used least-cost path (LCP) modelling to determine likely routes for the colonization of the New World. In this approach, a series of environmental variables in the form of gridded cell values, usually including topographic slope, are compiled to reflect the energetic cost of traversing a landscape. A Geographic Information System (GIS) is then used to compute the least-cost path from known start and destination points. The calculation of the 'friction' surface determines how the multiple environmental variables affect mobility. More typically, only a digital elevation model is used to derive first slope and then the caloric cost of climbing that slope. This approach generally assumes a complete prior knowledge of the environment and that mobility was consciously directed towards minimizing the total cost of the path, rather than minimizing the cost of each step. Since, in a dispersal context the landscape is not known in advance, Field et al. (2007), in their study of colonization routes into Southern Asia, developed an innovative 'wandering' method of computing least-cost paths in 60 km steps. Unlike Anderson and Gillam (2000), this method did not require that final destinations were known in advance, only that incremental destinations in sequential 60 km searches would be selected by the colonizing population.

A path that minimizes the energetic cost of walking through a landscape may be a good estimation of the routing of individuals on small time scales (for a trade network for example), but it is unclear if successive generations would determine their movements in the same way. A steep hill would not be a deterrent over the course of generations if a quality resource was at the top. Field et al. (2007) argued that the high cost areas would be accessed for resources, but would not be major channels of movement. While a good way to locate these preferred channels of movement, the model's assumption that energetic cost of movement is the primary factor in mobility decisions seems untenable over the inter-generational residential moves being modeled in hominin dispersal contexts.

2.3.3 Representing the environment

The field of ecology has been modelling dispersal processes much longer than archaeology and has developed a much greater variety of models and model assumptions (Johnson and Gaines, 1990). The resource patch is central to ecological theory and influences modelling frameworks. The patch is a homogeneous resource area, usually a food source, with none of that resource occurring in the inter-patch space. Patch-based analytical models focus on the effects of inter-patch distances, patch size, edge hardness, and clustering (e.g., Zollner and Lima, 1999) on dispersal. In a rare archaeological example, Grove (2013) explored the relationship between inter-patch distance and the natural selection of spatial memory.

Patches are useful for mathematical models due to their simplicity, but introduce somewhat artificial boundaries between some environmental zones. A gradual transition in abundance is not well represented by a patch edge, nor is degree of habitat quality. For example, patch distribution models may not be adequate if we assume hominins are interested in several resources in different proportions.

An alternative approach is to model heterogeneous landscapes of habitat suitability or quality, either as continuous variation, or discretely on a fine scale, usually on a grid. This has the advantage of more realistically representing many types of resource landscapes, while still being relatively simple to represent mathematically (Blackwell, 2007). For example, Mitchell and Powell (2004) represent a continuous heterogeneous resource landscape with a grid of cells varying in value from 0 to 1, and Holland et al. (2009) generate simulated continuous landscapes with varying degrees of spatial autocorrelation or clustering.

Archaeological wave of advance and LCP models represent environments as continuous variation (i.e., as carrying capacity and energetic cost, respectively), but derive their values from palaeoenvironmental or topographical variables, rather than generated environments with specific properties. In a simulation study of the evolution of cultural learning in hominins, Lake (2001) generated continuously varying landscapes of net energetic harvesting return ranging from -100 to +100 using a fractal algorithm. Using this method, he produced multiple landscapes for each of three different levels of environmental heterogeneity.

2.3.4 Cellular automata and agent-based models

Cellular automata models consist of a grid of cells which change state, from empty to colonized for example, based on the condition of their neighbouring cells (Mithen and Reed, 2002). As in wave of advance models, archaeological cellular automata models have focused on calculating the earliest arrival dates in a given location. Mithen and Reed (2002), and the related Nikitas and Nikita (2005) and Hughes et al. (2007), used a probabilistic cellular automata to model the dispersal of *Homo erectus* throughout the Old World using constant probabilities for movement, colonization (fission), and extinction. These models assumed mobility decisions were made irrespective of the environment, although this was a programming choice and not a limitation of the approach per se.

There have been a number of archaeological ABMs published since the 1970s (see reviews in Aldenderfer, 1981, 1991; Costopoulos and Lake, 2010), including several that model hunter-gatherer foraging patterns (e.g., Mithen, 1990). Comparatively few have dealt with dispersal explicitly. Lake (2000) simulated the first colonization of a small island of the coast of Britain using a custom-made ABM. This required a detailed palaeoenvironmental reconstruction to model the distribution of a hypothesized key food resource, hazelnuts. Simulations were run using several hypothesized origin points, and the distribution of simulated lithic assemblages resulting from model runs were compared with the known archaeological record. In a paper demonstrating the potential of ABMs for studying migration, Young (2002) developed a variety of simple models to show how random walks, biased migration, mobility speeds, population growth rates, and inter-group competition could result in complex patterning. He argued that basic models of foragers looking for food could result in large scale population dispersals without invoking "extraordinary circumstances or motivation" (Young, 2002: 157). Of particular relevance to the current study is Young's model of biased migrations. In this model, agents randomly selected a neighbouring location, and tested if that location offered an improvement. If it did, they were only allowed to move with a specified probability.

Most of the modelling frameworks discussed above have the drawback of not being able to represent evolutionary processes, such as the evolution of foresight, and dispersal through space simultaneously. However, agent-based models are particularly useful for studying the evolution of traits while modelling the underlying environment. The growth of computational power and the maturation of languages and packages specific for ABM (e.g., Netlogo (Wilensky, 1999) or Repast (North et al., 2007)) means that ABMs can look at the relationship of both processes (evolution and dispersal) within a single framework. It is for this reason that we develop an ABM to look at the relationship between spatial environmental heterogeneity, the evolution of foresight, and the dispersibility of hominin populations.

2.3.5 Role of environmental knowledge in dispersal models

In an early review of dispersal models in population ecology, Johnson and Gaines (1990) identified a series of key ‘push’ or ‘pull’ factors affecting dispersal rates and patterns. Some of the factors are incorporated into models used in archaeology such as population growth in wave of advance models and minimizing cost of movement in least-cost path models. Other factors, such as the probability of surviving a dispersal episode are highly relevant to hominin dispersal, but are extremely difficult to estimate from archaeological data since failed attempts are less likely to be archaeologically visible. Johnson and Gaines (1990) also propose a number of instructive general conclusions about environmental variability. Temporal variability tends to increase dispersal since the local environment will likely become worse. A spatially heterogeneous environment tends to reduce dispersal since any new location is likely worse.

Random directional movement, often from a ‘push’ such as population growth, is the most widely used approach in archaeology. However, Conradt et al. (2003) argued that random movement is costly in terms of survival due to its high probability of failure. Still, forays or reconnaissance trips before movement can increase success by informing dispersers of potential risks and locating resources. Such trips are commonly noted in ethnographic accounts of foraging, including the daisy pattern of daily return trips in the classic forager model or logistical information gathering trips in the collector model (Binford, 1980). The volume edited by Whallon and colleagues (2011) contains numerous examples of information sharing within and between groups, and of the importance of this information for success and survival. This pattern of exploratory migration has also been noted in contemporary ethnographic examples such as the classic study of Mexican migrants from Tzintzuntzan (Kemper, 1977).

The degree of environmental knowledge underlying mobility decisions in wave of advance and least-cost path models represent two ends of a spectrum. The former assumes random movement with no knowledge of the environment and the latter assumes directed movement with global knowledge. Models can vary along an information continuum from random walks (no information) to local information (spatially limited information) to agents with complex cognitive models or ideal-free distribution models (global knowledge)(Lima and Zollner, 1996). Agent-based models may be designed to fall anywhere along this informational continuum, but are particularly suited to local information. For example, Lake (2000) coded agents to learn about resource distributions from individual observations at the local-scale, and additionally to construct a broader collective memory by sharing that information with other agents.

2.4 Modelling spatial foresight in a variable environment

Our ABM approach is informed by results obtained from the above studies and includes an explicitly defined representation of space and resource abundance as continuous variables, and the use of information at a local scale when making mobility decisions. The model uses directed movement, or spatial foresight, but with a variable probability of accuracy. This is similar to the approach of Young (2002) discussed above (see Cellular automata and agent-based models). However, we make foresight a heritable trait varying from 0 to 100% accuracy, within a population of constant size. We then examine how the heterogeneity of the resource environment affects the selective pressure for increased or decreased spatial foresight and its implications for dispersal.

Spatial foresight as a mobility mechanism requires two basic assumptions. The first assumption is that hominin groups were able to evaluate the resource potential of their local, or neighbouring, environment. The second is the model's 'pull', that hominin groups made mobility decisions to improve upon the currently available resources, at least some proportion of the time. The first assumption is not onerous; hominins were certainly able to assess resource abundance or quality in surrounding habitats. However, the scale at which a landscape is expected to be assessed is relevant. Our model is designed to operate on a spatial grid, where a move to a new grid cell represents a residential move, and the scale may therefore be adapted to a reasonable distance. A small group of hominins could easily be expected to utilize a 5 to 10 km radius, or catchment, and assess the resource potential of a slightly larger radius (Vita-Finzi and Higgs, 1970; Kelly, 1995). Binford (2001) collated foraging radius measurements for a large number of ethnographic examples to derive an average 8.28 km radius for foragers. He found the average distance between residential camps ranged between approximately 25 km for plant foragers and 43 km for terrestrial animal collectors. For the sake of generality, we have chosen not to parameterize our model to a specific distance. However, it would be consistent with a 10 to 20 km grid cell and a 30 to 60 km local assessment area. In the current study, we are more concerned with the effect of environment heterogeneity than a specific spatial scale (see Model resource landscapes and results, below).

The proportion of mobility decisions that may be attributed to our second assumption, that resources acted as a 'pull' during mobility decisions (rather than any number of other factors) is difficult to determine from archaeological evidence, but we will explore this question with our model in the next section. For simplicity, our agents are programmed to make mobility decisions based upon resource abundance some proportion of the time, and that other mobility decisions are made without reference to the resource distribution.

2.4.1 Model outline

Our ABM, constructed using the Netlogo toolkit (Wilensky, 1999), begins with a population of five hundred agents distributed near one corner of a gridded resource landscape (see Model resource landscapes and results, below). Agents have one attribute, foresight, which is the probability that they will correctly assess the environment of their local (9-cell) landscape. Agents begin each run with perfect foresight, although the result is robust to changes in the initial condition. During each time step, the following schedule of events occurs:

1. Each agent differentially reproduces based on the abundance of resources available on its local cell (see Reproduction, below). There is no accumulation of resources.
    (a) Offspring inherit their parent's foresight value with a slight mutation.
    (b) A random empty neighbouring cell is chosen for each offspring agent.
    (c) If all neighbouring cells are occupied, the offspring agent is removed.
    (d) For every placed offspring, one random agent is removed.
2. Each agent's inherited foresight determines the probability of correctly predicting the highest resource cell of a 9-cell neighbourhood.

(a) If correct, and the highest resource cell is unoccupied, the agent moves to that cell (i.e., the agent has accurately moved to the best available cell).

(b) If incorrect, the agent moves to a random neighbouring cell as long as it is unoccupied (i.e., the agent has mistakenly moved to a suboptimal cell, possibly one worse than the starting point).

(c) In either case, if the selected cell is occupied, the agent stays.

The mean foresight and mean resource values of the agents are logged with the environmental heterogeneity value at the end of each run. Mean foresight represents the culmination of the evolutionary trend of the agent population. Mean resource value represents the agent population's collective ability to maximize the currently available resources, effectively their final level of adaptive success. Since the summed cell values of all gridded resource landscapes are equal, mean success measures the permissiveness of each level of heterogeneity.

2.4.2 Reproduction

Agents represent small groups rather than individual hominins. As such, reproduction occurs by asexual fission with a probability determined by the current success of the group. The ratio of the resource abundance of the cell the agent occupies, s, and the resource abundance of the most successful of all agents, $max(s)$, is multiplied by a base reproduction rate, r held constant at 0.1, to determine their individual probability of reproduction (Equation 2.3). Mutation of foresight occurs as a uniform random value with a specified maximum size, held constant at 0.01, to increase or lower the value.

$$\frac{s}{max(s)} \cdot r \tag{2.3}$$

The constant population size allows us to measure the effect of natural selection in the absence of demographic stochasticity. For the evolution of a trait to occur we need only to implement either differential reproduction or removal of agents. We chose to randomly 'kill' agents after successful reproductions, rather than removing those with the lowest resource abundance, to avoid doubling the fitness advantage of the resource landscape.

This process is a simplification of the population growth and fission dynamics of hunter-gatherers under the constraint of carrying capacity in either static or dispersal conditions. We assume simply that more abundant resources lead to a higher rate of population growth and group fission, but that a large number of groups in a small area reduces group fission.

2.5 Model resource landscapes and results

2.5.1 Cone

Our simulated environment is represented by a 100 x 100 cell grid of environmental resource values ranging from 0 to 100, where 100 is considered the highest resource value. Before experimenting with complex resource landscapes, we first consider a smooth sided resource cone or bull's eye where resource abundance decreases evenly away from a high centre area.

When the model is run, the high foresight agents cluster around the central area as they all try to maximize the resources available to them, and thus maximize their rate of reproduction. However, on this simple, relatively homogeneous resource landscape, foresight is strongly selected against and rapidly declines to very low levels (median of 14%, Figure 2–1).

2.5.2 Heterogeneous environments

We generated 1100 continuously varying gridded resource landscapes using a stochastic fractal algorithm in the r.surf.fractal module of GRASS

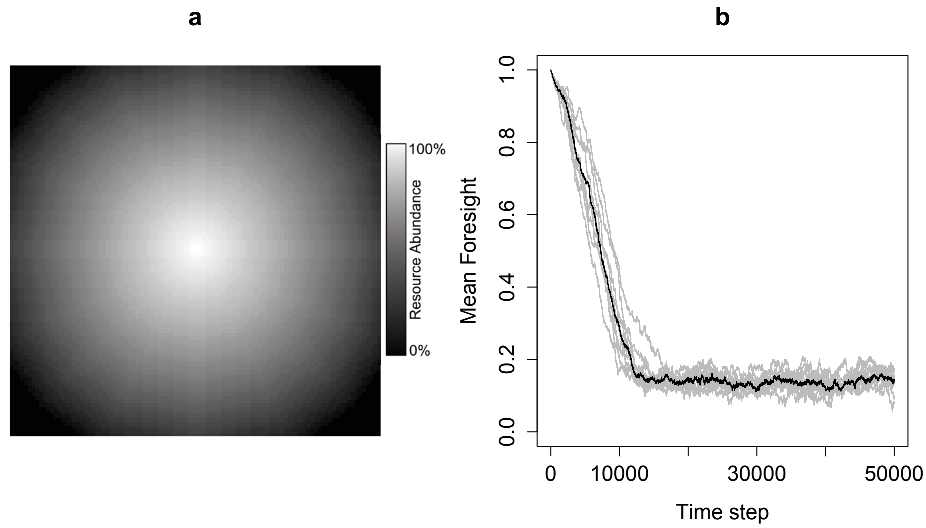


Figure 2–1. Natural selection of decreased foresight on simple resource cone. a) Resource landscape where shades of grey represent percent abundance of resources and white is the most abundant. b) Change in mean foresight over time from an initially perfect foresight (value of 1). Grey lines represent 10 runs with identical parameters, the black line is the median of those runs.

GIS (GRASS Development Team, 2012). The algorithm generates natural looking continuous landscapes with increasing environmental heterogeneity specified as increasing fractal dimension, ranging between 2 and 3 (n.b. Since fractal dimensions of 2 and 3 cannot be used in the algorithm, we used 2.001 and 2.999 as our least and most heterogeneous landscapes, respectively). We scaled the cell values produced from 0 to 100 for input into the model, such that every value was approximately equal in frequency and the sum of all cells in a landscape was equal irrespective of the degree of heterogeneity. We generated 100 different landscapes for each of the 0.1 increment increases in fractal dimension (Figure 2–2).

After 50 000 time steps of the ABM, a duration our experimental runs determined to be generally sufficient to stabilise at a relatively constant value, we took the mean foresight and resource values of all agents to represent the effect and result of natural selection for each of the 1100

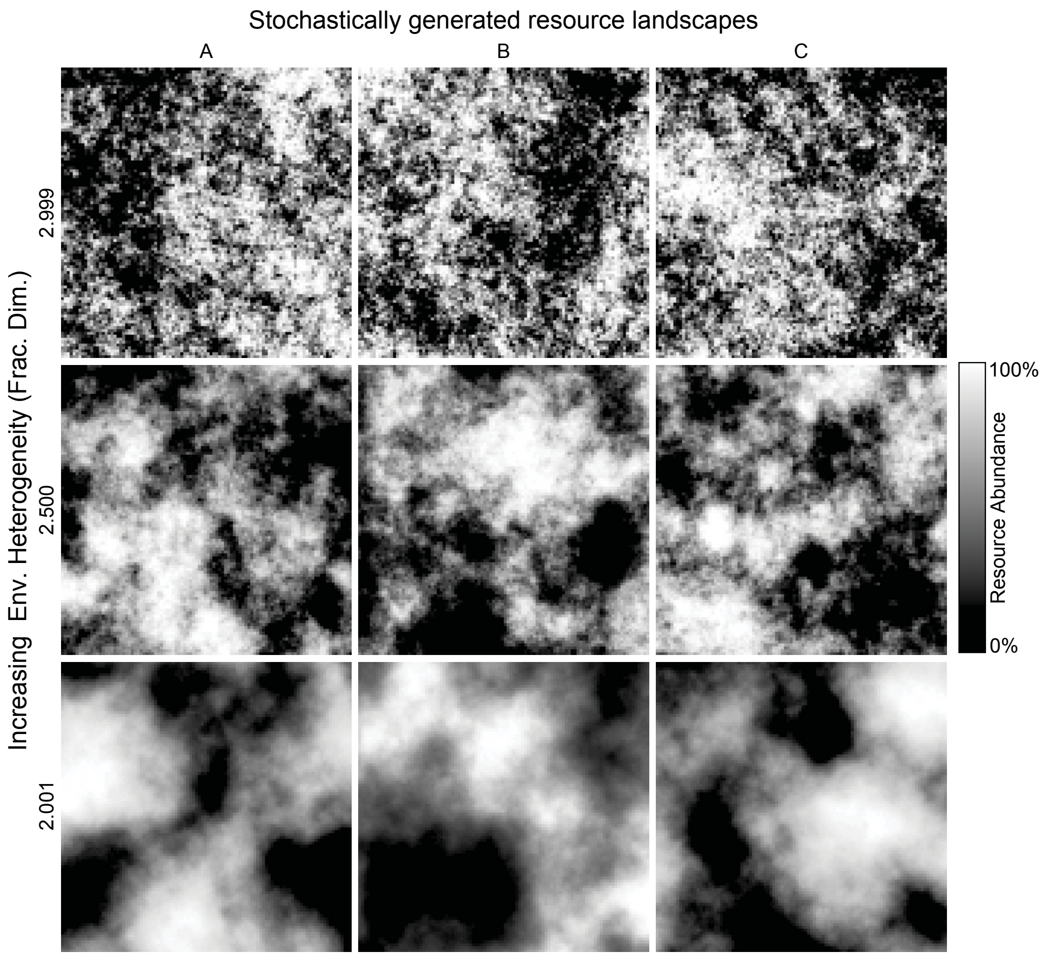


Figure 2–2. Example gridded resource landscapes used in the model. Rows illustrate the differences between three stochastically generated landscapes with the same environmental heterogeneity, while columns represent different degrees of heterogeneity. Note that similar cell values are spatially clustered in large patches when heterogeneity is low, and more in smaller, more distributed patches when heterogeneity is high.

heterogeneous landscapes (Figure 2–3). For less heterogeneous environments, mean foresight decreases to very low levels (median 24%), replicating our prior observation on the cone. As the degree of heterogeneity increases, the mean foresight level of the population increases to very high levels (median 85%).

Mean success was highest for less heterogeneous environments (median 95%), and only slightly lower success (median 88%) for the most heterogeneous environments (Figure 2–4). Since mean fitness is also increased due to differential reproduction, we ran a series of control runs where agents had no spatial foresight ability to differentiate the effect of foresight from reproduction. Mean success of the control runs was lower than those of foresight for all environments.

2.6 Discussion

2.6.1 Dynamics of foresight in heterogeneous environments

As the model progresses on the cone-shaped resource landscape, the highest foresight agents move to the centre where there is less space available to reproduce due to crowding. Since more space is available to lower foresighted agents around the edges of the cluster, they are more often successful in placing offspring, even though their reproduction rate is lower. In effect, a new resource of available reproductive space is generated and becomes a more important factor than resource value of the cell in the natural selection of foresight. Natural selection is not driven by who is able to acquire the best resources, but by who can reproduce most successfully. This mechanism, that reproductive space is selected over resource value, is replicated on the less heterogeneous landscapes where resource clusters are relatively wide but decrease in value towards the edges.

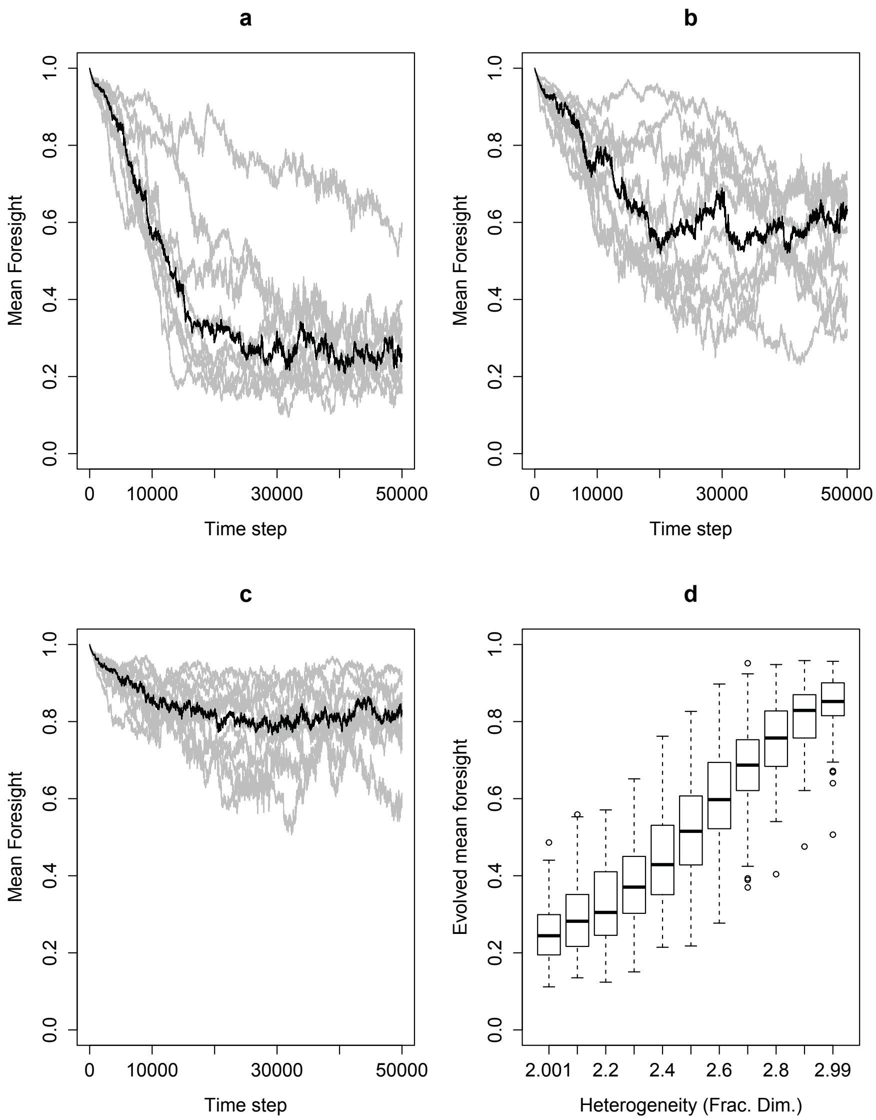


Figure 2–3. The ability to correctly predict the local environment, foresight, is selected against in less heterogeneous landscapes. Grey lines represent runs on 10 different generated landscapes, the black line is the median of those runs. a) Low heterogeneity (2.001). b) Medium heterogeneity (2.5). c) High heterogeneity (2.9). d) Each box plot represents the mean foresight value of 500 agents at the end of runs on 100 different simulated landscapes. Dark horizontal lines represent the median, horizontal edges of the boxes represent the 25th and 75th percentiles, top and bottommost horizontal lines represent 1.5 times the inter-quartile distance. Small circles represent outliers.

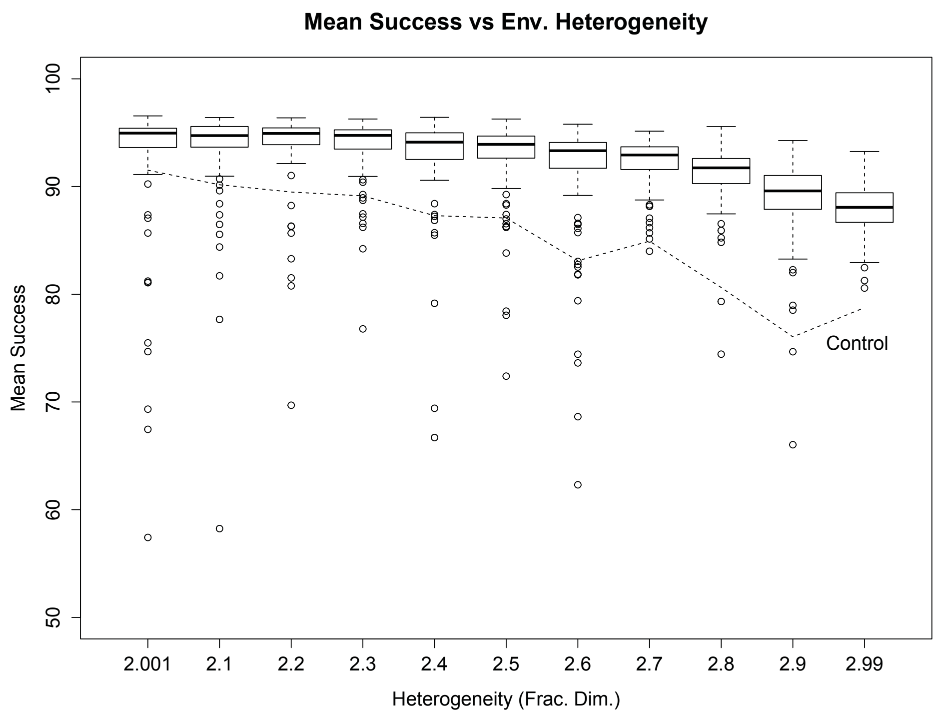


Figure 2–4. The mean resource abundance of agents, a measure of their success at locating resources, is inversely proportional to heterogeneity but remains high overall. The dotted line displays the effect of a series of control runs where agents have no spatial foresight.

As the degree of environmental heterogeneity increases, the clusters of agents become smaller and more dispersed and the availability of reproductive space increases overall. Further, foresight inaccuracies are less well tolerated as they more quickly move an agent onto a low resource cell, because of the steeper resource gradients. As a result, the selective pressure against the high foresight agents is mitigated and the mean foresight of the population increases significantly. These results demonstrate that the level of foresight is density-dependent (Hixon and Johnson, 2009) as a function of the degree of clustering of the resources (the level of heterogeneity), because the summed resource abundance was equal for all landscapes in this experiment.

The inverse relationship between success and heterogeneity is due to the decreased clustering of similar resource values in heterogeneous environments. In a highly heterogeneous environment, if an agent makes a few errors and moves a short distance away from a high resource value, its new environment will likely be a much lower resource location. On a less heterogeneous landscape, mistakes are better tolerated as resource values diminish much less quickly with distance.

Heterogeneity is inversely correlated to success even after the level of foresight has been naturally selected for an environment. Interestingly though, for all heterogeneity levels, the agents are generally more successful than in the control runs despite a widely differing level of foresight of the population (Figure 2–4). This suggests that a local environmental awareness, what we have called foresight, is a remarkably successful behaviour assuming it is sufficiently adapted to the characteristics of the resource landscape.

2.6.2 Effect of foresight on dispersal

While these dynamics explain the natural selection of foresight in different environmental patterns, they do not fully explain the relationship of foresight to dispersal. High foresight causes agents to 'hill-climb' to the nearest local optimum, a location on the resource landscape where all surrounding cells are lower in value. It also causes them to become stuck on local optima, because they can accurately predict that their entire accessible neighbourhood is worse than their current location and therefore do not move again. Lower foresight allows agents the potential to random-walk into a novel, and potentially higher, resource area. Agents with very low foresight may not realize they have reached a peak and may walk off the peak, resulting in lower resource abundance. This trade-off is well known elsewhere as a part of evolutionary optimization to adaptive or fitness landscapes (Wright, 1932; Fogel, 1994).

Natural selection of intermediate levels of foresight result in a stochastic hill-climbing behaviour that allows agents to strike an appropriate balance between exploration ('mistakes') and resource maximization (hill-climbing). If agents did not make mistakes in assessing the local resources, they would become fixed on the first local optimum they encountered even if was relatively low in resource abundance. Other possible stochastic strategies, like randomly choosing from the subset of better neighbouring cells also exist but were not chosen in this model for simplicity. Choosing from the best of the unoccupied cells would perhaps have been slightly more realistic for a rational agent. However, this would have increased computational time and would have crowded resource peaks even more tightly.

As noted in the introduction of this paper, dispersal should be seen as an emergent phenomenon arising from local scale mobility decisions. The model demonstrates that lower foresight, resulting from natural selection within a less heterogeneous resource landscape, will increase the probability of exploratory behaviour at the local scale, and therefore higher population dispersibility at the global scale. The inverse is also true, higher foresight, resulting from a highly heterogeneous resource landscape, reduces the probability that agents will explore beyond the immediate resource cluster; that is, the more 'sticky' the peaks of the resource landscape become. The model therefore predicts that less heterogeneous environments would radiate populations outwards, while more highly heterogeneous landscapes would, over time, capture those populations and adapt them into higher foresight populations. However, this poses an interesting question for future research since increased cognitive complexity, in the form of highly accurate foresight in foraging at least, reduces the dispersibility of the population.

2.7 Conclusion

Archaeology and palaeoanthropology continue to search for mechanisms that can connect the increased cognitive complexity of our genus to our success in colonizing complex novel environments. Behavioural flexibility (Potts, 2002), improved technology (Mellars, 2004, 2006b), language (Wynn and Coolidge, 2010), extended social networks (Gamble et al., 2004; Grove et al., 2012), and increased home range (Antón et al., 2002) are just a few of the many hypotheses suggested to account for this success.

Palaeoenvironmental reconstructions and hominin fossil and artefact distributions alone cannot provide a complete picture of the complex dynamics of hominin-environment interaction. Dispersal models, such as the model presented in this paper, provide a complementary approach for exploring hominin interactions with reconstructed environments. These models explore the potential mechanisms behind dispersal and begin to evaluate not just when and where, but how or why hominins might have decided to leave one environment in favour of an unknown and potentially risky environment.

The approach taken here illustrates the potential of agent-based modelling for connecting local scale cognitive decisions with observed global scale patterns to test hypotheses about dispersal. Rather than assuming that landscapes would become occupied when available, we model a population making deliberate decisions about foraging potential at the local scale, to varying degrees of accuracy, and we evaluate the impact of foresight on population dispersibility, i.e., whether it favours or inhibits global scale population dispersal. The model suggests that there is an intimate relationship between population dispersibility, foresight, and environmental heterogeneity. Under most conditions, dispersibility depends on a certain level of inaccuracy in mobility decisions based on resource abundance, or the presence of decision making mechanisms not based on resource abundance. This level of inaccuracy varies strongly with environmental heterogeneity, suggesting that we should look to the periods leading up to major dispersal events, not just during the dispersal, to see how the spatial patterning of the environment could have naturally selected hominin populations to have high or low dispersibility. The model predicts that environments with relatively low heterogeneity are required to naturally select a population with the characteristics necessary, i.e., low foresight, to disperse into unknown environments.

The next step in our research agenda is to look at the strength of the effect of foresight by quantifying dispersal rates of populations with varying levels of foresight, and with population growth, and compare this to expected rates of dispersal in other published dispersal models. This will allow us to explore how expected hominin arrival times in different regions would be altered by a population with foresight. Our future work will help us to clarify the apparent contradiction found by this paper, that environmental heterogeneity favours increased cognitive complexity but not dispersibility.

CHAPTER 3
Environmental knowledge inhibits hominin dispersal

3.1 Overview and context within thesis

In any computational model, there are a multitude of programming choices made for the sake of simplicity or expediency. This leaves many additional questions regarding what the model would do if other choices had been made. In particular, three aspects of the model presented in chapter 2 are worth revisiting to evaluate the robustness of the findings. Chapter 3 extends the model to attempt to address these questions:

- What if agents could see farther?
- What if agents could share information?
- What if the population could grow?

In chapter one, agents could only evaluate the resource potential of their immediate neighbourhood. The site catchment inspired this choice and the model design roughly replicated the behaviour of a hunter-gatherer group discovering better resources during its daily foraging tasks near camp. A reviewer asked what would happen if the agents had a larger assessment neighbourhood. Although I suspected it would not be beneficial, the first model of chapter two evaluates this question by holding foresight constant, and making the neighbourhood size or perceptual range a heritable trait. If it provides a fitness advantage, then a larger perceptual range should evolve over the course of a model run.

Lake (2000, 2001) presented an ABM in which agents, as individuals, would spend a day foraging before returning to camp to share information about the landscape with their group. As a dispersal model, this provided a way for a colonizing hunter-gatherer group to build up a collective memory of their new landscape over time and use it to forage more efficiently. Due to hardware limitations, Lake's model runs had only four agents. The results of chapter one suggest that a crowded landscape could add an interesting new dynamic to the hypothesised advantage of information sharing and collective memory.

As noted in the introduction, population growth is the one indisputable dispersal mechanism. The model needs to reflect this, rather than fix population size to an arbitrary number, to evaluate its effect on the natural selection of cognition and dispersibility. As will be noted in the following chapter, this didn't exactly go as planned, but results in a confirmation of the selective effect of crowding.

Overall, the models suggest that environmental knowledge inhibits dispersal by directing movement towards known resources instead of outwards into unknown territory. The same movement towards resources reduces available reproductive space around resource clusters (i.e. increases crowding) and results in the natural selection of lower levels of environmental knowledge. Smaller assessment neighbourhoods and low levels of cultural transmission of environmental knowledge result. Increased population size crowds the landscape even more and intensifies the selective effect against environmental knowledge.

3.2 Introduction

Under what behavioural strategies and environmental conditions will dispersing hominins fail to locate and colonize a desirable, resource rich, but unoccupied region? This question is fundamental to understanding hominin dispersal as it explicitly connects the local-scale mobility decisions of hominin foraging groups to the two broad-scale research avenues of the palaeoanthropological literature: palaeoenvironmental reconstruction (e.g. Palombo, 2013, and the references therein), and the location and timing of hominin fossils and artefacts (Bar-Yosef and Belfer-Cohen, 2013).

Using the baseline model for this study, Wren et al. (2014) showed that the connection between foraging related mobility decisions and the emergent pattern of a dispersing (or non-dispersing) population is not necessarily intuitive. Cognitively sophisticated agents accurately read the resource potential of the landscape at a local scale, but demonstrated lower dispersibility than agents that selected patches at random. Natural selection of heritable resource assessment accuracy, referred to as spatial foresight, resulted in very low levels of accuracy and high dispersibility for environments with relatively low heterogeneity. The more heterogeneous the environment, the more spatial foresight was advantageous, while also lowering group dispersibility. This reminds us that dispersal is an emergent phenomenon that, under the proper conditions, may result from local scale mobility decisions.

This paper builds on the findings of Wren et al. (2014) by extending how groups acquire knowledge of their environment before making mobility decisions. The first model varies the size of the agent's resource assessment area, giving them access to more of the environment before deciding where to move, and perhaps letting them see beyond some of the local scale landscape variability. The second model allows agents to learn about the resource landscape through social interactions instead of direct observation. This could allow them to make use of extensive social networks to acquire environmental knowledge, and to thereby capitalise on the success of the population as a whole. Each model allows the agent's level of environmental knowledge to vary, and then evaluates how the resource distribution affects the natural selection of environmental knowledge. By extension, this allows us to evaluate what impact environmental knowledge has on the dispersibility of the population.

Our previous work also demonstrated that since dispersibility is relatively low in many environments (Wren et al., 2014) , some type of push, a factor which decreases the attractiveness of the current location (Anthony, 1990), may be needed for dispersal to take place. Three principal push factors have been identified in the palaeoanthropological and dispersal ecology literature. The most often cited is population growth causing diminishing returns within a local area and making movement into a new area more advantageous (e.g. Ammerman and Cavalli-Sforza, 1971; Steele et al., 1998; Mellars, 2006b). We therefore add a small degree of population growth to the previous two models to evaluate its effect on mobility strategies. Two other possible pushes are temporal environmental change, such as a latitudinal shift of a resource distribution, and local resource depletion, but will not be addressed here (Rockman, 2003).

The current paper only considers the natural selection of the level of environmental knowledge and its effect on dispersibility. Later work will consider other model results, such as the quantification of dispersal rates under different conditions.

3.3 Models

In each of the following two models the resource environment consists of a 100 by 100 cell grid with each cell containing a fixed resource abundance or habitat quality ranging from 0 to 100%. We generated resource landscapes with different degrees of heterogeneity using a fractal algorithm and varying the fractal dimension from 2.001 to 2.999 in 0.2 increments (GRASS Development Team, 2012). Due to the stochastic nature of the module, 30 landscapes of each heterogeneity level were generated to make a total 'run set' of 180 landscapes. We scaled the cell values of each landscape to have an approximately equal cell count of each resource value and the same summed resource abundance.

A population of agents, each representing a hominin foraging group, begins each run clustered in one corner to simulate entry into the novel territory. Reproduction occurs as asexual fission at a fixed base probability, r_b, adjusted by the ratio of the cell's resources, s, to the maximum resource value of all agents (Equation 3.1). A change in their trait value, which determines the level of environmental knowledge they have access to, occurs by increase or decrease of the trait value in the offspring at a specified probability, m_r, by size, m_s. This is a slight departure from the baseline model of Wren et al. (2014), for which mutation occurred in every offspring with a uniform random m_s up to a specified maximum size. The new method decreases the amount of random drift of the trait value by having mutations occur less often, but with a larger effect if the mutation increases fitness.

$$r_a = \frac{s}{max(s)} \cdot r_b \tag{3.1}$$

Each of the models runs three times. First with population size, n, held constant and a full run set of 180 landscapes, second with different population sizes on a subset of low heterogeneity landscapes, and finally with a variable population function which allows for population growth and a full run set (Table 3–1). In all models, the probability of removal, or death, of an agent is equal for all agents, irrespective of their resource value. Natural selection by the environment is therefore only counted once, during reproduction, rather than being counted at birth and death.

The models only vary in how agents access environmental knowledge. In each case the optimal trait value is naturally selected as the run progresses. Small mutations in trait value lead to a reproductive advantage or disadvantage for the agents, and over time the optimal level of environmental knowledge evolves. In effect, the model lets natural selection act as an optimizer, refining the level of environmental knowledge until it provides the most optimal solution for the population. This is similar to evolutionary optimization algorithms, which let a system make small changes to an algorithm until it finds the best solution.

3.4 Model 1: Assessment Radius

3.4.1 Introduction

The baseline model constrained the radius over which agents assessed the resource potential of their landscape to an 8-cell neighbourhood (Wren et al., 2014). A common assumption is that increasing this radius to include a larger assessment area would provide more detailed information about the overall landscape and would therefore provide an adaptive advantage to foraging groups. This hypothesis was suggested by an anonymous reviewer of the baseline model and by several others who saw preliminary model results in conference presentations.

Var.	Description	Assessment radius			Cult. transmission		
		Const. Pop.	Var. Init. Pop.	Pop. Growth	Const. Pop.	Var. Init. Pop.	Pop. Growth
N	Initial population size	500	100, 1000, 2000	500	500	100, 1000, 2000	500
r_b	Base reproductive rate	0.1	0.1	0.1	0.1	0.1	0.1
d	Removal probability	0	0	0.06	0	0	0.06
m_r	Mutation probability	0.001	0.001	0.001	0.001	0.001	0.001
m_s	Mutation size	0.5 (cells)	0.5 (cells)	0.5 (cells)	0.1	0.1	0.1
f	Assessment accuracy	0.25 0.75	0.25 0.75	0.25 0.75	n/a n/a	n/a n/a	n/a n/a
Env	Range of hetero-geneities in run-set	All	2.001 only	All	All	2.001 only	All
Steps	Number of time steps for each run	100 000					

Table 3–1. Parameters used to initialize model runs.

The first model tests whether increasing the assessment radius would improve the ability of agents to navigate through a complex resource surface, and if this would impact the foraging success or dispersibility of the population. An increased visual range increases the overall amount of environmental knowledge that an individual group has access to when making mobility decisions. It seems intuitive that groups would be less likely to be stuck on local resource optima, places where all surrounding cells are lower in value, if they were able to evaluate a greater number of cells before moving (Figure 3–1).

Lima and Zollner (1996) review ecological models of perceptual range, an equivalent concept to what this article refers to as assessment radius. They suggest that increased perceptual range could increase dispersal since search time and risk of mortality would be reduced, but that empirical data is lacking (see also Zollner and Lima, 1999).

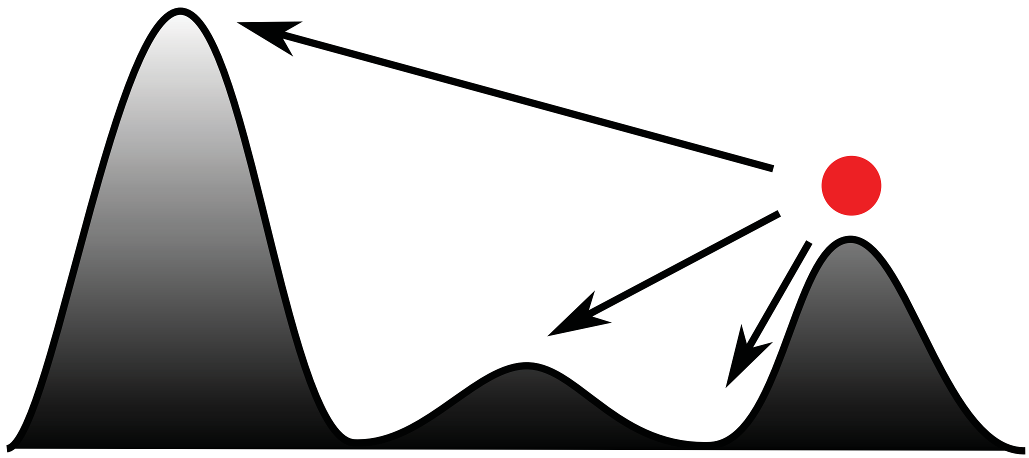


Figure 3–1. Increasing the assessment range when making foraging decisions may allow agents to escape local optima and locate higher peaks. Dot represents an agent and peak height represents resource abundance.

Binford (2001) notes that the distance between residential moves of hunter-gatherer groups varied depending on the resource base and the subsistence strategy. This suggests that the distribution of resources is an important factor in the optimal radius being taken into account by humans when making mobility decisions. In an ethnographic study of the Yup'ik Eskimo, Funk (2011) describes the high level of landscape detail known, particularly by men, over a wide area. However, of particular relevance is her observation that knowledge of subsistence resources (i.e., seasonality and variations in abundance or quality) was restricted to their immediate area of use, although the precise range of that area was not given (Funk, 2011, p. 48).

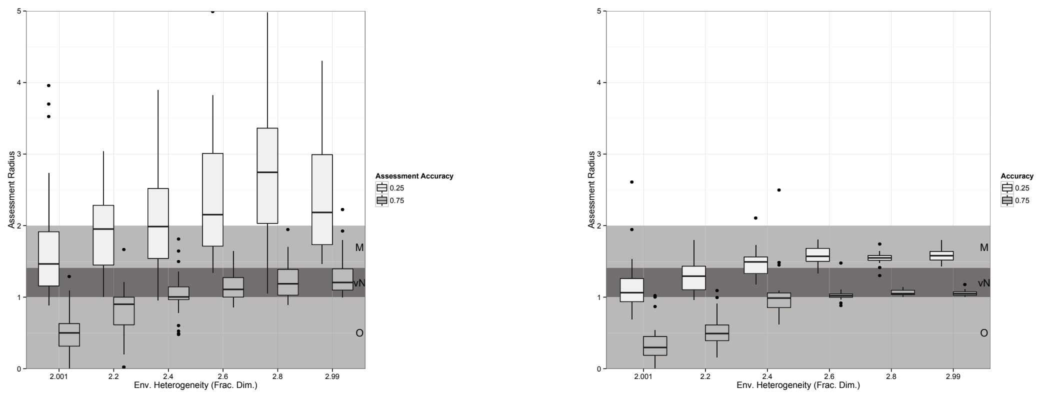
3.4.2 Model Description

Model 1 evaluates the natural selection of assessment radius by making radius a heritable trait subject to small random increases or decreases. Since the baseline model demonstrated that foraging accuracy varies with environmental heterogeneity, the model holds foraging accuracy constant. The model runs through all 600 landscapes twice, once with low foraging accuracy ($f = 0.25$) and once with high foraging accuracy ($f = 0.75$). The model output includes the median assessment radius and cell value of all surviving agents at the end of each run (See Table 3–1 for model parameters). At each time step of the run, each agent follows this schedule:

1. At probability, r_a, produce an offspring (Eq. 3.1).
   (a) Offspring inherit their parent's assessment radius trait value, f_r.
   (b) At probability, m_r, offspring's trait value will increase or decrease by m_s.
   (c) Offspring choose a random unoccupied neighbouring cell.
   (d) If all neighbouring cells are occupied, offspring is removed.
   (e) Fixed pop. only: if offspring is successfully placed, one random agent is removed.
2. At probability, f, correctly predict the highest resource cell within their inherited radius f_r .
   (a) If correct, attempt to move one cell directly towards the selected cell.
   (b) If incorrect, attempt to move to a random neighbouring cell.
   (c) In either case, stay if another agents blocks the move.
3. Variable pop. only: be removed with probability, d.

3.4.3 Results

The model shows that there is strong selection to keep assessment radius at low levels in all landscapes (Figure 3–2). Evolved median assessment radius ranged between 0.5 and 1.2 for high foraging accuracy runs and between 1.5 and 2.2 with a higher variance for low accuracy runs. Assessment radius increased slightly with environmental heterogeneity. Agents with an assessment radius below 1 would only be able to assess the currently occupied cell which would result in no movement except on foraging errors,



(a) Fixed population size

(b) Variable population size

Figure 3–2. Natural selection favours low assessment radius (the radius over which groups assess the resource potential of the landscape) across all types of environments, and with fixed or variable population sizes. Each box plot represents the assessment radius value of agents at the end of runs on 100 different simulated surfaces. Bottom, middle, and top of boxes represent the 25th, median, and 75th percentiles respectively, vertical whiskers extend to 1.5 times the inter-quartile distance. Dots represent outliers. Shaded horizontal bands represent the radii of: a 9-cell Moore neighbourhood (M), a 5-cell von Neumann (vN), and only the current cell (O) .

essentially equivalent to a random walk. A radius between 1 and 1.41 represents a 5-cell von Neumann neighbourhood, while a radius between 1.42 and 2 represents the 9-cell Moore neighbourhood used in (Wren et al., 2014).

Repeating model 1 with a variable population function resulted in lower median radii as with fixed populations, and reduced variance between the various surfaces of the same heterogeneity (Figure 3–2b). In these runs the population went through an initial period of flux and then stabilized between 50 and 3000 agents with a median around 2000. This generally larger population size smoothed some of the stochasticity of the smaller fixed population runs resulting in reduced variance and a lower median, with almost all high radius outliers belonging to runs with low population (Figure 3–3).

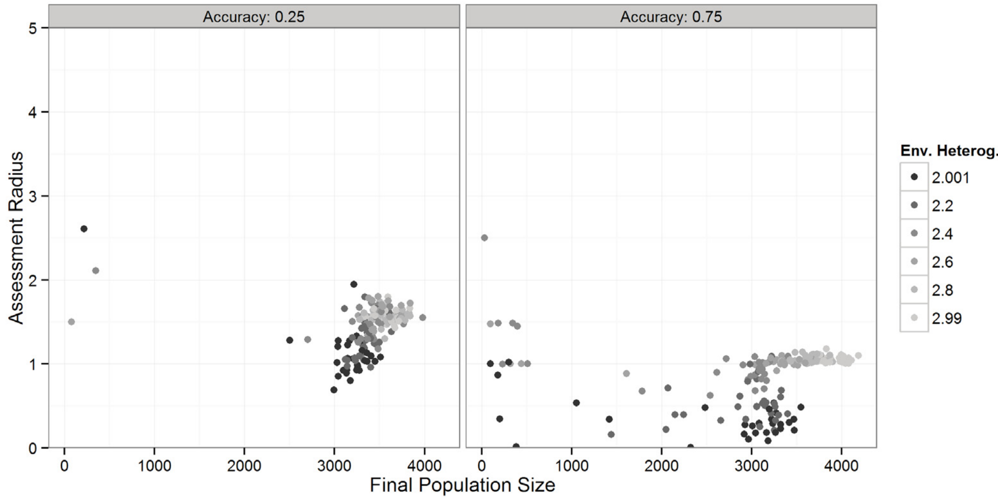


Figure 3–3. Assessment radius was not significantly affected by the final population size as nearly all runs were below 2. However, higher foraging accuracy results in increased crowding, more variable final population, and slightly reduces assessment radius.

To evaluate a hypothesis that the population growth function simply increases crowding, or population density, we re-ran the model with different initial population sizes and the same landscape dimensions (Figure 3–4). As expected, increasing the fixed population size decreases the value, and variance, of assessment radius.

3.4.4 Mechanisms of selection

The strong selection against increased assessment radius is a counter-intuitive result. It seems logical that ever increasing spatial range would improve the ability of groups to find quality resource patches. However, several factors diminish the potential advantage of increased assessment radius. First, if a distant patch is selected, especially one with only marginally increased resource abundance, the intermediate cells the group must pass through to reach that patch may be of lower quality. This poses a significant risk that may not overcome the potential resource advantage of the distant patch.

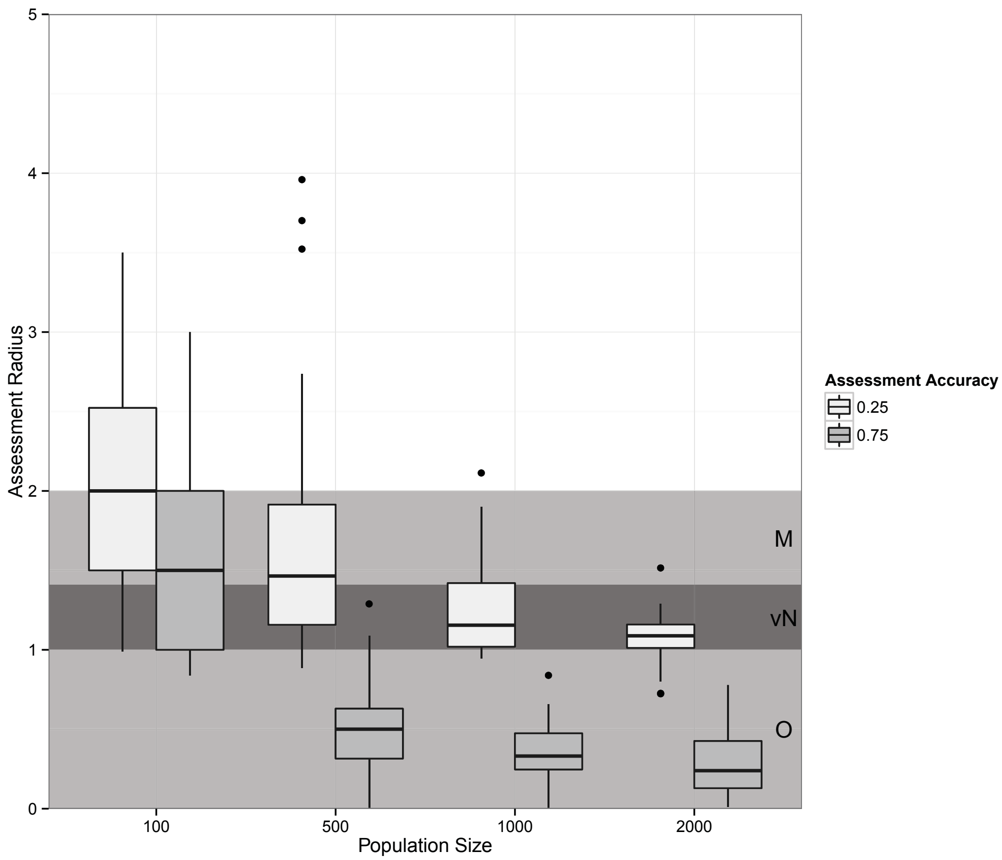


Figure 3–4. As the landscape remains the same size, increasing the fixed population size increases crowding. As a result, natural selection further decreases assessment radius.

Second, the model suggests that considering the optimality of a group acting in isolation may not be a good approach. Rather, a crowded resource landscape in which competition and reproductive advantages are measured against neighbouring groups gives a better picture. In other words, the fitness of foraging strategies is strongly affected by the density of the population. Note that our crowded landscape does not necessarily suggest a high total population. Rather, under basic assumptions of population growth and mobility, carrying capacity would be quickly reached, whatever that capacity might be, and available quality habitat would become a rare commodity.

Given a crowded and competitive landscape, it should no longer be surprising that increased assessment radius provides little advantage. In the baseline model, the mechanism driving the natural selection of low foraging accuracy was the limited availability of reproductive space in the center of clusters. This caused the evolutionary trajectory to be driven by the agents around the fringes of clusters where reproductive space was more readily available (Figure 3–5). In the assessment radius model, the most advantageous strategy is to keep assessment radius to the immediately accessible surroundings (8-cell neighbourhood), or even to stop moving entirely. For higher radii, the probability that a distantly selected patch will be available when the group arrives even a couple of time steps later is too low to provide any advantage. Similarly, there is little likelihood that the intermediate patches will be available to pass through. This is supported by Figure 3–3 where assessment radius is inversely related to final population size and high foraging accuracy, which both increase crowding. For agents with low foraging accuracy, a greater proportion of mobility is random, reducing the degree of crowding. Less crowding means less chance of having intermediate cells be occupied, and an advantage to groups with a slightly larger radius.

Unlike the baseline model, the heterogeneity of the environment does not greatly affect the natural selection of assessment radius. While crowding is reduced on a highly heterogeneous surface, the spatial autocorrelation of resources is also reduced such that resource clusters are relatively small and peaks are close together. Given this spatial distribution, increasing assessment radius beyond the inter-peak distance provides no advantage. This aspect is somewhat speculative, and likely needs a new type of resource surface to interrogate it further.

We attempted to model population growth to simulate a push factor for dispersal by setting the base reproductive probability slightly higher than the removal probability (i.e., $b_r > d$). However, since probability of reproduction is a product of available resources, the population grew until only cells with the adjusted reproductive probability below the removal probability were left (Eq. 3.1). On average, this caused the population to grow to a higher population size than the fixed runs, but then to stabilise. Higher population within the same bounded space resulted in more crowding and slightly increased selection against assessment radius but this did not change the underlying mechanism. To evaluate this result, we increased the fixed population size and as predicted, the selection against assessment radius was increased.

3.5 Model 2: Information Sharing

3.5.1 Introduction

Cultural transmission is a significant way through which humans acquire knowledge of their environment (Mithen, 1990; Whallon et al., 2011; Rockman, 2003). Fitzhugh et al. (2011) and others have suggested that

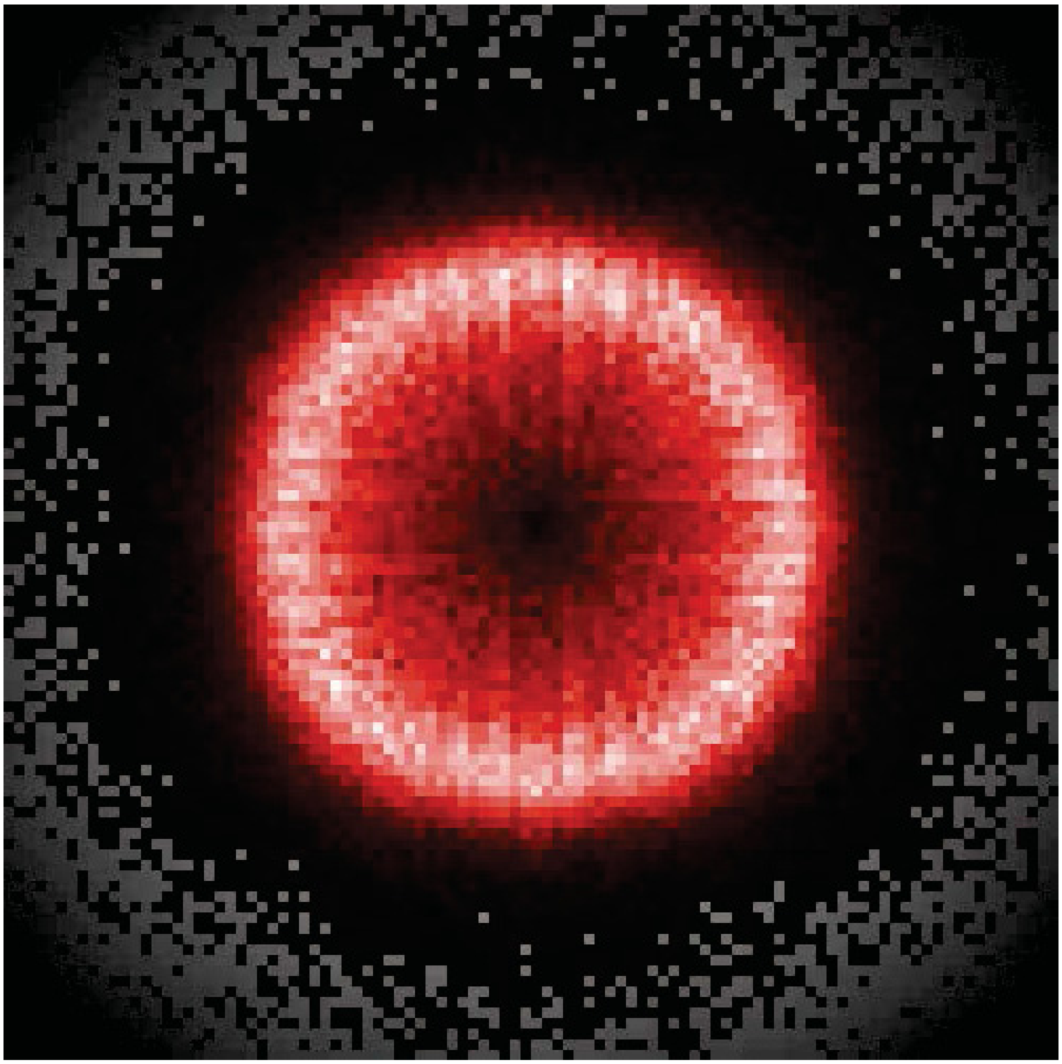


Figure 3–5. Example spatial frequency distribution of successfully placed offspring on a cone shaped landscape where lighter shades represent higher frequency. Note the crowded center area which has the most abundant resources, has a relatively low frequency of offspring agents.

acquiring and disseminating information through social networks would be an essential component of the colonization of novel landscapes as it could increase the speed of landscape learning (Veth et al., 2011; Rockman and Steele, 2003). The second model changes the source of environmental knowledge from direct observation of the environment to indirect socially acquired information. Instead of examining the resource abundance of the local landscape, groups examine the success of other groups. In effect, the unit of comparison remains the resource abundance of each cell, however, which cells are observable has shifted from a spatially local neighbourhood to any currently occupied cell.

Cultural transmission is an immensely complex process and involves at least four distinct phases: acquisition, circulation, storage, and use (Whallon et al., 2011; Lake, 2001). For example, decisions about how much information and what level of detail to circulate to other groups can be strategic and political. Larger regions and rare environmental changes may be more costly to maintain information about, compared to the low cost involved in the individual monitoring of a local landscape (Fitzhugh et al., 2011). This suggests that socially acquired information may be complimentary to individual observation as a source of information outside the local area.

In the cultural transmission model, we assume that the current level of success is always assessable, rather than having groups choose whether or not to share their information. Additionally, each group may assess any other group in the population rather than just the neighbouring ones. This is more simplified than the complex connectivity depicted in Fitzhugh et al. (2011, Fig. 4.2) in that information can percolate to any point in the network. Interestingly, the usefulness of information decreases with distance

Learning mechanism	Individual or group	Description
Individual learning	I	No cultural transmission (null hypothesis)
Unbiased random	I	Copy random target
Independent decisions	I	Copy random strategy, freq. independent
Success/Prestige bias	I	Choose random target and copy if better
Conformity	G	Majority preferentially copied
Copy successful individuals	G	Variant of conformity
Copy successful behaviours	G	Variant of conformity
Anti-conformity	G	Traits of intermediate frequency preferred
Frequency trimming	Hybrid	Ignore most or least popular, then copy random

Table 3–2. Mechanisms of cultural transmission. Adapted and expanded from Mesoudi and Lycett (2009).

in the model, although this occurs not as an explicitly programmed part of the model but as an emergent phenomenon.

A significant branch of cultural evolutionary theory is focused on modelling the mechanisms of cultural transmission. This work originated with Boyd and Richerson (1985) and was later expanded and thoroughly tested by others (McElreath et al., 2005; Mesoudi and O Brien, 2008; Mesoudi and O'Brien, 2008; Mesoudi and Lycett, 2009; Mesoudi, 2008; Henrich and McElreath, 2003). Mechanisms vary based on whether the whole group or one individual is chosen to model and whether or not the "copier" can assess the success of the "copied" (Table 3–2). These mechanisms are compared to each other and to independent learners, to see what trait frequency curve would be expected and which mechanism fares best on different adaptive landscapes.

Mesoudi (2008) found that individual learning performed best on a unimodal fitness landscape, but that strategies of social learning (e.g. success bias), especially when the whole population is known (e.g. conformity), performed best on multi-modal landscapes. This is because social learning allowed individuals to jump from a low local optima to the global optima (or a higher local optima) (Mesoudi and O Brien, 2008, p.8). In the adaptive landscape of cultural traits, such as dimensions, shape, and colour of projectile points, many or all individuals may occupy the same trait space and there is no penalty for being similar to others. Frequency-dependent trimming is a slight variation where the most popular trait is preferentially avoided (see Mesoudi and Lycett, 2009).

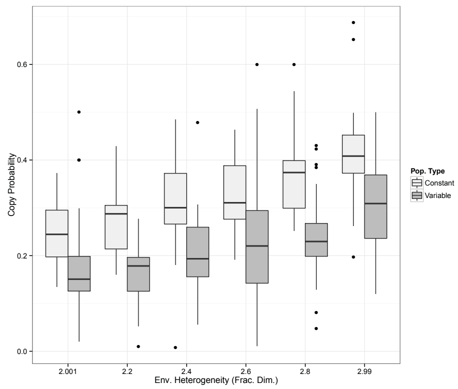
When the adaptive landscape is also a physical landscape, it puts significant additional constraints on trait selection. While our model could have made all social information available (e.g. conformity), if every group learned about the same, already occupied, location is obviously a maladaptive strategy. Therefore, our model uses a spatial equivalent of *success bias* by allowing a group to acquire information about one randomly selected group at a time. This models the chance acquisition of a piece of information, and naturally selects the probability at which it is adaptive to act upon it by moving towards that location.

Like the baseline model, this model assumes movement is random with respect to the resource distribution when groups are not learning through cultural transmission. This allowed us to isolate the effects of cultural transmission from individual foraging bias, and is also a reasonable assumption. Among other reasons, Whallon (2006) notes that some proportion of mobility is focused on maintaining social networks to provide a flow of information about resources to protect against times of scarcity, perhaps becoming more important at broader spatial scales or when the environment is less predictable. While still resource related, this movement would appear unrelated to the resource distribution.

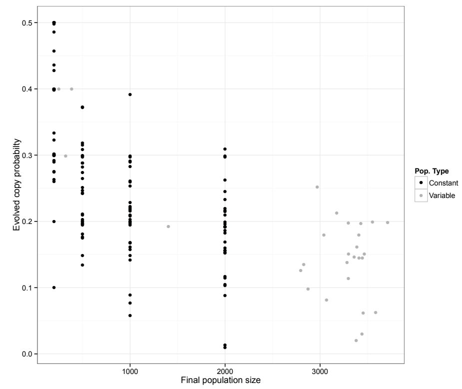
3.5.2 Model Description

Model 2 evaluates the natural selection of cultural transmission of resource information using a simple form of mobility behaviour, which is based on the observed success of other groups. Like foraging bias, a balance between the frequency of movements based on cultural transmission and other movements is necessary to avoid becoming stuck on local optima. Therefore, each agent has one heritable trait, c, which is the probability that they will assess (copy) another agent and move towards that agent if it has more resources. We recorded the mean copy probability and cell value for all surviving agents at the end of each run of the 180 landscape run set. Then with the heterogeneity held constant at 2.001, the model ran with fixed populations of 100, 1000, and 2000, and with a variable population function (See Table 3–1 for model parameters). At each time step of each run, each agent follows this schedule:

1. At probability, r_a, produce an offspring (Eq. 3.1).
   (a) Offspring inherit their parent's copy probability trait value, c.
   (b) At probability, m_r, offspring's trait value will increase or decrease by m_s.
   (c) Offspring choose a random unoccupied neighbouring cell.
   (d) If all neighbouring cells are occupied, offspring is removed.
   (e) Fixed pop. only: if offspring is successfully placed, one random agent is removed.
2. At probability, c, select a random target agent and compare resources.
   (a) If target has more, attempt to move one cell towards them.



(a)



(b)

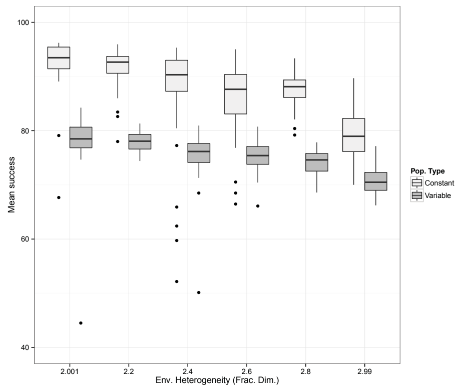
Figure 3–6. a) Evolved copy probability is strongly correlated with environmental heterogeneity. Each box plot represents the median copy probability of all agents at the end of runs on 30 different simulated landscapes. b) Inverse relationship between population size N and copy probability c, further emphasizing the role of crowding. Constant and variable population sizes for $env = 2.001$ are shown.

   (b) If target has less or another agent blocks the movement, the agent stays.

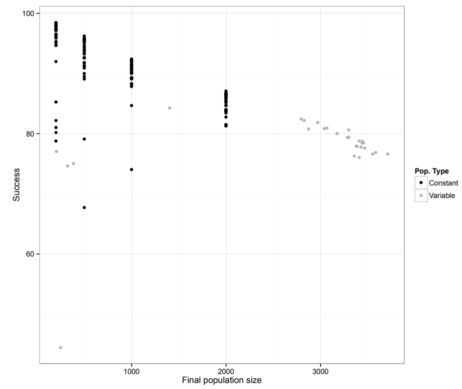
3. Variable pop. only: be removed with probability, d.

3.5.3 Results

Model 2 shows that the heterogeneity of the environment strongly affects the evolution of copy probability, although with relatively high variance between surfaces of the same heterogeneity. For the lowest heterogeneity environments, the median copy probability is 25%, with the other 75% of movements being of random direction. For the highest heterogeneity, the median copy probability is higher but still relatively low at 40% (Figure 3–6). Allowing the population size to change generally increased population size, to around 3000-3500, and lowered median copy probability by about 10% for each environment. The fixed population runs of different population sizes illustrated the same pattern of increased population, i.e. increased crowding, decreasing the evolved copy probability (Figure 3–6b).



(a)



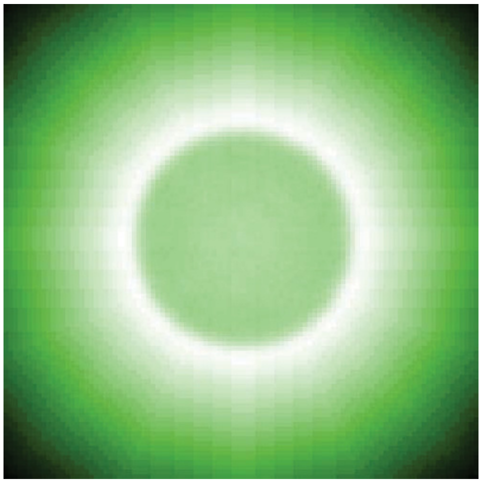
(b)

Figure 3–7. a) Mean success is inversely correlated with environmental heterogeneity. Each box plot represents the foraging accuracy of all agents at the end of runs on 30 different simulated surfaces. b) The inverse relationship between population size and success is not surprising since available resources does not increase with population.

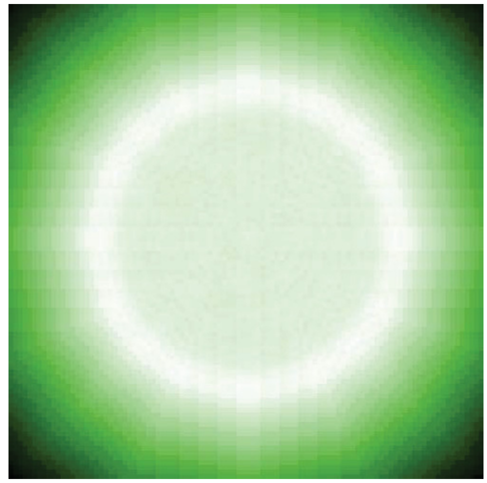
As with model 1 and the baseline model, the success of the population is inversely correlated with heterogeneity, although relatively high overall. This suggests that the evolved copy probability, in combination with resource related reproduction rates, is highly successful across a wide variety of environments, but that surfaces with relatively low heterogeneity are the most permissive. The variable population function generally resulted in increased population. This predictably decreased success overall since a larger population was competing over the same resources, forcing a greater proportion of the population onto low resource cells (Figure 3–7a).

3.5.4 Mechanisms of selection

The mechanism behind the natural selection of copy probability is the same as the baseline model. The availability of reproductive space around an agent is more important than their current resource value. The fitness of a trait is determined by its ability to have offspring, which is not necessarily related to acquiring resources. Considered from another perspective, the effective reproductive probability, or fitness, is determined by a combination



(a) $c = 0.75$



(b) $c = 0.25$

Figure 3–8. Spatial distribution of cumulative probability of successfully placing an offspring on a cone shaped resource landscape where lighter shades represent higher probability. The crowded center area has the most abundant resources, but has lower probability of offspring agents a) with high copy probability versus b) low copy probability. The near plateau of probability occurs when copy probability reaches an approximately optimal level. n.b. These example runs held copy probability constant.

of adjusted reproductive rate and the probability of finding an unoccupied neighbouring cell. The adjusted reproductive rate is dependent only on the home cell, whereas finding an unoccupied cell is dependent on the degree of crowding (Figure 3–8).

Given this understanding of crowding, the agent that consistently has available reproductive space is the fittest. Agents with below average copy probability will be near the edge of the population cluster and less crowded and will thus drive the copy probability of the population down by reproducing more frequently. As with assessment radius, agents below a certain copy probability threshold are also maladaptive as they approximate a random walk. The copy probability of the population stabilises when the effective reproductive probability is relatively constant over space, although this occurs at different levels depending on the spatial heterogeneity of the environment (Figure 3–8b).

The effect of cultural transmission as a mobility strategy is that the population always clusters together. This is best explained from the perspective of the mean direction of mobility from one agent to all other agents. The mean direction of every agent, whether on the outside of the cluster or in the center, will be towards the cluster's center (Figure 3–9). Since non-copying random movements have no mean directionality, any copying will result in increased clustering. This will keep the population in one large cluster, rather than dispersing across the peaks of the resource landscape. Lower copy probabilities increase the proportion of movement away from the center resulting in a more diffuse cluster.

A variety of other programming choices could change the way information is shared within the model. Agents could have access to information about the whole population or all agents in a certain radius, allowing the most successful agent instead of a random agent to be copied. However, the net result would be approximately the same no matter the form of cultural transmission modelled (except perhaps frequency-dependent trimming (Mesoudi and Lycett, 2009)), namely one large cluster of agents would form and stick closely together.

In this sense, dispersibility is inversely related to copy probability, and dispersal is generally unlikely to occur for a population that bases its mobility on culturally acquired environmental knowledge. Lower copy probabilities result in a higher amount of time in exploratory random walks, and these lower rates are naturally selected by lower heterogeneities. Like the baseline model, less heterogeneous landscapes could radiate populations outwards to a certain extent. However, given the tight grouping behaviour

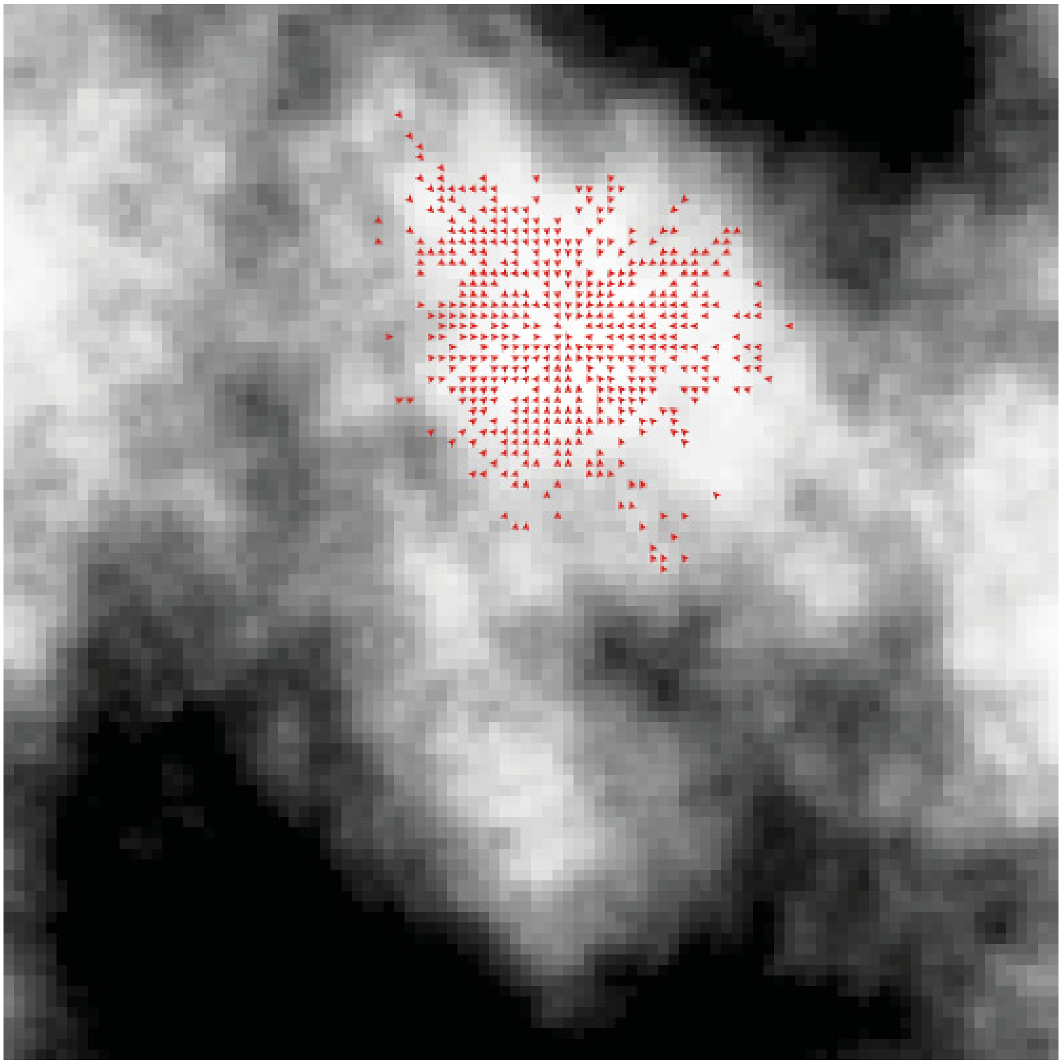


Figure 3–9. Illustration of the clustering effect of cultural transmission. Image produced by *asking* each agent to face towards the mean of all other agents' locations.

driven by copying, the dispersibility of even low copy probability agents would be much lower than low individual foraging bias agents in the baseline model. This is suggested by the relatively high number of low success outlier runs, especially on low heterogeneity surfaces. In these cases, the starting corner of the map formed a low resource local optimum from which the population of agents never escaped.

3.6 Discussion

The model dynamics illustrate a seemingly general pattern that it is better to know less, but more than nothing, about a resource landscape. This is a counter-intuitive result as it runs contrary to the hypothesis that increased cognitive complexity, at least in the form of foraging accuracy or cultural transmission, gave hominins a unique ability to disperse rapidly into novel landscapes. The literature discussing the mechanisms of dispersal assume that increased cognitive capacity was necessary for, or at least enabled, hominin dispersal (Dunbar, 1998; Müller et al., 2011; Barton and Riel-Salvatore, 2012; Grove et al., 2012; Stewart and Stringer, 2012; Bar-Yosef and Belfer-Cohen, 2013). Another common claim is that acquisition of information about the environment, whether through individual learning or cultural transmission, would have been crucial for dispersal (Rockman and Steele, 2003).

In contrast, our results demonstrate that natural selection of foraging related mobility strategies tends to reduce dispersibility, since these traits (e.g. foraging accuracy, assessment radius, and cultural transmission) are adaptive to some degree and thus bias agents to move towards valued resource patches. The antithesis to foraging based mobility decisions, and the only way to maximize the likelihood of dispersal, is to move randomly with respect to the environment (i.e. a random walk) or to purposefully explore regions away from populated areas by venturing blindly into the unknown. This agrees with Barton et al. (2004), who find that in colonizing a novel landscape the lack of knowledge of the landscape would increase dispersal since no location, including the currently occupied place, would be particularly well known. However, this is a highly risky and likely maladaptive strategy, and certainly does not employ hominins' impressive cognitive capacity.

The models presented here also demonstrate that the optimal foraging strategies within a crowded landscape are different from a single group on a landscape since foraging and mobility traits are necessarily density-dependent at multiple spatial scales (Ray and Hastings, 1996). Natural selection favours traits that enable successful reproduction, which are traits that provide reproductive space as well as sufficient resources. In low heterogeneity landscapes with a single large smooth resource patch, the degree and selective effect of crowding is very strong. This reduces the probability of accurate foraging and the probability of cultural transmission and makes dispersal more likely. The degree of crowding decreases at higher levels of environmental heterogeneity, dramatically changing the selective pressure on traits, and making dispersal less likely.

Highly heterogeneous landscapes typically decrease dispersal of plants and animals since neighbouring locations are likely lower in resources (Johnson and Gaines, 1990). Since crowding is reduced in heterogeneous landscapes, and this favours foraging accuracy and cultural transmission, dispersal is reduced via a very different mechanism, but with the same effect. The inverse relationship between heterogeneity and dispersibility from the baseline model is therefore a robust result as the pattern is repeated under several different mobility strategies. This further strengthens our hypothesis that low heterogeneity resource distributions should characterise the period leading up to major dispersal events (Wren et al., 2014).

Our experiments with population growth as a stimulus for dispersal resulted in some unexpected conclusions. Since the model landscape was bounded, population size tended to follow a logistic curve where a period of relatively rapid growth was followed by stability at a higher level. This is not the constant population pressure we were looking for and this will be addressed with a new model in a future article. However, the results do show a strong effect of population size on the natural selection of traits since increased population size is linked to crowding.

Assessment radius in particular was low for all environments when the population was large, but increased assessment radius did evolve in some of the smaller populations. This suggests that a small colonizing population could benefit from increased assessment radius, bringing to mind the rapid colonization of the Americas, which is assumed to involve a small population. It also adds the requirement of a small population size to the leap-frog (Anthony, 1990; Anderson and Gillam, 2000; Fiedel and Anthony, 2003) and saltation models (Gamble et al., 2004) of colonization where large patches of inhospitable territory are quickly skipped over. Gamble et al. (2004) claims that *H. sapiens* were "released from social proximity" by establishing extended social networks and were therefore uniquely able to assess large radii to find suitable habitat while maintaining contact with a parent group.

This pattern is also the solution to 'Reid's paradox' in ecology where the mean distance of dispersal multiplied by the generation length was insufficient to explain the observed rate of post-glacial tree dispersal. Rather, rare but long distance dispersals (e.g. carried by a storm or animal) were a necessary component of the explanatory model (Clark, 1998). Future models could be extended to test these hypotheses using a 'Lévy flight' model (Viswanathan et al., 1996; Raichlen et al., 2013), which makes walking time a fat-tailed distribution that allows for occasional long duration moves (also see Edwards et al., 2007).

3.6.1 Note on memory

One component seemingly missing from the above models is the ability to remember the location of resources. Information could be acquired through either individual learning, cultural transmission, or both, and then compiled into a mental map of the landscape. This was the objective of MAGICAL, an agent-based model of a foraging driven Mesolithic colonization of the island of Islay in Southern Scotland, although due to limitations of computer hardware the published runs of MAGICAL contained only four agents per run (Lake, 2000, 2001).

However, the combination of results from models one and two suggests that this would not increase the dispersibility of the population. The more information is shared, the more populations are alike in their chosen destinations and the more crowded they become. Further, the more distant the chosen destination, the less likely the intermediate territory will be favourable or available. While mobility strategies like increased foraging accuracy, greater assessment radius, cultural transmission, and memory seem like they would be highly adaptive, their use in a crowded landscape is greatly constrained.

3.6.2 Note on resource landscapes

This article has only explored one dimension of landscapes, namely the spatial distribution or heterogeneity of resources assuming actual differences in the heterogeneity of the physical environment. The ABM approach could also enable a new approach to understanding and modeling other hypotheses of hominin-environment interaction. For example, within the same biogeographic landscape, a generalist's perception of that landscape would look less heterogeneous (since resources have different distributions) and have lower peaks than that of a specialist. Potts's (1998) variability selection hypothesis implies that hominins would experience less heterogeneity as well but with higher peaks than a generalist. A shift in technology enabling more efficient extraction of energy, could also be represented spatially by increasing the height of peaks without a change in heterogeneity.

This way of representing resource distributions is relevant to dispersal since we have already demonstrated that the spatial distribution of resources affects both the fitness and dispersibility of populations. Changes in technology have already been suggested to increase dispersal (Mellars, 2004, 2006b), and our results suggest a new way to evaluate that hypothesis. These ideas will be explored further in future work.

3.7 Conclusion and next steps

The selective pressure to reduce environmental knowledge, particularly in low heterogeneity environments, is a surprising result. However, it does present a number of explicitly testable predictions stemming from the selective pressures of the resource landscape. First, high heterogeneity environments increase the selective pressure for complex cognition. Second, since dispersibility is higher in low heterogeneity environments, high heterogeneity environments should have greater population sizes. If these two hypotheses were true, we should expect the evolution of cognitively complex hominins to occur preferentially in spatially heterogeneous environments. Similar claims have been made by Winder et al. (2013) and for temporal heterogeneity by Potts (1998, 2002). Third, major dispersal episodes should emanate from, and be preceded by a period with, low spatial heterogeneity. In fact, we should expect that dispersal corridors should be relatively low heterogeneity as well, although this has yet to be explicitly modelled. Fourth, cultural transmission as a source of information decreases dispersibility. Thus, archaeological indicators of social network strength, such as presence of exotic materials, should be low during dispersal episodes (although social networks could be useful for other purposes, c.f. Fitzhugh et al., 2011).

The model presented here is highly abstract and it is easy to imagine any number of factors that could confound the model's dynamics, particularly the rigid way a crowded landscape inhibits reproduction. However, we are not attempting to recreate the entirety of past mobility patterns and nor should we try to do so. Rather, the goal is to identify each element in the hypotheses and interpretations of others, and make how they are thought to interact explicit in a computer model. Some assumptions may be overly restrictive in the models and may need to be relaxed in future models and some implementations will function better than others will. For example, our population pressure function merely increased the stable population size. Since population pressure is thought to be a critical aspect of dispersal itself, rather than the evolution of a population's dispersibility, this needs to be revised. We will tackle this question in a future article and finally have a quantification of the rate of dispersal under different conditions which will be comparable to the archaeological record.

CHAPTER 4
Putting (hominin) thought into hominin dispersal models

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4.1 Overview and context within thesis

As described in previous chapters, Fisher's (1937) equation predicts a wave of advance of an organism from the dynamics of population growth and random movement. Its first appearance as a human dispersal model was by Ammerman and Cavalli-Sforza (1971), who adopted the equation as a mathematical model to describe the advance of early farming into Europe. Others applied the model to several other case studies to show that the same model of random movement creating a wave of advance is consistent with the archaeological appearance of early humans in different locales.

A basic tenet of modelling is to determine whether the model elements are necessary and sufficient to explain the phenomenon (Epstein, 1999). The model elements are necessary if removing one of them results in a different outcome, and they are sufficient if together they generate the important dynamics of the phenomenon in question. By assuming human cognition would have a negligible effect on mobility patterns, the wave of advance model may be insufficient, even if it is consistent with the archaeological record at a coarse scale. In this article, I incorporate human decision making into a replication of the wave of advance model to evaluate its effect on the expected dispersal velocity in different environments.

In some ways, this chapter would have made a better first step than the model in chapter 2. It certainly would have been a smaller departure from the established modelling approach and thus the conclusions more easily understood and accepted. However, I needed to go through the evolutionary models to develop my understanding of foraging biased mobility, and why the random movement of the other published dispersal models had left me unconvinced. The natural selection of dispersibility through low levels of environmental knowledge is an important backdrop to the following study. The previous models suggest that it is logical to assume that cognition inhibits dispersal velocity, and the following model provides a quantification of this.

4.2 Abstract

Wave of advance dispersal models (Ammerman and Cavalli-Sforza, 1971; Steele et al., 1998; Fort et al., 2004; Silva and Steele, 2012) depict humans and other hominins as passive agents spreading randomly across palaeo-landscapes. This seems to contradict both our assumptions about the importance of hominin cognition in dispersal, and the characteristics of palaeoenvironments in channelling movement. We use an abstract agent-based model to add a simple form of cognitive complexity to the wave of advance, by enabling hominins to direct movements towards resource rich parts of the landscape. Although in a few specific cases cognition increases the dispersal velocity slightly, overall the model suggests that increases in cognition would have decreased dispersal velocity significantly.

Keywords: Dispersal; Wave of advance; Environmental heterogeneity; Simulation; Agent-based modelling; Hominin cognition

4.3 Introduction

Two main types of narratives emerge from the study of human and other hominin dispersals. One sees humans as active agents adapting to novel environments, the other sees them as passive agents diffusing according to environmental constraints.

The active narrative suggests that dispersals were successful due to the increased cognitive abilities of early humans (Bar-Yosef and Belfer-Cohen, 2001). Bigger and more complex brains facilitated technological innovations that increased adaptation to, and helped shape, the environment (Gaudzinski, 2004; Mellars, 2006b; Shea and Sisk, 2010; Banks et al., 2013; d'Errico and Banks, 2013), extended social networks as a source of information and a buffer against risk (Aiello and Dunbar, 1993), as well as developing other social traits such as cooperation (Bar-Yosef and Belfer-Cohen, 2013). This increased brain power is assumed to be connected to the increasingly rapid dispersal rates observed in the archaeological record, although the specific mechanism is much debated. The actual impact of increased cognitive capacity on hominin dispersal rate has never been explicitly tested through modelling and simulation until this study.

The passive narrative depicts human populations expanding when resources were present and spreading to new regions when ecological conditions permitted. Rather than consciously selecting preferred habitats, humans diffused or expanded as climatic changes increased the boundaries of their ecological niche (e.g., Drake et al., 2013; Pearson, 2013; Rohling et al., 2013). This narrative sees hominin dispersal as a biogeographic phenomenon, albeit with behavioural innovations indirectly contributing to the changing range boundaries (Roebroeks, 2006). The dichotomy between the two narratives is partially a product of their respective analytical scales, as the passive narrative is typical of palaeoenvironmental studies which focus on broad spatial and temporal scales, rather than the local scale behaviour of individuals.

Computational models of human dispersals are largely based on the passive narrative. The standard dispersal model is a wave of advance, based on Fisher's (1937) equation, in which population growth radiates out from an origin like ripples on a pond. As movement is assumed to be random in direction, environmental characteristics do not affect the velocity or direction of the wave's travel, except when an environment is completely uninhabitable. This contradicts a common assumption of the passive narrative, that hominins disperse more rapidly through resource rich locales (Pearson, 2013). Wave of advance models seem to be at odds with aspects of both narratives since they contradict hypotheses that connect increased cognition with dispersal success, and palaeoenvironmental conditions with dispersal patterns and timing.

Active cognition may be added to Fisher's wave of advance model by assuming that cognition would direct movement towards resource rich locales. An increasingly complex brain would result in a more accurate understanding of the resource landscape, and thus bias movement with increasing accuracy. In this article, we use an agent-based model with a variety of simulated resource landscapes to explore how increasing cognitive complexity in this way could affect the relative dispersal velocity of a population of hominins.

The results show that increased cognition will actually slow down dispersal rate in most environments. This has important implications for the general understanding of dispersal mechanisms and suggests that estimates of population growth rate, diffusivity, and the importance of cognition in dispersal research should be reconsidered.

Wave of advance model

The standard dispersal model is a partial differential equation known by a number of names: reaction-diffusion, Fisher, Fisher–Kolmogorov, Fisher–KPP (Kolmogorov-Petrovsky-Piskounov), or Fisher–Skellam. The equation describes a travelling wave, or 'wave of advance', where a population is simultaneously increasing and spreading into new territory. There are two terms to equation 4.1, the first is population growth, often logistic, and the second is an even diffusion of that population into surrounding space (i.e., the cumulative effect of individual random dispersal directions).

$$\frac{\partial n}{\partial t} = \alpha n \left(1 - \frac{n}{K}\right) + D\nabla^2 n \tag{4.1}$$

where K is local carrying capacity, α is intrinsic maximum population growth, D is a diffusion constant which determines the dispersal distance per generation, ∇ is the mechanism of even outward spreading from a local density, and n denotes population size at a given time, t, and place (Steele, 2009).

Logistic population growth up to a local carrying capacity, K, is a reasonable assumption although the growth rate, α, will be revisited later. The appropriateness of the second term is the primary subject of this article, particularly the assumption that a dispersing group or individual will move randomly, which appears even given sufficient time, with respect to the social and environmental landscape. This is a logical first approximation, but given our understanding of hunter-gatherer decision making and movement, we will revisit this assumption here.

Many of the foundational papers on dispersal models in biology and ecology (e.g., Fisher, 1937; Levin et al., 2003; Kolmogorofl et al., 1989), and even some archaeological applications of the model (Hazelwood and Steele, 2004), acknowledge that the assumption of random directionality is an over simplification. Some justify this by assuming that it is approximately true at broad spatial and temporal scales, or by arguing that randomness is the simplest assumption in the absence of empirical evidence suggesting a more specific mechanism. A few articles have discussed the effect of a directional bias along rivers (Davison et al., 2006), away from population densities (Lika and Hallam, 1999), or towards suitable habitat (Bowler and Benton, 2005). Rowell (2009) examined the impact of rational local searching behaviour (i.e., for greater resource availability) and found that it could limit the speed and extent of an organism's spread. He derived a new partial differential equation to describe the resource gradient climbing behaviour resulting from rational decision making (Eq. 4.2).

$$\frac{\partial n}{\partial t} = -k\nabla \cdot (n\nabla S) + n(rS - \mu) \tag{4.2}$$

where S is landscape of resource availability (i.e., resource abundance value affected by local population density n), k is a constant which controls sensitivity to variations in resource availability, r affects the population growth rate, and μ is a density-independent per capita mortality.

Archaeological applications

The most direct material evidence of hominin dispersals are the earliest dated occupations at increasing distances from an assumed origin. Ammerman and Cavalli-Sforza (1971) used regression on a date versus distance plot to estimate the velocity of the spread of farming into Europe shortly after Clark (1965) published a compilation of early Neolithic radiocarbon dates.

An important prediction of the Fisher equation is that wave velocity is proportional to population growth rate and dispersal distance (Eq. 4.3).

Ammerman and Cavalli-Sforza (1971) used this and the Fisher equation as a model to explain the process of Neolithic diffusion, namely as a 'demic' wave of population growth and spread (also see Ammerman and Cavalli-Sforza, 1973, 1984). Since reasonable estimates for diffusivity and population growth rate (derived from ethnographic literature) were compatible with the archaeologically observed velocity, they accepted the 'demic', or population, wave-of-advance as a reasonable model of Europe's Neolithisation.

$$v = 2\sqrt{D\alpha} \tag{4.3}$$

This work has been extensively cited in the literature of the spread of farming into Europe (e.g., Fedotov et al., 2008; Fort et al., 2012; Isern and Fort, 2012; Bocquet-Appel et al., 2012; Lemmen et al., 2011; Rowley-Conwy, 2011; Pinhasi et al., 2005). The Fisher equation has also been applied to several other case studies including, the Palaeoindian colonization of the New World (Steele et al., 1998; Hazelwood and Steele, 2004; Hamilton and Buchanan, 2007), the reoccupation of northern Europe by modern humans after the last-glacial maximum (Fort et al., 2004), the initial colonization of the western Pacific (Fort, 2003), the spread of farming through southern Africa (Silva and Steele, 2012), and the spread of anatomically modern humans globally (Young and Bettinger, 1995).

Interestingly, almost no attempt has been made to test alternative models such as 'leapfrogging', 'migration streams', or 'Markov models' suggested in a frequently cited article by Anthony (1990). Only a few papers have expanded or adjusted the Fisher equation, to account for a pre-existing Mesolithic population for example (Isern and Fort, 2012), and these tend not to be widely cited. One exception is Davison et al. (2006), who modified the equation to increase the per generation dispersal distance, D, along rivers

Case study	v (km/ year)	D (km^2/ generation)	α (%)	Citation
Erectus Eurasia	0.01-0.02	n/a	n/a	Hughes et al. (2007)*
AMH Europe	0.4-0.5	n/a	n/a	Mellars (2006a)
Europe Post-LGM	0.7-1.4	1 400- 3 900	1.7-2.7	Fort et al. (2004)
New World	3-10	900	0.3-3	Steele et al. (1998)
New World	5-8	n/a	n/a	Hamilton and Buchanan (2007)
Neolithic Europe	0.6-1.3	1 400- 3 900	2.9-3.5	Pinhasi et al. (2005)
Western Pacific	8	3 600- 300 000	2.9-3.5	Fort (2003)

Table 4–1. Variations in published parameters for (4.3), compiled from Steele (2009). *Estimated from straight line distances and provided table of arrival dates.

and coastlines in their model of Neolithic dispersal up the Rhine–Danube and along sea coasts. Another is James Steele, who has published several papers exploring different versions and expansions of the Fisher model, including variations in the demographic and mobility constants, multiple populations, and spatial and temporal heterogeneity (Hazelwood and Steele, 2004; Steele, 2009; Silva and Steele, 2012).

The velocity of the wave front is an attractive tool for archaeologists because it provides a concrete comparison to the archaeological record, and thus a way to empirically validate the model. However, the range of ethnographic and archaeological examples which are used to estimate diffusivity, D, and population growth rate, α, as well as the uncertainty in dating, provides significant wiggle room in the comparison of the model's prediction to the velocity calculated from the distribution and timing of archaeological sites. This range can be seen in Steele (2009), where he collated estimates for these parameters and for wave velocity, v, from papers published on a variety of case studies (Table 4–1). Given this uncertainty, a substantial change in the dispersal model could still produce a velocity in line with the predictions from archaeological record.

In STEPPINGOUT, Mithen and Reed (2002) used a cellular automata model and global climate simulation data to construct a complex grid of triangular cells representing the Old World palaeoenvironment. STEPPINGOUT modelled hominin population movement as a constant probability of colonizing neighbouring grid cells with the environment influencing a variable probability of extinction (see Nikitas and Nikita, 2005; Hughes et al., 2007, for related approaches). This is similar to Fisher models' use of a reconstructed map of variable carrying capacity to limit population growth in certain locations, or movement if $K = 0$. In either case, the selection of which cell to occupy occurs randomly and without reference to the environment. The only exceptions are models that bias movement along coastal or river routes, by increasing either the probability of colonization (Mithen and Reed, 2002; Hughes et al., 2007) or the dispersal distance (Davison et al., 2006).

Contrary to these approaches, this study assumes that mobility decisions, that is the choice of where the group will move their residential base, are not made randomly with respect to the environmental landscape (Lake, 2000, 2001; Grove, 2009). This approach re-frames dispersal as an emergent phenomenon, rather than the goal of a population, and emphasises that the direction of dispersers will likely not be random at the local scale.

Fisher-based models tend to strive towards realism (Costopoulos, in press) by using maps of coast lines, rivers, mountain ranges, and adjusted sea levels, as well as detailed palaeoenvironmental reconstructions, and demographic and mobility rates taken from ethnographic and archaeological case studies (Mithen and Reed, 2002; Steele et al., 1998). Their goal is to test the correlation of the models with arrival dates taken from archaeological sites; what Premo (2010) calls emulation or hypothesis testing.

Here we use an abstract heuristic model to explore the role of cognition in dispersal, and in hominin-environment interactions more generally. The goal is to understand the mechanisms of dispersal in more depth, rather than to make specific predictions about the arrival of hominins in any given locale (Premo, 2010; Costopoulos and Lake, 2010; Lake, 2013).

4.4 Modelling cognition-based dispersal

The mathematical basis of the Fisher dispersal models (i.e., with partial differential equations), has some significant limitations particularly in representing complex environments and variability in modelled individuals or their behavioural responses (Romanowska, 2013). Agent-based modelling, while somewhat less simple, is a useful tool for representing the same dispersal process but with additional elements which are difficult to represent mathematically. An agent-based model (ABM) is a dynamic computational simulation of autonomous agents that allows us to study the broader scale effects of a large number of local scale individual actions. Agents, which in our case represent foraging hunter-gatherer groups, are programmed with simple traits and behaviours that may change over time in response to their interaction with the social and physical environment (Conolly and Lake, 2006; Rouse and Weeks, 2011). In this article, we present an ABM of how hunter-gatherers acquire information about the resource environment and make mobility decisions based on that information (Code available at openabm.org).

ABM replication of Fisher's model

We first implement an ABM version of the classic wave of advance model using the Netlogo toolkit (Wilensky, 1999). This model establishes a baseline that we will use to evaluate the dispersal velocity of our cognition-based dispersal models. The model environment consists of a 100 by 100 cell landscape where cell values represent carrying capacity. For simplicity, cell values in each simulated landscape range from 1 to 100. This relatively small range may still over estimate potential population density during dispersals (data from Kelly 1995 cited in Steele et al., 1998).

Each run begins with one agent, which represents a hunter-gatherer group occupying a cell, in the center of the landscape. During each time step, each agent first increases its size, n, logistically towards the carrying capacity of its cell (i.e., the first term of eq. 2.1). Second, each individual in each agent (i.e., each agent repeats n times) moves their residential camp to a randomly selected cell in their 8-cell neighbourhood. Individuals will either add 1 to the n of another agent or create a new agent with $n = 1$ depending on whether or not the selected cell is already occupied. This simulates ∇^2 in the second term of eq. 2.1. The diffusivity constant, D, is represented by the cell size and we did not correct for the increased distance of diagonal movements.

During each time step, each agent repeats the following n times:

1. Pop. growth: Increase n by one if random(0 to 1) $< 1 - \frac{n}{K}$
2. Movement: Select a random neighbouring cell
    (a) If cell is occupied, $n + 1$ for the occupying agent
    (b) If unoccupied, create a new agent with $n = 1$

The model creates the classic travelling wave of population dispersal from the initial population center. This article uses the baseline velocity from this ABM replication of the wave of advance model to determine how cognition may accelerate or inhibit dispersal. ABM wave velocity is defined as the number of time steps it takes for the first agent to reach the edge of the landscape divided by the 50 cell distance. We do not parameterize diffusivity and population growth rate explicitly (i.e., by inputting values from Table 4–1). Instead, we hold these values constant and compare the relative differences in velocity with and without cognition.

Foraging bias model

The foraging bias model replaces the random cell selection, i.e., random dispersal direction, with an individual agent's choice. We assume that movement will be towards the cell with the highest resource abundance within the surrounding 8-cell neighbourhood (Lake, 2001, 2000). Wren et al. (2014) established that perfect accuracy in choosing the highest resource cell decreased evolutionary fitness and mobility. Instead, an intermediate foraging accuracy was more adaptive, that is only choosing the best cell some of the time, with the heterogeneity of the resource landscape playing a role in the natural selection of the optimal level.

Since a dispersal wave occurs over a relatively short period of time, we chose not to include the evolution of foraging accuracy in this model. Instead, we test the effect of a range of fixed foraging accuracy rates (i.e., 0%, 25%, 50%, 75%, and 99.9%) which could have evolved over a longer period of time in the source population. At each time step, each agent's population grows as in the baseline model, but then at the fixed rate each individual (i.e. each agent repeats n times) has a probability of moving to the highest resource cell in its local neighbourhood, or to a random neighbouring cell otherwise. In the Fisher model, population cannot exceed carrying capacity but in foraging biased movement it could. To correct this, we stop movements to cells already at carrying capacity.

During each time step, each agent repeats the following n times:

1. Pop. growth: Increase n by one if random(0 to 1) $< 1 - \frac{n}{K}$
2. Movement: If random(0 to 1) $<$ foraging accuracy, select best neighbouring cell, otherwise select a random cell
   (a) If cell is occupied and $n < K$, $n + 1$ for the occupying agent
   (b) If unoccupied, create a new agent with $n = 1$

4.5 Carrying capacity landscapes

In the Fisher model, wave velocity is unaffected by the spatial distribution of the carrying capacity landscape (Eq. 4.3). However, Rowell's (2009) results suggest that this may not be the case for non-random dispersal strategies. Given the emphasis on the characteristics of palaeoenvironments in discussions of hominin dispersal, we simulate several different types of resource landscapes to evaluate their impact on wave velocity. To establish a baseline, we first use a homogeneous resource landscape where all cell values equal 100. We run the model 30 times to account for stochasticity in the model.

We then wanted to evaluate the effect of a dispersal corridor on a travelling wave, whether a coast line (Mithen and Reed, 2002; Field et al., 2007), river (Davison et al., 2006), or other geographic bottleneck. Using GRASS GIS (GRASS Development Team, 2012), we generate a homogeneous horizontal corridor (cell value of 100) that decreases gradually in value to the north and south. Since this may be an unrealistically uniform environment, we create a noisy corridor by adding a small degree of random variability (±5%) to the smooth corridor. The final landscape is a gradient that begins with a cell value of 1 and increases gradually up to 100. The model runs 30 times on each of these landscapes, varying the random seed each time, to account for model stochasticity.

Next, the model runs once on each of a set of 150 continuously varying landscapes representing different environmental heterogeneities. Following Wren et al. (2014), GRASS generates these using a random fractal algorithm, *r.surf.fractal*. We chose five degrees of heterogeneity (from lowest, by fractal dimension: 2.001, 2.25, 2.5, 2.75, and 2.999) and generated 30 landscapes for each, for a total set of 150 landscapes. GRASS scales the cell values of each landscape such that each cell value is equal in frequency and the summed carrying capacity of all cells on the landscape is equal (see figure 4–4 for example landscapes).

4.6 Results

The velocity of the foraging-biased dispersal wave is strongly affected by foraging accuracy and, for non-random movement, by the spatial patterning of the resource landscape. The baseline behaviour of the Fisher model, the median from 0% foraging accuracy on the homogeneous plain, is represented as 1.0 on the y-axis of figure 4–1. This plot summarizes the relative velocities over the 150 landscapes of varying heterogeneity and illustrates that increased foraging accuracy, which represents increased cognition, substantially decreases wave velocity. Indeed, this suggests that the random dispersal in a Fisher wave is probably over-estimating the wave velocity of a cognitively advanced human population.

Sub-dividing these results by environmental heterogeneity shows that wave velocity is further decreased by increased heterogeneity of the resource landscape (Figure 4–2). With intermediate to high accuracy, wave velocity is faster than baseline when travelling up a gradient (median 106–110%).

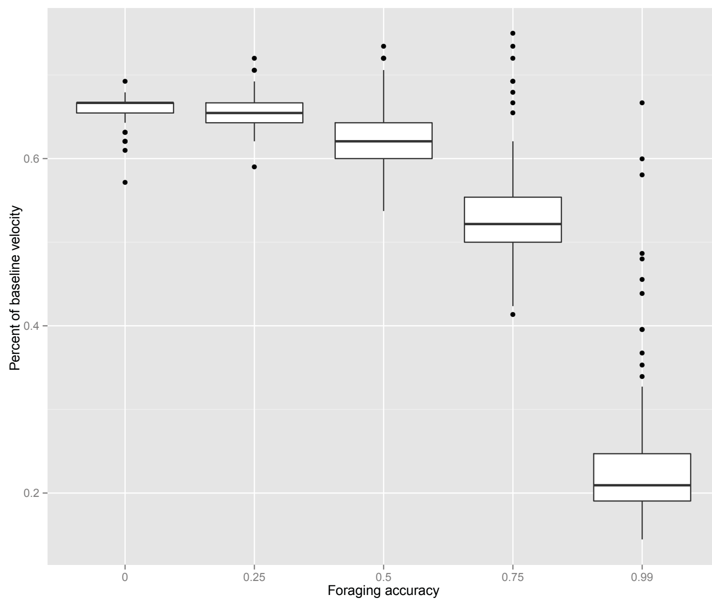

Figure 4–1. Foraging accuracy decreases wave velocity across heterogeneous landscapes such that the fastest velocities come from random mobility. Each box plot represents the wave velocity for 30 different runs. Dark horizontal lines represent the median, horizontal box edges represent the 25th and 75th percentiles, top and bottom most horizontal lines represent 1.5 times the inter-quartile distance. Small circles represent outliers.

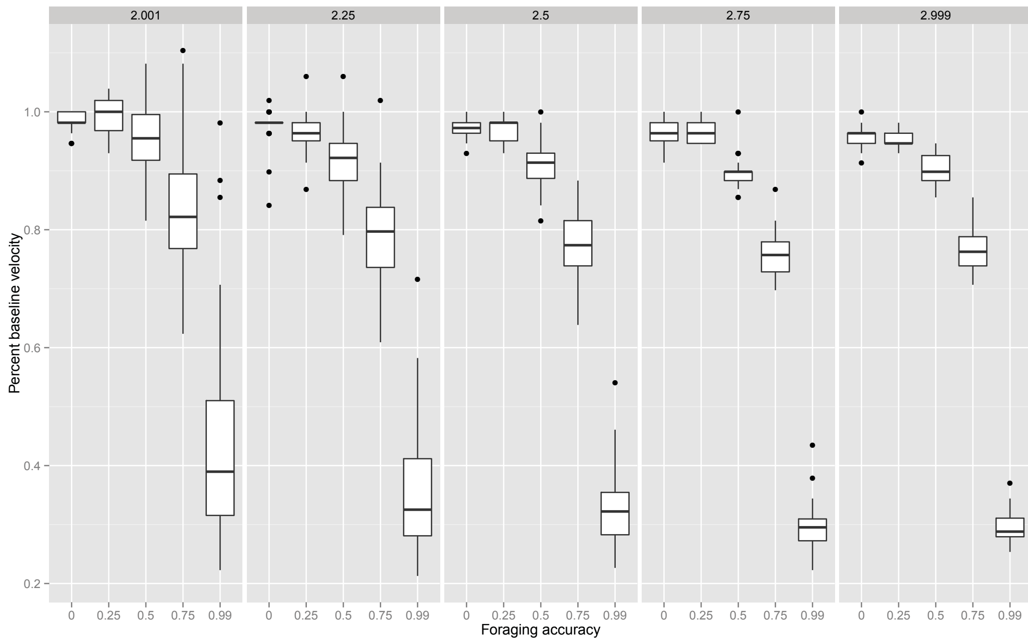

Figure 4–2. Increased resource heterogeneity (panels from left to right) decreases wave velocity. Also note the decreased variance in velocity for increased heterogeneity.

At the highest accuracy velocity is slightly faster along a smooth corridor (102%), but this reduces to only 30% of baseline in the noisy corridor (Figure 4–3).

There is a high degree of wave velocity variance on the low heterogeneity landscapes, including some landscapes where foraging biased dispersal exceeds random dispersal velocity. These landscapes often have only one large resource patch which gradually decreases away from a central point. The position of this patch relative to the starting cell can result in a gradient leading towards the map edge. In these instances, an intermediate foraging accuracy can increase velocity over random dispersal. The randomized placement of this patch leads to the high degree of variance. While equation 4.3 suggests that the value and spatial distribution of the resource landscape is not a factor in wave velocity, these results show that it becomes important when cognition is involved in dispersal.

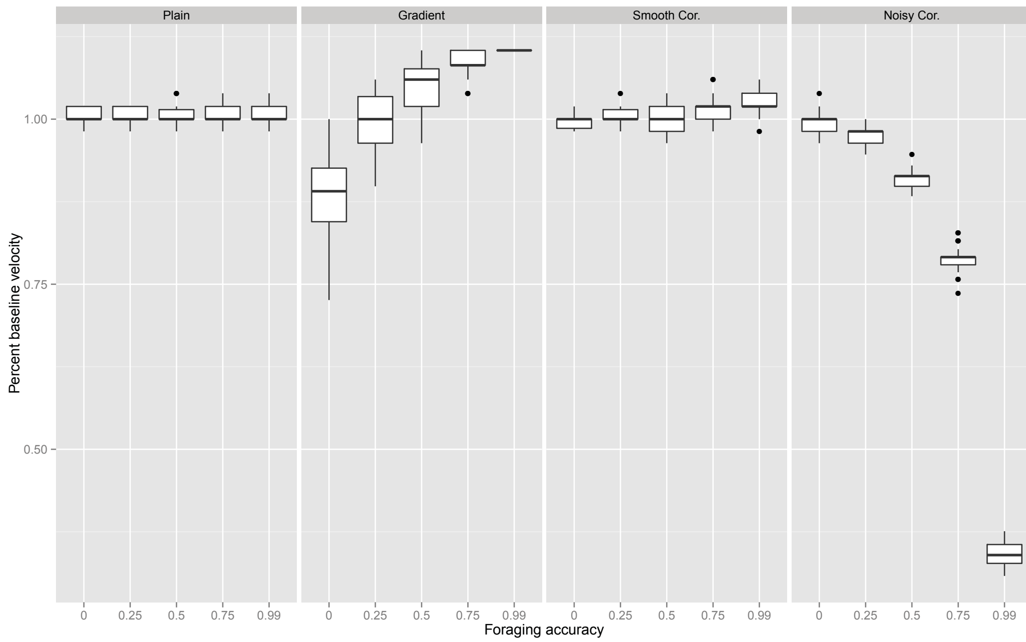

Figure 4–3. Wave velocity across simulated plains, gradients, and corridors. Velocity only exceeds the baseline (1.0) on the gradient when foraging accuracy relatively high.

So far we have reported the wave velocity for each model run by dividing the time taken to reach the map edge by that distance. However, wave velocity varies spatially according to resource gradients at the local scale. Foraging bias increases wave velocity as the front moves towards the center of resource patches (i.e., up local gradients), and slows considerably when moving away from resource patches (i.e., down local gradients). This effect is highest when the heterogeneity is low and resource patches are large. On these landscapes, the wave does not appear as an evenly expanding radius like in a Fisher wave, but as an uneven front which becomes more sinuous and asymmetrical with increasing foraging bias (Figure 4–4 & 4–5).

Our results also show that velocity decreases in heterogeneous landscapes even with random dispersal, contrary to eq. 4.3 (Figure 4–6). The mathematical models assume continuous and fractional population values, n,

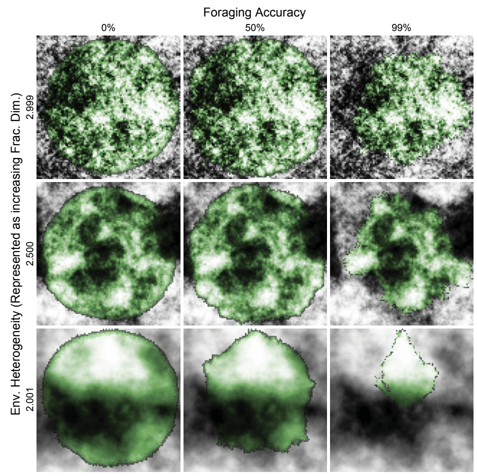

Figure 4–4. Wave front sinuosity increases with increased foraging accuracy on resource landscapes with large patches (low heterogeneity).

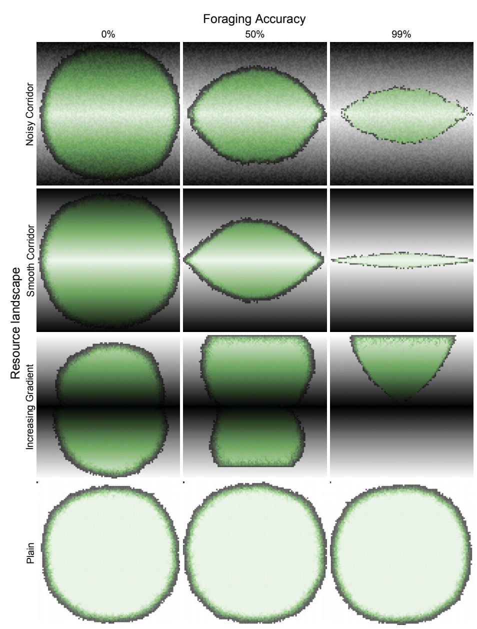

Figure 4–5. Increased foraging accuracy allows agents more directionality up gradients and along corridors. Note the wider spread of agents on the noisy versus smooth corridor.

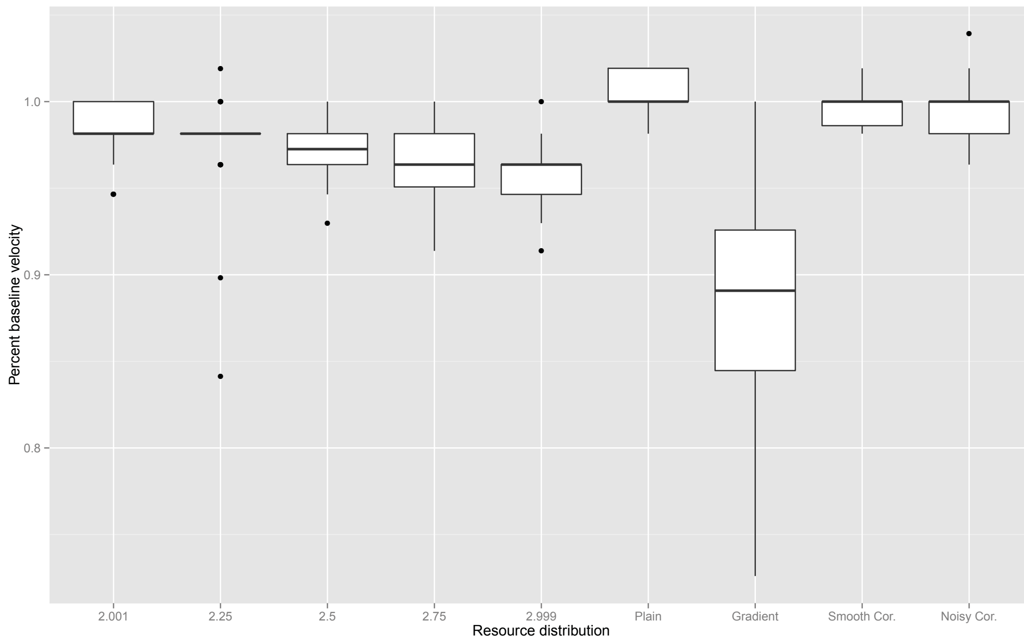

Figure 4–6. Wave velocity decreases with environmental heterogeneity even with random dispersal when carrying capacity has a very low value.

which means that a single individual can disperse fractions of itself to surrounding cells. This cannot occur when individuals are discrete, such as in an ABM. This distinction becomes important whenever there are cells with very low carrying capacity. Since low carrying capacity and low population density are often the default assumptions for the initial human dispersals, this suggests that we should not discount the range or distribution of carrying capacity in the determination of wave velocity, even in non-cognitive dispersals. To confirm this result, we increased the carrying capacity range from 1 - 100, to 101 - 200 and re-ran the model. As expected, wave velocity was the same for all landscapes in the latter case (not shown).

4.7 Discussion

This article investigates the relationship between the importance ascribed to hominin cognition in major dispersal events and Fisher equation-based dispersal models that assume mobility occurred without reference to the environment. Here we present a model where human agents acquire information about their environment, to varying degrees of accuracy based on their level of cognition, and then make mobility decisions based on resource abundance. The results of the agent-based model shows that cognition-based mobility significantly alters the velocity and pattern of waves of advance. Overall, the greater the role of cognition in mobility, the slower the wave of advance (as much as an 80% reduction of non-cognitive wave velocity).

The spatial distribution of the resource landscape plays an important role in wave velocity in the foraging bias model. At the local scale, foraging biased mobility can result in a faster wave than random mobility when there is a smooth gradient of increasing resources to follow, and slower than random when the resource gradient declines. On heterogeneous landscapes, or even in a slightly noisy corridor, wave velocity decreases significantly with increased cognition. The model's complex resource landscapes are difficult to represent mathematically, but these ABM results generally correspond with Rowell (2009) who found that a mobility strategy based on maximizing available resources resulted in a wave front velocity that varied considerably on the local scale according to the slope of the resource gradient.

Since these results suggest that cognition should generally have an inhibiting effect on wave velocity, this suggests that population growth, α, or inter-generational mobility distance, D, need to be much higher to account for the wave velocity observed in the archaeological record. It is beyond the scope of this paper to determine appropriately higher values for α and D, or a cognition-based version of eq. 4.3 (although see Rowell, 2009, Eq. 8), but the results clearly show that the role of cognition on mobility decisions cannot be discounted in dispersal models.

Gradients, corridors, and low heterogeneity resource landscapes, i.e., large resource patches, with intermediate-high foraging accuracy generated the most sinuous and asymmetrical waves of advance. However, asymmetrical wave fronts were relatively uncommon in the suite of model runs conducted. Davison et al. (2006) suggests that the archaeological record of the Neolithic expansion into Europe was asymmetrical. It is currently unclear if this reflects a difference in the mobility decision making process of the population from earlier hominin populations (agriculturalist versus hunter-gatherer, or difference in cognition), or merely a more detailed archaeological record.

The conclusion that cognition inhibits dispersal is unexpected given the frequent assumption that cognitive advances are causally related to major dispersal events. Indeed, the trend of encephalization (Grove, 2012), as well as increases in cultural complexity and other proxies for cognition (McBrearty and Brooks, 2000), is clear, as is the increasing geographic scale and velocity of dispersal events (Steele, 2009; Bar-Yosef and Belfer-Cohen, 2013). Computational models are an important method for testing the narrative explanations of dispersal events' causes and constraints, although this article has shown that the frequently used Fisher equation is insufficient. We need to continue borrowing, adapting, and developing new models to test the various ways in which the complex cognition of hominins may have enhanced or inhibited dispersal. For example, this article has not accounted for pre-existing populations in later dispersal events. In future work we plan to adapt the multiple-population Lokta-Volterra model (Young and Bettinger, 1992; Steele, 2009) to include cognition-based mobility.

CHAPTER 5
Conclusion

5.1 Summary of findings

It is unnecessary to assume humans have an inherent drive to explore or that humans are unaware of their environment to explain patterns of dispersal. However, the mechanisms connecting increases in cognitive complexity with dispersal, are not necessarily intuitive.

This dissertation uses an agent-based modelling approach to incorporate cognition into a model of human dispersal. The goal is to evaluate the assumed causal relationship between increases in hominin cognitive complexity, palaeoenvironmental change, and increasingly geographically expansive and rapid waves of dispersing human populations.

Published computational models of human dispersal generally assume that the movement of individuals and groups occurs without reference to the resource landscape, modelled as a random walk. To incorporate human cognition, this dissertation assumes that human mobility is biased towards foraging-related mobility decisions made by individuals or groups. Foraging-biased mobility involves assessing the surrounding landscape for resource potential and making mobility decisions that maximize available resources. If this resource assessment has perfect accuracy (referred to as spatial foresight in chapter 2), then mobility ceases when agents encounter local optima. An imperfect assessment accuracy allows agents to effectively search out better resources on the landscape by spending some proportion of their time exploring. With the assumption that increased cognitive complexity would increase assessment accuracy, this dissertation explores the natural selection of cognitive complexity, the resulting dispersal potential of the population, and the spatial and temporal pattern of a cognitive wave of advance.

Chapter 2 presents a model where agents make decisions about foraging potential at the local scale to varying degrees of assessment accuracy. Their accuracy is a heritable trait and is subject to natural selection over the course of each model run. When accuracy is high, agents crowd around the resource clusters and reduce reproductive space. Agents with slightly lower accuracy have more reproductive space and are more adaptive as a result. Through this mechanism, natural selection favours less accurate agents, as long as they are still able to maintain sufficient proximity to resources. When the heterogeneity of the environment increases, crowding is reduced and natural selection favours a higher accuracy level. The dispersal potential, or dispersibility, of the population is inversely related to assessment accuracy as it is only through non-resource related mobility decisions (modelled here as random walking) that agents disperse away from resource clusters.

These results suggest that natural selection requires a long duration of low environmental heterogeneity to evolve a population with high dispersibility, and that this occurs through the natural selection of relatively low cognitive complexity. High environmental heterogeneity favours increased cognitive complexity, but low dispersibility.

Chapter 3 extends the way agents acquire environmental knowledge of their environment in two distinct ways, one individual and one social. In both cases natural selection favours decreased levels of environmental knowledge, particularly in low heterogeneity environments. Detailed environmental knowledge being shared or acquired from a larger area, results in agents choosing similar locations and increasing crowding. As in the previous chapter, agents with less environmental knowledge move away from resource clusters and into areas with more space available for reproduction. These results suggest a different role for the cultural transmission of environmental knowledge. Rather than being a requirement for successful dispersal (Gamble et al., 2004), cultural transmission strengthens the bond to particular locations and significantly reduces dispersibility as a result.

Finally, chapter 4 combines the model of cognitive dispersal and the classic wave of advance model. While the previous chapters focus on the evolution of dispersibility, this chapter quantifies the impact of cognition on dispersal velocity and the wave pattern. The model suggests that the greater the level of cognitive complexity, i.e. the more accurate the resource assessment, the slower the wave of advance. The spatial heterogeneity of the environment also decreases wave velocity to a lesser degree when cognition is involved in mobility. Random movement, i.e. non-cognitive mobility, provides the highest velocity across all landscapes except an increasing gradient.

This model suggests that a cognitively complex human disperses much slower than a less cognitively complex human, all other things being equal. However, the archaeological record tells us that dispersal velocity increased as humans became more cognitively complex. Estimates for the variables of Fisher's (1937) equation, inter-generational movement distance and population growth rate, are too low to account for the decreased velocity of cognitive dispersal. Many hypotheses about the cognitive advantage of humans suggest technology and social networks increased the survivability of novel environments. This is compatible, and even complementary, to the results presented here, as this could increase the population growth rate and movement distances significantly.

5.2 Next steps

Agent-based modelling offers a rigorous method for evaluating the mechanisms connecting human cognition and local scale mobility to dispersal events. However, resource assessment accuracy and cultural transmission are only two of many proxies for cognition. In future work, I plan to evaluate other hypotheses connecting increased cognition to dispersal, such as increasing survivability of novel environments or redefining the human ecological niche with technology.

While this dissertation focused on spatial environmental heterogeneity, I also plan to investigate the impact of temporal variability on hominin dispersal. How did shifts in the mean, range, or variability of key resources (i.e. climate change) affect the pattern of dispersal and subsequent settlement? The goal will be to identify the selective pressures affecting the human capacity to adapt to different modes of temporal change. For example, to what extent do humans learn to avoid highly variable locations that are unpredictable and risky (Fitzhugh, 2001), as opposed to adapting their behaviour to make a variable environment more survivable by altering their resource base, technology, mobility, or social organization (Potts, 1998, 2002, 2013; Stewart and Stringer, 2012)?

The models in this dissertation are kept purposefully abstract. However, I also plan to investigate specific dispersal and settlement patterns in the archaeological record. A future applied model will make use of fine scale reconstructed climate simulation data for the Iberian peninsula during the last glacial period (approximately 60 to 19 thousand years ago). The goal is to evaluate how the Iberian glacial refugium could have impacted the evolution of dispersibility, and then to evaluate what effect this had on the recolonization of northern Europe in the post-glacial period.

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APPENDIX A
Agent-based model code

The following sections contain the computer code, written in the Netlogo programming language (Wilensky, 1999), for the agent-based models described in each chapter. This language is designed to be relatively readable without any prior knowledge of programming. To further clarify, I have added comments to the code to explain the key parts of the models. Finally, download links precede the code in each section.

A.1 Code for chapter 2

Download link: `http://www.openabm.org/model/3846/`

```
extensions [ gis ]

breed [agents agent]

globals
[
  elevation-dataset
  stable?
  nummap
]

agents-own
[
  aforesight
]

patches-own
[
  elevation
]

;##############################

to setup
```

```
  ;random-seed 1
  ca
  set nummap 0
  if first fmap = "2"
  [
    gis:load-coordinate-system (word "surfeq/surf.prj")
    set elevation-dataset gis:load-dataset (word "surfeq/" fmap "/" run# ".asc")
    gis:set-world-envelope (gis:envelope-of elevation-dataset)
    set nummap read-from-string fmap
  ]
  if fmap = "cone"
  [
    gis:load-coordinate-system (word "surfeq/surf.prj")
    set elevation-dataset gis:load-dataset (word "surfeq/" fmap "/" run# ".asc")
    gis:set-world-envelope (gis:envelope-of elevation-dataset)
  ]
  gis:apply-raster elevation-dataset elevation
  display-elevation

  create-agents N
  [
    set shape "square"
    set size 1
    setxy max-pxcor - round(abs(random-normal 0 10)) max-pycor - round(abs(random-normal 0 10))
    while [ elevation < 0 OR count agents-here > 1 ] [ setxy max-pxcor - round(abs(random-normal 0 10)) max-pycor - round(abs(random-normal 0 10)) ]
    set aforesight foresight
    color-gradient aforesight
  ]
  reset-ticks
end

to go
  fit-hill-w-evo

  ;plot map
  if one-of [hidden?] of agents = TRUE [display-elevation]

```

```
  tick
end

to fit-hill-w-evo
  let numbabies 0
  ask agents
  [
    ;Reproduction
    let maxfit max [elevation] of agents
    let birth-adjust ( elevation / maxfit ) * birth-rate
    if (random-float 1 < birth-adjust) [
      hatch 1 [
        set aforesight aforesight + mutation-size - random-float (mutation-size * 2) ;mutation
        if aforesight > 1 [set aforesight 1]
        if aforesight < 0 [set aforesight 0]
        color-gradient aforesight

        ;random drop hatching
        let p patch 0 0
        set p one-of neighbors with [not any? agents-here = TRUE]
        ifelse (p != nobody) [
          move-to p
          ask one-of agents [die]
        ][;else p=nobody
          die
        ]
      ] ;close hatch
    ];close birthrate

    ;Mobility
    ifelse (random-float 1 < aforesight)
      [;hill-climb if foresight correct
        let p max-one-of neighbors [elevation]
        if elevation < [elevation] of p
        [
          if not any? agents-on p [ move-to p ]
        ]
      ]
      [;else random movement if foresight wrong
        let p one-of neighbors ;with [pcolor != 99]
        if not any? agents-on p [ move-to p ]
      ]
  ];close ask agents
```

```
end

to display-elevation
  let min-elevation gis:minimum-of elevation-dataset
  let max-elevation gis:maximum-of elevation-dataset
  ask patches
  [ ;
    set pcolor 99 ;in case some cells are inaccessible (e.g. water)
    if (elevation > 0) [set pcolor scale-color black elevation min-elevation max-elevation ]
  ]
  ask agents [set hidden? false]
end

to color-gradient [number]
  ifelse (number <= 0.5) [set color red + ( number * 9.99 )] [set color 114 - (number * 9.99) ]
end
@#$#@#$#@
GRAPHICS-WINDOW
304
10
814
541
-1
-1
5.0
1
10
1
1
1
0
0
0
1
0
99
0
99
1
1
1
ticks
```

```
1000.0

BUTTON
15
9
78
42
setup
setup
NIL
1
T
OBSERVER
NIL
S
NIL
NIL
1

BUTTON
15
41
78
74
go
ifelse ticks != 50000 [go][stop]\n;go\n
T
1
T
OBSERVER
NIL
G
NIL
NIL
1

BUTTON
15
74
78
107
step
go
NIL
1
```

```
T
OBSERVER
NIL
NIL
NIL
NIL
1

SLIDER
82
92
254
125
N
N
0
1000
500
100
1
NIL
HORIZONTAL

CHOOSER
82
10
221
55
fmap
fmap
"2.001" "2.10" "2.20" "2.30" "2.40" "2.50" "2.60" "2.70"
    "2.80" "2.90" "2.999" "cone"
5

SLIDER
82
125
254
158
foresight
foresight
0
1
1
.05
```

```
1
NIL
HORIZONTAL

PLOT
12
357
253
477
AvgFitness
ticks
AvgFitness
0.0
10.0
50.0
55.0
true
false
"" ""
PENS
"default" 1.0 0 -16777216 true "" "plot mean [elevation] of agents"
"biased" 1.0 0 -13345367 true "" ";if (mode = \"infoshare\" AND count agents with [strategy = \"biased\"] > 0) [plot mean [elevation] of agents with [strategy = \"biased\"]]"
"unbiased" 1.0 0 -2674135 true "" ";if (mode = \"infoshare\" AND count agents with [strategy = \"unbiased\"] > 0) [plot mean [elevation] of agents with [strategy = \"unbiased\"]]"

SLIDER
82
55
220
88
run#
run#
1
100
1
1
1
NIL
HORIZONTAL
```

```

SLIDER
82
191
253
224
birth-rate
birth-rate
0
.5
0.1
.1
1
NIL
HORIZONTAL

PLOT
12
226
253
357
AvgForesight
NIL
NIL
0.0
10.0
0.0
1.0
true
false
"" ""
PENS
"default" 1.0 2 -13345367 true "" ";ask n-of 10 agents [plotxy ticks aforesight]"
"Dist" 100.0 0 -16777216 true "" "plotxy ticks mean [aforesight] of agents"

MONITOR
252
226
302
271
AvgForesight
mean [aforesight] of agents
2
```

```
1
11

SLIDER
82
158
254
191
mutation-size
mutation-size
0
.1
0.01
0.001
1
NIL
HORIZONTAL

BUTTON
220
55
275
88
rand
set run# random 100 + 1
NIL
1
T
OBSERVER
NIL
NIL
NIL
NIL
1

@#$#@#$#@
## WHAT IS IT?

Agent-based model evaluating the natural selection of foresight, the accuracy at which agents are able to assess their environment, under different degrees of environmental heterogeneity.

```

The model is designed to connect a mechanism of local scale mobility, namely foraging, with the global scale phenomenon of population dispersal.

HOW IT WORKS

Agents are assigned the initial "foresight" parameter to their individual "aforesight" trait. This value controls the probability of either moving randomly to one of their 9-cell neighbours ("a mistake"), or choosing the neighbouring cell with the highest value. This value is mutated slightly either up or down with each successful reproduction, controled by the "birth-rate" parameter. Agents on high valued cells reprouced more frequently. This allows the population to find an optimal value for the foresight parameter.

HOW TO USE IT

Maps are not generated by NetLogo. Download my map set from (includes a bash script for generating your own with GRASS GIS): https://dl.dropboxusercontent.com/u/1360468/surfaces.zip

Unzip the surfeq folder into the same folder as this nlogo file.

Choose a heterogeneity value from the "fmap" list running from 2.001 (least heterogeneous) to 2.999 (most heterogenous). Click rand to choose 1 of the 100 randomly generated surfaces at the selected heterogeneity level. Optionally also adjust the base birth-rate, mutation-size, and initial foresight parameters. Then click "setup". Assuming everything works, run with the "Go" button.

See the BehaviourSpace dialog for the run sets used in the article.

THINGS TO NOTICE

```
The high resource clusters get crowded from high foresight agents which reduces the rate of successful reproductions. As a result, high levels of foresight are maladaptive due to reducing the available reproductive space and the mean foresight of the population falls to relatively low levels.

As heterogeneity is increased, the number of clusters increases while the size of them decreases. This disperses the population across the landscape which reduces the crowding, and favours higher foresight.

Success remains relatively high for all runs.

## THINGS TO TRY

Playing with the parameters for birth-rate and mutation-size alters the final values and variance of the runs but not the overall result. Higher birth-rate reduces the number of moves an individual agent has time for before being replaced. Lower mutation-size reduces the stochasticity of the mean, but requires a much longer run time before the mean foresight value stabilizes.

## EXTENDING THE MODEL

Try importing different types of surfaces, or even a landscape you're interested in classified by its presumed habitat quality.

Introduce population growth, increase the range of the evaluated neighbourhood, or work out a way to share information between agents. Does increased information about the environment increase success or foresight?

## CREDITS AND REFERENCES

This model was designed for a paper submitted to the Journal of Human Evolution, submitted for publication in 2013.
@#$#@#$#@
default
true
```

```
0
Polygon -7500403 true true 150 5 40 250 150 205 260 250

airplane
true
0
Polygon -7500403 true true 150 0 135 15 120 60 120 105 15 165 15 195 120 180 135 240 105 270 120 285 150 270 180 285 210 270 165 240 180 180 285 195 285 165 180 105 180 60 165 15

arrow
true
0
Polygon -7500403 true true 150 0 0 150 105 150 105 293 195 293 195 150 300 150

box
false
0
Polygon -7500403 true true 150 285 285 225 285 75 150 135
Polygon -7500403 true true 150 135 15 75 150 15 285 75
Polygon -7500403 true true 15 75 15 225 150 285 150 135
Line -16777216 false 150 285 150 135
Line -16777216 false 150 135 15 75
Line -16777216 false 150 135 285 75

bug
true
0
Circle -7500403 true true 96 182 108
Circle -7500403 true true 110 127 80
Circle -7500403 true true 110 75 80
Line -7500403 true 150 100 80 30
Line -7500403 true 150 100 220 30

butterfly
true
0
Polygon -7500403 true true 150 165 209 199 225 225 225 255 195 270 165 255 150 240
Polygon -7500403 true true 150 165 89 198 75 225 75 255 105 270 135 255 150 240
```

```
Polygon -7500403 true true 139 148 100 105 55 90 25 90 10 105 10 135 25 180 40 195 85 194 139 163
Polygon -7500403 true true 162 150 200 105 245 90 275 90 290 105 290 135 275 180 260 195 215 195 162 165
Polygon -16777216 true false 150 255 135 225 120 150 135 120 150 105 165 120 180 150 165 225
Circle -16777216 true false 135 90 30
Line -16777216 false 150 105 195 60
Line -16777216 false 150 105 105 60

car
false
0
Polygon -7500403 true true 300 180 279 164 261 144 240 135 226 132 213 106 203 84 185 63 159 50 135 50 75 60 0 150 0 165 0 225 300 225 300 180
Circle -16777216 true false 180 180 90
Circle -16777216 true false 30 180 90
Polygon -16777216 true false 162 80 132 78 134 135 209 135 194 105 189 96 180 89
Circle -7500403 true true 47 195 58
Circle -7500403 true true 195 195 58

circle
false
0
Circle -7500403 true true 0 0 300

circle 2
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240

cow
false
0
Polygon -7500403 true true 200 193 197 249 179 249 177 196 166 187 140 189 93 191 78 179 72 211 49 209 48 181 37 149 25 120 25 89 45 72 103 84 179 75 198 76 252 64 272 81 293 103 285 121 255 121 242 118 224 167
Polygon -7500403 true true 73 210 86 251 62 249 48 208
Polygon -7500403 true true 25 114 16 195 9 204 23 213 25 200 39 123

```

```
cylinder
false
0
Circle -7500403 true true 0 0 300

dot
false
0
Circle -7500403 true true 90 90 120

face happy
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 255 90 239 62 213 47
    191 67 179 90 203 109 218 150 225 192 218 210 203 227
     181 251 194 236 217 212 240

face neutral
false
0
Circle -7500403 true true 8 7 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Rectangle -16777216 true false 60 195 240 225

face sad
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 168 90 184 62 210 47
    232 67 244 90 220 109 205 150 198 192 205 210 220 227
     242 251 229 236 206 212 183

fish
false
0
Polygon -1 true false 44 131 21 87 15 86 0 120 15 150 0
    180 13 214 20 212 45 166
Polygon -1 true false 135 195 119 235 95 218 76 210 46
    204 60 165
```

```
Polygon -1 true false 75 45 83 77 71 103 86 114 166 78 135 60
Polygon -7500403 true true 30 136 151 77 226 81 280 119 292 146 292 160 287 170 270 195 195 210 151 212 30 166
Circle -16777216 true false 215 106 30

flag
false
0
Rectangle -7500403 true true 60 15 75 300
Polygon -7500403 true true 90 150 270 90 90 30
Line -7500403 true 75 135 90 135
Line -7500403 true 75 45 90 45

flower
false
0
Polygon -10899396 true false 135 120 165 165 180 210 180 240 150 300 165 300 195 240 195 195 165 135
Circle -7500403 true true 85 132 38
Circle -7500403 true true 130 147 38
Circle -7500403 true true 192 85 38
Circle -7500403 true true 85 40 38
Circle -7500403 true true 177 40 38
Circle -7500403 true true 177 132 38
Circle -7500403 true true 70 85 38
Circle -7500403 true true 130 25 38
Circle -7500403 true true 96 51 108
Circle -16777216 true false 113 68 74
Polygon -10899396 true false 189 233 219 188 249 173 279 188 234 218
Polygon -10899396 true false 180 255 150 210 105 210 75 240 135 240

house
false
0
Rectangle -7500403 true true 45 120 255 285
Rectangle -16777216 true false 120 210 180 285
Polygon -7500403 true true 15 120 150 15 285 120
Line -16777216 false 30 120 270 120

leaf
false
```

```
0
Polygon -7500403 true true 150 210 135 195 120 210 60 210 30 195 60 180 60 165 15 135 30 120 15 105 40 104 45 90 60 90 90 105 105 120 120 120 105 60 120 60 135 30 150 15 165 30 180 60 195 60 180 120 195 120 210 105 240 90 255 90 263 104 285 105 270 120 285 135 240 165 240 180 270 195 240 210 180 210 165 195
Polygon -7500403 true true 135 195 135 240 120 255 105 255 105 285 135 285 165 240 165 195

line
true
0
Line -7500403 true 150 0 150 300

line half
true
0
Line -7500403 true 150 0 150 150

pentagon
false
0
Polygon -7500403 true true 150 15 15 120 60 285 240 285 285 120

person
false
0
Circle -7500403 true true 110 5 80
Polygon -7500403 true true 105 90 120 195 90 285 105 300 135 300 150 225 165 300 195 300 210 285 180 195 195 90
Rectangle -7500403 true true 127 79 172 94
Polygon -7500403 true true 195 90 240 150 225 180 165 105
Polygon -7500403 true true 105 90 60 150 75 180 135 105

plant
false
0
Rectangle -7500403 true true 135 90 165 300
Polygon -7500403 true true 135 255 90 210 45 195 75 255 135 285
```

```
Polygon -7500403 true true 165 255 210 210 255 195 225 255 165 285
Polygon -7500403 true true 135 180 90 135 45 120 75 180 135 210
Polygon -7500403 true true 165 180 165 210 225 180 255 120 210 135
Polygon -7500403 true true 135 105 90 60 45 45 75 105 135 135
Polygon -7500403 true true 165 105 165 135 225 105 255 45 210 60
Polygon -7500403 true true 135 90 120 45 150 15 180 45 165 90

sheep
false
0
Rectangle -7500403 true true 151 225 180 285
Rectangle -7500403 true true 47 225 75 285
Rectangle -7500403 true true 15 75 210 225
Circle -7500403 true true 135 75 150
Circle -16777216 true false 165 76 116

square
false
0
Rectangle -7500403 true true 30 30 270 270

square 2
false
0
Rectangle -7500403 true true 30 30 270 270
Rectangle -16777216 true false 60 60 240 240

star
false
0
Polygon -7500403 true true 151 1 185 108 298 108 207 175 242 282 151 216 59 282 94 175 3 108 116 108

target
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240
Circle -7500403 true true 60 60 180
```

```
Circle -16777216 true false 90 90 120
Circle -7500403 true true 120 120 60

tree
false
0
Circle -7500403 true true 118 3 94
Rectangle -6459832 true false 120 195 180 300
Circle -7500403 true true 65 21 108
Circle -7500403 true true 116 41 127
Circle -7500403 true true 45 90 120
Circle -7500403 true true 104 74 152

triangle
false
0
Polygon -7500403 true true 150 30 15 255 285 255

triangle 2
false
0
Polygon -7500403 true true 150 30 15 255 285 255
Polygon -16777216 true false 151 99 225 223 75 224

truck
false
0
Rectangle -7500403 true true 4 45 195 187
Polygon -7500403 true true 296 193 296 150 259 134 244 104 208 104 207 194
Rectangle -1 true false 195 60 195 105
Polygon -16777216 true false 238 112 252 141 219 141 218 112
Circle -16777216 true false 234 174 42
Rectangle -7500403 true true 181 185 214 194
Circle -16777216 true false 144 174 42
Circle -16777216 true false 24 174 42
Circle -7500403 false true 24 174 42
Circle -7500403 false true 144 174 42
Circle -7500403 false true 234 174 42

turtle
true
0
```

```
Polygon -10899396 true false 215 204 240 233 246 254 228 266 215 252 193 210
Polygon -10899396 true false 195 90 225 75 245 75 260 89 269 108 261 124 240 105 225 105 210 105
Polygon -10899396 true false 105 90 75 75 55 75 40 89 31 108 39 124 60 105 75 105 90 105
Polygon -10899396 true false 132 85 134 64 107 51 108 17 150 2 192 18 192 52 169 65 172 87
Polygon -10899396 true false 85 204 60 233 54 254 72 266 85 252 107 210
Polygon -7500403 true true 119 75 179 75 209 101 224 135 220 225 175 261 128 261 81 224 74 135 88 99

wheel
false
0
Circle -7500403 true true 3 3 294
Circle -16777216 true false 30 30 240
Line -7500403 true 150 285 150 15
Line -7500403 true 15 150 285 150
Circle -7500403 true true 120 120 60
Line -7500403 true 216 40 79 269
Line -7500403 true 40 84 269 221
Line -7500403 true 40 216 269 79
Line -7500403 true 84 40 221 269

x
false
0
Polygon -7500403 true true 270 75 225 30 30 225 75 270
Polygon -7500403 true true 30 75 75 30 270 225 225 270

@#$#@#$#@
NetLogo 5.0
@#$#@#$#@
@#$#@#$#@
@#$#@#$#@
<experiments>
  <experiment name="Evo" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <timeLimit steps="50000"/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
```

```
    <metric>mean [aforesight] of agents</metric>
    <enumeratedValueSet variable="N">
      <value value="500"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="foresight">
      <value value="1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="fmap">
      <value value="&quot;2.001&quot;"/>
      <value value="&quot;2.10&quot;"/>
      <value value="&quot;2.20&quot;"/>
      <value value="&quot;2.30&quot;"/>
      <value value="&quot;2.40&quot;"/>
      <value value="&quot;2.50&quot;"/>
      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.70&quot;"/>
      <value value="&quot;2.80&quot;"/>
      <value value="&quot;2.90&quot;"/>
      <value value="&quot;2.999&quot;"/>
    </enumeratedValueSet>
    <steppedValueSet variable="run#" first="1" step="1" last="100"/>
    <enumeratedValueSet variable="mutation-size">
      <value value="0.01"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="birth-rate">
      <value value="0.1"/>
    </enumeratedValueSet>
  </experiment>
  <experiment name="Evo - control" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <timeLimit steps="50000"/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [aforesight] of agents</metric>
    <enumeratedValueSet variable="N">
      <value value="500"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="foresight">
      <value value="1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="fmap">
      <value value="&quot;2.001&quot;"/>
```

```
      <value value="&quot;2.10&quot;"/>
      <value value="&quot;2.20&quot;"/>
      <value value="&quot;2.30&quot;"/>
      <value value="&quot;2.40&quot;"/>
      <value value="&quot;2.50&quot;"/>
      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.70&quot;"/>
      <value value="&quot;2.80&quot;"/>
      <value value="&quot;2.90&quot;"/>
      <value value="&quot;2.999&quot;"/>
    </enumeratedValueSet>
    <steppedValueSet variable="run#" first="1" step="1" last="100"/>
    <enumeratedValueSet variable="mutation-size">
      <value value="0.01"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="birth-rate">
      <value value="0.1"/>
    </enumeratedValueSet>
  </experiment>
  <experiment name="Evo - fsplot" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <final>export-plot "AvgForesight" (word "evo/fsplot/f" nummap "_" run# ".csv")</final>
    <timeLimit steps="50000"/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [aforesight] of agents</metric>
    <enumeratedValueSet variable="N">
      <value value="500"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="foresight">
      <value value="1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="fmap">
      <value value="&quot;2.001&quot;"/>
      <value value="&quot;2.10&quot;"/>
      <value value="&quot;2.20&quot;"/>
      <value value="&quot;2.30&quot;"/>
      <value value="&quot;2.40&quot;"/>
      <value value="&quot;2.50&quot;"/>
      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.70&quot;"/>
```

```
        <value value="&quot;2.80&quot;"/>
        <value value="&quot;2.90&quot;"/>
        <value value="&quot;2.999&quot;"/>
      </enumeratedValueSet>
      <steppedValueSet variable="run#" first="1" step="10" last="100"/>
      <enumeratedValueSet variable="mutation-size">
        <value value="0.01"/>
      </enumeratedValueSet>
      <enumeratedValueSet variable="birth-rate">
        <value value="0.1"/>
      </enumeratedValueSet>
    </experiment>
    <experiment name="Evo - fsplot - cone" repetitions="10" runMetricsEveryStep="false">
      <setup>setup</setup>
      <go>go</go>
      <final>export-plot "AvgForesight" (word "evo/fsplot/cone_" behaviorspace-run-number ".csv")</final>
      <timeLimit steps="50000"/>
      <metric>mean [elevation] of agents</metric>
      <metric>mean [aforesight] of agents</metric>
      <enumeratedValueSet variable="N">
        <value value="500"/>
      </enumeratedValueSet>
      <enumeratedValueSet variable="foresight">
        <value value="1"/>
      </enumeratedValueSet>
      <enumeratedValueSet variable="fmap">
        <value value="&quot;cone&quot;"/>
      </enumeratedValueSet>
      <enumeratedValueSet variable="run#">
        <value value="1"/>
      </enumeratedValueSet>
      <enumeratedValueSet variable="mutation-size">
        <value value="0.01"/>
      </enumeratedValueSet>
      <enumeratedValueSet variable="birth-rate">
        <value value="0.1"/>
      </enumeratedValueSet>
    </experiment>
  </experiments>
@#$#@#$#@
@#$#@#$#@
default
```

```
0.0
-0.2 0 1.0 0.0
0.0 1 1.0 0.0
0.2 0 1.0 0.0
link direction
true
0
Line -7500403 true 150 150 90 180
Line -7500403 true 150 150 210 180

@#$#@#$#@
0
@#$#@#$#@
```

A.2 Code for chapter 3

Download link: `http://www.openabm.org/model/4176/`

```
extensions [ gis ]

breed [agents agent]

globals
[
  elevation-dataset
  max-elev
  nummap
]

agents-own
[
  trait
  pop
  aforesight
  acopyrate
  fsdist
]

patches-own
[
  elevation
  currentelev
  timestamp
  occfreq
  cum-effit
]

```

```
; SETUP CODE ##################################

to setup
  ;random-seed 1
  ca
  set nummap 0
  if first fmap = "2"
  [
    gis:load-coordinate-system (word "surfeq/surf.prj")
    set elevation-dataset gis:load-dataset (word "surfeq/" fmap "/" run# ".asc")
    gis:set-world-envelope (gis:envelope-of elevation-dataset)
    set nummap read-from-string fmap
  ]
  if fmap = "cone"
  [
    gis:load-coordinate-system (word "surfeq/surf.prj")
    set elevation-dataset gis:load-dataset (word "surfeq/" fmap "/" run# ".asc")
    gis:set-world-envelope (gis:envelope-of elevation-dataset)
  ]
  gis:apply-raster elevation-dataset elevation
  display-elevation
  set max-elev gis:maximum-of elevation-dataset

  create-agents N
  [
    ifelse colonize? = TRUE [ ;begin with agents distributed around one corner
      setxy max-pxcor - round(abs(random-normal 0 10)) max-pycor - round(abs(random-normal 0 10))
      while [ elevation < 0 OR count agents-here > 1 ] [
        setxy max-pxcor - round(abs(random-normal 0 10)) max-pycor - round(abs(random-normal 0 10))
      ]
    ]
    [;else random placement
      setxy round random-xcor round random-ycor
      while [ elevation <= 0 OR count agents-here > 1] [ setxy round random-xcor round random-ycor ]
    ]

```

```
    ifelse randTrait? = false  ;set all trait values to same value, as specified by interface slider
    [
      if mode = "info" [set acopyrate copyrate color-gradient acopyrate]
      if mode = "radius" [set fsdist 1 color-gradient ( fsdist / 2 )]
    ]
    [;else randTrait? = true, assign random trait value
      if mode = "info" [set acopyrate random-float 1 color-gradient acopyrate]
      if mode = "radius" [
        set fsdist 1 + plus-or-minus mutation-size
        if fsdist < 0 [set fsdist 0]
        color-gradient ( fsdist / 2 )
      ]
    ];close randTrait?

    set aforesight foresight ; I retain the original term for resource assessment accuracy, foresight, within the model code
  ]; close agents

  ;;; for quantifying reproductive potential (cumulative reproductive fitness) more comments in go code
  ;  ask patches [set timestamp 0 set occfreq 0 set currentelev elevation ]
  ask patches [set cum-effit 0]
  reset-ticks
end

; GO CODE #####################################

to go
  if (mode = "info") ;set run type to information sharing
  [
    go-info
  ]
  if (mode = "radius") ;set run type to assessment radius
  [
    go-radius
  ]

```

```
  if not any? agents [stop]

  tick
end

to go-radius
  let maxfit max [elevation] of agents + 1 ; addition protects against crash by div zero
  let maxdist max [fsdist] of agents + 0.001
  ask agents
  [
    let birth-adjust ( elevation / maxfit ) * birth-rate ;differential reproduction, decreases probability of reproduction for agents with low resources
    if (random-float 1 < birth-adjust) [
        hatch 1 [
          if (random-float 1 < mutation-rate) [ ;at the specified rate, change parent's trait value by mutation-size, otherwise inhereit parent's value
            set fsdist fsdist + plus-or-minus mutation-size
            if fsdist < 0 [set fsdist 0]
            color-gradient ( fsdist / maxdist )
          ] ;close mutation-rate

            ;;;;;;;; drop offspring on any empy neighbouring cell, or die if all are full
            let p one-of neighbors with [not any? agents-here = TRUE]
            ifelse (p != nobody) [
              move-to p
              if death-rate = 0 [ask one-of agents [die]] ;if population size is fixed
            ][;else p=nobody
              die
            ]

        ] ;close hatch
    ];close birth-adjust

    ;;;;;;;;; mobility
    ifelse (random-float 1 < aforesight)
    [;hill-climb if foresight correct
```

```
      let p max-one-of patches in-radius fsdist [elevation] ;choose best cell within assessment radius
      if (p != patch-here)
      [
        face p
        if not any? agents-on patch-ahead 1 [ move-to patch-ahead 1 ] ;move towards it if there is an empty cell
      ]

    ]
    [;else random movement if foresight wrong (inaccurate assessment)
      let p one-of neighbors
      if not any? agents-on p [ move-to p ]
    ]

    if death-rate > 0 [ ;for variable population size, kill of random agents at specified probability
      if (random-float 1 < death-rate) [die]
    ];close death
  ];close ask agents

  ;;;; Commented out code below used for quantifying the cumulative effective fitness (reproductive availability) of cells during a run.
  ;;;; Too compuatationally expensive to leave running all the time
  ;  let effit 0
  ;  ask patches
  ;  [
  ;    if timestamp = 0 AND any? agents-here = TRUE [set timestamp ticks ]
  ;    if timestamp > 0 AND any? agents-here = TRUE [set occfreq occfreq + count agents-here]
  ;    let basefit ( elevation / maxfit * birth-rate)
  ;    ifelse (count agents-on neighbors < 8) [set effit basefit][set effit 0]
  ;    set cum-effit cum-effit + effit
  ;  ]

  if ticks mod 100 = 0 AND count agents > 2 [ ;plotting
    let fsdist_med median [fsdist] of agents
    set-current-plot "Trait"
```

```
    set-current-plot-pen "Median"
    plotxy ticks fsdist_med
  ]
end

to go-info ;go code for information sharing model, comments from above generally apply
  let maxfit max [elevation] of agents + 1 ; addition protects against crash by div zero
  ask agents
  [
    let birth-adjust ( elevation / maxfit ) * birth-rate
    if (random-float 1 < birth-adjust) [
      hatch 1 [
        if (random-float 1 < mutation-rate) [
          set acopyrate acopyrate + plus-or-minus mutation-size ;mutation
          if acopyrate > 1 [set acopyrate 1]
          if acopyrate < 0 [set acopyrate 0]
          color-gradient acopyrate
        ] ;close mutation-rate

        ;random drop hatching
        let p one-of neighbors with [not any? agents-here = TRUE]
        ifelse (p != nobody) [
          move-to p
          if death-rate = 0 [ask one-of agents [die]]
        ][;else p=nobody
          die
        ]
      ] ;close hatch
    ];close birthadjust

    ;Movement
    ifelse random-float 1 < acopyrate [ ;inherited probability of copying another agent vs exploration
      let a one-of other agents ;randomly pick a target agent from population
      if (a != nobody AND [elevation] of a > elevation) [ ; if target's resource value is higher than the agent's, then try to move
        face a
```

```
        if not any? agents-on patch-ahead 1 [move-to patch-ahead 1] ;step towards if there is an empty cell
      ]
    ]
    [;else: move randomly if chose not to copy / copy error
      let p one-of neighbors
      if not any? agents-on p [move-to p]
    ];close acopyrate

    if death-rate > 0 [
      if (random-float 1 < death-rate)
      [
        die
      ]
    ];close death
  ];close ask agents
  if not any? agents [stop]

;  let effit 0
;  ask patches
;  [
;    if timestamp = 0 [if any? agents-here = TRUE [set timestamp ticks]]
;    if timestamp > 0 AND any? agents-here = TRUE [set occfreq occfreq + count agents-here]
;    let basefit ( elevation / maxfit * birth-rate)
;    ifelse (count agents-on neighbors < 8) [set effit basefit][set effit 0]
;    set cum-effit cum-effit + effit
;  ]


  if ticks mod 100 = 0 [
  ;if plots-on? = TRUE [
    let cp_med median [acopyrate] of agents
    set-current-plot "Trait"
    set-current-plot-pen "Median"
    plotxy ticks cp_med
  ]
end


;DISPLAY MODULES ####################################
```

```
to display-ticks ;mapping the pattern of initial occupation, not used in article
  ask agents [set hidden? true]
  ask patches
  [
    if (timestamp > 0)
    [
      set pcolor scale-color red timestamp 0 ticks
    ]
  ]
end

to display-occfreq ;mapping the cumulative occupation history of each cell, not used in article
  let max-occfreq max [occfreq] of patches
  ask agents [set hidden? true]
  ask patches
  [
    if (occfreq > 0)
    [
      set pcolor scale-color red occfreq 0 max-occfreq
    ]
  ]
end

to display-elevation ;display landscape code borrowed from GIS code example, elevation represents the resource value
  let min-elevation gis:minimum-of elevation-dataset
  let max-elevation gis:maximum-of elevation-dataset

  ask patches
  [ ;
    set pcolor 99
    if (elevation > 0) [set pcolor scale-color black elevation min-elevation max-elevation ]
  ]
  ask agents [set hidden? false]
end


to display-effit
  ;init set cum-effit 0 in setup
  ;add cum-effit to patches-own
```

```
  ;add to maptype chooser
  ;add display to go
  ;let effit 0
  ;let maxfit max [elevation] of agents + 1
  let max-cum-effit max [cum-effit] of patches
  ask agents [set hidden? true]
  ask patches
  [
  ;  let basefit ( elevation / maxfit )
  ;  ifelse (count agents-on neighbors < 8) [set effit basefit][set effit 0]
  ;  set cum-effit cum-effit + effit
     set pcolor scale-color green cum-effit 0 max-cum-effit
  ]
end

;HELPER MODULES ########################################

to export-map [folder] ;this section is a bit sloppy. Exports a raster of the cumulative occupation history, a proxy for the archaeological record. Not used in article.
  ;** Create raster dataset
  let occraster gis:create-raster world-width world-height gis:world-envelope
  ;** Transfer agent's trait value of each netlogo patch to the occraster layer
  set occraster gis:patch-dataset occfreq

  ;** At last store the data in file
  ;gis:store-dataset occraster (word "occraster/" nummap "_" run# "_f" round (foresight * 100) ".asc")
;  ifelse (mode = "infoshare")
;  [
;    gis:store-dataset occraster (word folder remove "f" fmap "_" run# "_cr" round (copyrate * 100) "_f" round (foresight * 100) ".asc")
;    gis:store-dataset occraster (word "infoshare/occraster/uh/" remove "f" fmap "_" run# "_cr" round (copyrate * 100) ".asc")
;    gis:store-dataset occraster (word "infoshare/occraster/br/" remove "f" fmap "_" run# "_cr" round (copyrate * 100) ".asc")
;  ]
```

```
;   [;else
      ;gis:store-dataset occraster (word "occraster/" remove "f" fmap "_" run# "_f" round (foresight * 100) ".asc")
      ;gis:store-dataset occraster (word folder "/" fmap "_" run# "m_" mutation-size ".asc")
      gis:store-dataset occraster (word folder "/" fmap "_" run# "br_" birth-rate ".asc")
;   ]
;   gis:store-dataset occraster (word "occraster/" fmap "_f" round (foresight * 100) ".asc")
    ;(word "occraster/" fmap "/" colonize? "/" "f" round (foresight * 100) ".png")
end

to screenshots ;export series of images during a run
    if ticks mod 10 = 0
    [
      export-view (word "screenshots/" fmap "/ticks/img" round (ticks / 10) ".png")
    ]
end

to color-gradient [number] ;agent colour-scheme, creates a bi-polar colour gradient from dark red through white through dark blue
    ;ifelse (number < 0.5) [set color [255 ( number * 255) ( number * 255)]] [set color [( number * 255) ( number * 255) 255]]
    ifelse (number <= 0.5) [set color red + ( number * 9.99 )] [set color 114 - (number * 9.99) ]
end

to-report plus-or-minus [ value ] ;used in trait mutation to randomly increase or decrease the mutation-size
      ; randomly reports either +value or -value
      report value * (((random 2) * 2) - 1)
      ; explanation of "(((random 2) * 2) - 1)"
      ; Operation:     Yields:
      ; random 2   -> 0             or 1
      ;       * 2   -> 0 * 2 =  0   or 1 * 2 = 2
      ;       - 1   -> 0 - 1 = -1   or 2 - 1 = 1
      ; thus, returns -1 or +1
end
```

```
@#$#@#$#@
GRAPHICS-WINDOW
304
10
814
541
-1
-1
5.0
1
10
1
1
1
0
0
0
1
0
99
0
99
1
1
1
ticks
1000.0

BUTTON
15
9
78
42
setup
setup
NIL
1
T
OBSERVER
NIL
S
NIL
NIL
1
```

```
BUTTON
15
41
78
74
go
;ifelse ticks != 50000 [go][stop]\nifelse ticks != 100000 [go][stop]\n;go\n
T
1
T
OBSERVER
NIL
G
NIL
NIL
1

BUTTON
15
74
78
107
step
go
NIL
1
T
OBSERVER
NIL
NIL
NIL
NIL
1

SLIDER
118
180
290
213
N
N
0
2000
500
```

```
100
1
NIL
HORIZONTAL

CHOOSER
118
12
281
57
mode
mode
"info" "radius"
0

CHOOSER
118
57
256
102
fmap
fmap
"2.001" "2.05" "2.10" "2.15" "2.20" "2.25" "2.30" "2.35" "2.40" "2.45" "2.50" "2.55" "2.60" "2.65" "2.70" "2.75" "2.80" "2.85" "2.90" "2.95" "2.99" "cone"
0

SLIDER
118
213
290
246
foresight
foresight
0
1
1
.05
1
NIL
HORIZONTAL

CHOOSER
118
135
```

```
256
180
maptype
maptype
"fitness" "ticks" "occfreq" "effit"
0

SLIDER
118
102
256
135
run#
run#
1
100
1
1
1
NIL
HORIZONTAL

SLIDER
814
10
984
43
birth-rate
birth-rate
0
1
0.1
0.1
1
NIL
HORIZONTAL

SLIDER
814
43
984
76
death-rate
death-rate
0
```

```
birth-rate
0.06
0.01
1
NIL
HORIZONTAL

SWITCH
15
140
105
173
colonize?
colonize?
0
1
-1000

SLIDER
118
246
290
279
copyrate
copyrate
0
1
0
0.05
1
NIL
HORIZONTAL

PLOT
3
509
244
629
Pop
ticks
Pop
0.0
10.0
0.0
10.0
```

```
true
false
"" ";ask agents [measure-total-distance]"
PENS
"Default" 1.0 0 -16777216 true "" "if plots-on? = TRUE [plotxy ticks count agents]"

MONITOR
244
509
294
554
Pop
count agents
0
1
11

PLOT
3
378
245
509
Trait
ticks
Trait
0.0
100000.0
0.0
1.0
true
false
"" ""
PENS
"Median" 100.0 0 -16777216 true "" ";plotxy ticks mean [acopyrate] of agents"

MONITOR
245
378
295
423
MedC
median [acopyrate] of agents
2
```

```
1
11

SLIDER
118
279
290
312
mutation-size
mutation-size
0.01
.5
0.1
0.01
1
NIL
HORIZONTAL

BUTTON
250
103
305
136
rand
set run# random 100 + 1
NIL
1
T
OBSERVER
NIL
NIL
NIL
NIL
1

PLOT
304
541
504
691
Effective fitness
NIL
NIL
0.0
100.0
```

```
0.0
1.0
true
false
"" ""
PENS
"default" 1.0 0 -16777216 true "" "clear-plot\nif plots-on? = TRUE [\nlet env 0\nwhile [env <= 100 AND ticks > 0][\n  set env env + 1\n  let patch-env patch-set patches with [elevation = env]\n  if any? patch-env [plotxy env mean [cum-effit] of patch-env ]\n  ]\n  ]"

SWITCH
15
206
105
239
randTrait?
randTrait?
0
1
-1000

SLIDER
118
311
290
344
mutation-rate
mutation-rate
0
.1
0.0010
.001
1
NIL
HORIZONTAL

SWITCH
15
239
105
272
plots-on?
plots-on?
```

```
1
1
-1000

MONITOR
245
423
295
468
MedR
median [fsdist] of agents
2
1
11

@#$#@#$#@
## WHAT IS IT?

Agent-based model extending an earlier model found here: http://www.openabm.org/model/3846/

The models are designed to connect a mechanism of local scale mobility, namely foraging, with the global scale phenomenon of population dispersal. This model adds to the ability of agents to acquire information about their environment, one individual and one social.

## HOW IT WORKS

See the earlier model for the basic description. There are two variations of the model here, "radius" and "info". In "radius", an agent trait fsdist, determines the radius of the resource assessment neighbourhood. They choose the highest resource cell out of these patches at probability "foresight", and move one step towards it if empty, or move randomly otherwise. The median trait value evolves over time through natural selection by the distribution of the spatial resource environment.

```

```
In "info", an agent trait copyrate, determines the probability of copying information about resources from another random agent, or moving randomly otherwise. When copying, agents move one step towards another agent if they occupy a higher resource cell. Again, the trait value evolves over the course of a run.

## HOW TO USE IT

Maps are not generated by NetLogo. Download the map set as well which (includes a bash script for generating your own with GRASS GIS). Unzip the surfeq folder into the same folder as this nlogo file.

Choose a heterogeneity value from the "fmap" list running from 2.001 (least heterogeneous) to 2.999 (most heterogenous). Click rand to choose 1 of the 100 randomly generated surfaces at the selected heterogeneity level. Optionally also adjust other initial parameters. Setup and Go to run.

See the BehaviourSpace dialog for the run sets used in the dissertation.

## THINGS TO NOTICE

Resource assessment radius and copyrate evolve to relatively low levels, especially for low heterogeneity landscapes.

## CREDITS AND REFERENCES

Colin D. Wren wrote this model as a part of his PhD dissertation at McGill University.
@#$#@#$#@
default
true
0
Polygon -7500403 true true 150 5 40 250 150 205 260 250

airplane
true
0
```

```
Polygon -7500403 true true 150 0 135 15 120 60 120 105 15 165 15 195 120 180 135 240 105 270 120 285 150 270 180 285 210 270 165 240 180 180 285 195 285 165 180 105 180 60 165 15

arrow
true
0
Polygon -7500403 true true 150 0 0 150 105 150 105 293 195 293 195 150 300 150

box
false
0
Polygon -7500403 true true 150 285 285 225 285 75 150 135
Polygon -7500403 true true 150 135 15 75 150 15 285 75
Polygon -7500403 true true 15 75 15 225 150 285 150 135
Line -16777216 false 150 285 150 135
Line -16777216 false 150 135 15 75
Line -16777216 false 150 135 285 75

bug
true
0
Circle -7500403 true true 96 182 108
Circle -7500403 true true 110 127 80
Circle -7500403 true true 110 75 80
Line -7500403 true 150 100 80 30
Line -7500403 true 150 100 220 30

butterfly
true
0
Polygon -7500403 true true 150 165 209 199 225 225 225 255 195 270 165 255 150 240
Polygon -7500403 true true 150 165 89 198 75 225 75 255 105 270 135 255 150 240
Polygon -7500403 true true 139 148 100 105 55 90 25 90 10 105 10 135 25 180 40 195 85 194 139 163
Polygon -7500403 true true 162 150 200 105 245 90 275 90 290 105 290 135 275 180 260 195 215 195 162 165
Polygon -16777216 true false 150 255 135 225 120 150 135 120 150 105 165 120 180 150 165 225
Circle -16777216 true false 135 90 30
```

```
Line -16777216 false 150 105 195 60
Line -16777216 false 150 105 105 60

car
false
0
Polygon -7500403 true true 300 180 279 164 261 144 240 135 226 132 213 106 203 84 185 63 159 50 135 50 75 60 0 150 0 165 0 225 300 225 300 180
Circle -16777216 true false 180 180 90
Circle -16777216 true false 30 180 90
Polygon -16777216 true false 162 80 132 78 134 135 209 135 194 105 189 96 180 89
Circle -7500403 true true 47 195 58
Circle -7500403 true true 195 195 58

circle
false
0
Circle -7500403 true true 0 0 300

circle 2
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240

cow
false
0
Polygon -7500403 true true 200 193 197 249 179 249 177 196 166 187 140 189 93 191 78 179 72 211 49 209 48 181 37 149 25 120 25 89 45 72 103 84 179 75 198 76 252 64 272 81 293 103 285 121 255 121 242 118 224 167
Polygon -7500403 true true 73 210 86 251 62 249 48 208
Polygon -7500403 true true 25 114 16 195 9 204 23 213 25 200 39 123

cylinder
false
0
Circle -7500403 true true 0 0 300

dot
false
```

```
0
Circle -7500403 true true 90 90 120

face happy
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 255 90 239 62 213 47 191 67 179 90 203 109 218 150 225 192 218 210 203 227 181 251 194 236 217 212 240

face neutral
false
0
Circle -7500403 true true 8 7 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Rectangle -16777216 true false 60 195 240 225

face sad
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 168 90 184 62 210 47 232 67 244 90 220 109 205 150 198 192 205 210 220 227 242 251 229 236 206 212 183

fish
false
0
Polygon -1 true false 44 131 21 87 15 86 0 120 15 150 0 180 13 214 20 212 45 166
Polygon -1 true false 135 195 119 235 95 218 76 210 46 204 60 165
Polygon -1 true false 75 45 83 77 71 103 86 114 166 78 135 60
Polygon -7500403 true true 30 136 151 77 226 81 280 119 292 146 292 160 287 170 270 195 195 210 151 212 30 166
Circle -16777216 true false 215 106 30
```

```
flag
false
0
Rectangle -7500403 true true 60 15 75 300
Polygon -7500403 true true 90 150 270 90 90 30
Line -7500403 true 75 135 90 135
Line -7500403 true 75 45 90 45

flower
false
0
Polygon -10899396 true false 135 120 165 165 180 210 180 240 150 300 165 300 195 240 195 195 165 135
Circle -7500403 true true 85 132 38
Circle -7500403 true true 130 147 38
Circle -7500403 true true 192 85 38
Circle -7500403 true true 85 40 38
Circle -7500403 true true 177 40 38
Circle -7500403 true true 177 132 38
Circle -7500403 true true 70 85 38
Circle -7500403 true true 130 25 38
Circle -7500403 true true 96 51 108
Circle -16777216 true false 113 68 74
Polygon -10899396 true false 189 233 219 188 249 173 279 188 234 218
Polygon -10899396 true false 180 255 150 210 105 210 75 240 135 240

house
false
0
Rectangle -7500403 true true 45 120 255 285
Rectangle -16777216 true false 120 210 180 285
Polygon -7500403 true true 15 120 150 15 285 120
Line -16777216 false 30 120 270 120

leaf
false
0
Polygon -7500403 true true 150 210 135 195 120 210 60 210 30 195 60 180 60 165 15 135 30 120 15 105 40 104 45 90 60 90 90 105 105 120 120 120 105 60 120 60 135 30 150 15 165 30 180 60 195 60 180 120 195 120 210 105 240 90 255 90 263 104 285 105 270 120 285 135 240 165 240 180 270 195 240 210 180 210 165 195
```

```
Polygon -7500403 true true 135 195 135 240 120 255 105 255 105 285 135 285 165 240 165 195

line
true
0
Line -7500403 true 150 0 150 300

line half
true
0
Line -7500403 true 150 0 150 150

pentagon
false
0
Polygon -7500403 true true 150 15 15 120 60 285 240 285 285 120

person
false
0
Circle -7500403 true true 110 5 80
Polygon -7500403 true true 105 90 120 195 90 285 105 300 135 300 150 225 165 300 195 300 210 285 180 195 195 90
Rectangle -7500403 true true 127 79 172 94
Polygon -7500403 true true 195 90 240 150 225 180 165 105
Polygon -7500403 true true 105 90 60 150 75 180 135 105

plant
false
0
Rectangle -7500403 true true 135 90 165 300
Polygon -7500403 true true 135 255 90 210 45 195 75 255 135 285
Polygon -7500403 true true 165 255 210 210 255 195 225 255 165 285
Polygon -7500403 true true 135 180 90 135 45 120 75 180 135 210
Polygon -7500403 true true 165 180 165 210 225 180 255 120 210 135
Polygon -7500403 true true 135 105 90 60 45 45 75 105 135 135
```

```
Polygon -7500403 true true 165 105 165 135 225 105 255 45 210 60
Polygon -7500403 true true 135 90 120 45 150 15 180 45 165 90

sheep
false
0
Rectangle -7500403 true true 151 225 180 285
Rectangle -7500403 true true 47 225 75 285
Rectangle -7500403 true true 15 75 210 225
Circle -7500403 true true 135 75 150
Circle -16777216 true false 165 76 116

square
false
0
Rectangle -7500403 true true 30 30 270 270

square 2
false
0
Rectangle -7500403 true true 30 30 270 270
Rectangle -16777216 true false 60 60 240 240

star
false
0
Polygon -7500403 true true 151 1 185 108 298 108 207 175 242 282 151 216 59 282 94 175 3 108 116 108

target
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240
Circle -7500403 true true 60 60 180
Circle -16777216 true false 90 90 120
Circle -7500403 true true 120 120 60

tree
false
0
Circle -7500403 true true 118 3 94
Rectangle -6459832 true false 120 195 180 300
```

```
Circle -7500403 true true 65 21 108
Circle -7500403 true true 116 41 127
Circle -7500403 true true 45 90 120
Circle -7500403 true true 104 74 152

triangle
false
0
Polygon -7500403 true true 150 30 15 255 285 255

triangle 2
false
0
Polygon -7500403 true true 150 30 15 255 285 255
Polygon -16777216 true false 151 99 225 223 75 224

truck
false
0
Rectangle -7500403 true true 4 45 195 187
Polygon -7500403 true true 296 193 296 150 259 134 244 104 208 104 207 194
Rectangle -1 true false 195 60 195 105
Polygon -16777216 true false 238 112 252 141 219 141 218 112
Circle -16777216 true false 234 174 42
Rectangle -7500403 true true 181 185 214 194
Circle -16777216 true false 144 174 42
Circle -16777216 true false 24 174 42
Circle -7500403 false true 24 174 42
Circle -7500403 false true 144 174 42
Circle -7500403 false true 234 174 42

turtle
true
0
Polygon -10899396 true false 215 204 240 233 246 254 228 266 215 252 193 210
Polygon -10899396 true false 195 90 225 75 245 75 260 89 269 108 261 124 240 105 225 105 210 105
Polygon -10899396 true false 105 90 75 75 55 75 40 89 31 108 39 124 60 105 75 105 90 105
Polygon -10899396 true false 132 85 134 64 107 51 108 17 150 2 192 18 192 52 169 65 172 87
```

```
Polygon -10899396 true false 85 204 60 233 54 254 72 266 85 252 107 210
Polygon -7500403 true true 119 75 179 75 209 101 224 135 220 225 175 261 128 261 81 224 74 135 88 99

wheel
false
0
Circle -7500403 true true 3 3 294
Circle -16777216 true false 30 30 240
Line -7500403 true 150 285 150 15
Line -7500403 true 15 150 285 150
Circle -7500403 true true 120 120 60
Line -7500403 true 216 40 79 269
Line -7500403 true 40 84 269 221
Line -7500403 true 40 216 269 79
Line -7500403 true 84 40 221 269

x
false
0
Polygon -7500403 true true 270 75 225 30 30 225 75 270
Polygon -7500403 true true 30 75 75 30 270 225 225 270

@#$#@#$#@
NetLogo 5.0.3
@#$#@#$#@
@#$#@#$#@
@#$#@#$#@
<experiments>
  <experiment name="info fp" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <final>export-plot "Trait" (word "infoshare/screenshots/fp" fmap "_" run# ".csv")
display-elevation
export-view (word "infoshare/screenshots/fp" fmap "_" run# ".png")</final>
    <timeLimit steps="100000"/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [acopyrate] of agents</metric>
    <metric>(word "screenshots/fp" fmap "_" run# ".csv")</metric>
```

```
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    </enumeratedValueSet>
    <enumeratedValueSet variable="N">
      <value value="500"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="maptype">
      <value value="&quot;fitness&quot;"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mode">
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      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.80&quot;"/>
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    <enumeratedValueSet variable="copyrate">
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    <enumeratedValueSet variable="death-rate">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-rate">
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    </enumeratedValueSet>
  </experiment>
  <experiment name="info pp" repetitions="1" runMetricsEveryStep="false">
```

```
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    <go>go</go>
    <final>export-plot "Trait" (word "infoshare/screenshots/pp" fmap "_" run# ".csv")
display-elevation
export-view (word "infoshare/screenshots/pp" fmap "_" run# ".png")</final>
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    <metric>count agents</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [acopyrate] of agents</metric>
    <metric>(word "screenshots/pp" fmap "_" run# ".csv")</metric>
    <metric>(word "screenshots/pp" fmap "_" run# ".png")</metric>
    <enumeratedValueSet variable="random-seed">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mode">
      <value value="&quot;info&quot;"/>
    </enumeratedValueSet>
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    <enumeratedValueSet variable="fmap">
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      <value value="&quot;2.40&quot;"/>
      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.80&quot;"/>
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    <enumeratedValueSet variable="colonize?">
      <value value="true"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="copyrate">
      <value value="0"/>
    </enumeratedValueSet>
```

```
    <enumeratedValueSet variable="birth-rate">
      <value value="0.1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="death-rate">
      <value value="0.06"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-size">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-rate">
      <value value="0.0010"/>
    </enumeratedValueSet>
  </experiment>
  <experiment name="info fp &gt; N" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <final>export-plot "Trait" (word "infoshare/screenshots/fixed" fmap "_" run# "_" N ".csv")</final>
    <timeLimit steps="100000"/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [acopyrate] of agents</metric>
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      <value value="2000"/>
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mode">
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    </enumeratedValueSet>
    <steppedValueSet variable="run#" first="1" step="10" last="100"/>
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    </enumeratedValueSet>
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      <value value="0.2"/>
```

```
    </enumeratedValueSet>
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    <enumeratedValueSet variable="colonize?">
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    <enumeratedValueSet variable="mutation-size">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-rate">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="copyrate">
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    </enumeratedValueSet>
  </experiment>
  <experiment name="radius pp" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <final>export-plot "Trait" (word "fsdist/screenshots/pp" fmap "_" run# "_" foresight ".csv")
display-elevation
export-view (word "fsdist/screenshots/pp" fmap "_" run# "_" foresight ".png")</final>
    <timeLimit steps="100000"/>
    <metric>nummap</metric>
    <metric>count agents</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [fsdist] of agents</metric>
    <metric>(word "screenshots/pp" fmap "_" run# "_" foresight ".csv")</metric>
    <metric>(word "screenshots/pp" fmap "_" run# "_" foresight ".png")</metric>
    <enumeratedValueSet variable="random-seed">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="N">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="maptype">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mode">
```

```
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      <value value="&quot;2.99&quot;"/>
      <value value="&quot;2.20&quot;"/>
      <value value="&quot;2.40&quot;"/>
      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.80&quot;"/>
    </enumeratedValueSet>
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    <enumeratedValueSet variable="birth-rate">
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    <enumeratedValueSet variable="death-rate">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-size">
      <value value="0.5"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-rate">
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    </enumeratedValueSet>
  </experiment>
  <experiment name="radius fp" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
    <final>export-plot "Trait" (word "fsdist/screenshots/fp" fmap "_" run# "_" foresight ".csv")
display-elevation
export-view (word "fsdist/screenshots/fp" fmap "_" run# "_" foresight ".png")</final>
    <timeLimit steps="100000"/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [fsdist] of agents</metric>
    <metric>(word "screenshots/fp" fmap "_" run# "_" foresight ".csv")</metric>
```

```
    <metric>(word "screenshots/fp" fmap "_" run# "_" foresight ".png")</metric>
    <enumeratedValueSet variable="random-seed">
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    </enumeratedValueSet>
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    </enumeratedValueSet>
    <enumeratedValueSet variable="maptype">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mode">
      <value value="&quot;radius&quot;"/>
    </enumeratedValueSet>
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    <enumeratedValueSet variable="fmap">
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      <value value="&quot;2.99&quot;"/>
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      <value value="&quot;2.60&quot;"/>
      <value value="&quot;2.80&quot;"/>
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    <enumeratedValueSet variable="birth-rate">
      <value value="0.1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="death-rate">
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    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-size">
      <value value="0.5"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-rate">
      <value value="0.0010"/>
    </enumeratedValueSet>
  </experiment>
  <experiment name="radius fp &gt; N" repetitions="1" runMetricsEveryStep="false">
    <setup>setup</setup>
    <go>go</go>
```

```
    <final>export-plot ”Trait” (word ”fsdist/screenshots/fp” fmap ”_” run# ”_” foresight ”_” N ”.csv”)</final>
    <timeLimit steps=”100000”/>
    <metric>nummap</metric>
    <metric>mean [elevation] of agents</metric>
    <metric>mean [fsdist] of agents</metric>
    <enumeratedValueSet variable=”random-seed”>
      <value value=”1”/>
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      <value value=”1000”/>
      <value value=”2000”/>
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    <enumeratedValueSet variable=”mode”>
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    </enumeratedValueSet>
    <steppedValueSet variable=”run#” first=”1” step=”10” last=”100”/>
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    </enumeratedValueSet>
    <enumeratedValueSet variable=”foresight”>
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    </enumeratedValueSet>
    <enumeratedValueSet variable=”mutation-size”>
      <value value=”0.5”/>
    </enumeratedValueSet>
    <enumeratedValueSet variable=”mutation-rate”>
      <value value=”0.0010”/>
    </enumeratedValueSet>
    <enumeratedValueSet variable=”birth-rate”>
      <value value=”0.5”/>
    </enumeratedValueSet>
    <enumeratedValueSet variable=”death-rate”>
      <value value=”0”/>
    </enumeratedValueSet>
  </experiment>
</experiments>
@#$#@#$#@
@#$#@#$#@
```

```
default
0.0
-0.2 0 1.0 0.0
0.0 1 1.0 0.0
0.2 0 1.0 0.0
link direction
true
0
Line -7500403 true 150 150 90 180
Line -7500403 true 150 150 210 180

@#$#@#$#@
0
@#$#@#$#@
```

A.3 Code for chapter 4

Download link: http://www.openabm.org/model/4178/

```
extensions [ gis profiler ]

breed [agents agent]

globals
[
  elevation-dataset
  max-elev
  nummap
  speed
  exits
  total-exits
  total-exit-trait
  exit-first-tick
  exit-maxpop-tick
  poplist
]

agents-own
[
  trait
  pop
  aforesight
  acopyrate
  fsdist
]

patches-own
```

```
[
  elevation
  currentelev
  timestamp
  occfreq
  cum-effit
]

;SETUP CODE ########################################

to setup
  ;random-seed 1
  ca
  set nummap 0
  if first fmap = "2"
  [
    gis:load-coordinate-system (word "surfeq/surf.prj")
    set elevation-dataset gis:load-dataset (word "surfeq/" fmap "/" run# ".asc")
    gis:set-world-envelope (gis:envelope-of elevation-dataset)
    set nummap read-from-string fmap
  ]
  if fmap = "cone"
  [
    if run# > 9 [set run# 1]
    gis:load-coordinate-system (word "surfeq/surf.prj")
    set elevation-dataset gis:load-dataset (word "surfeq/" fmap "/" run# ".asc")
    gis:set-world-envelope (gis:envelope-of elevation-dataset)
  ]
  gis:apply-raster elevation-dataset elevation

  ;Test of the hypothesis that cells with very small values were affecting wave velocity
  ;ask patches [set elevation elevation + 100]

  display-elevation
  set max-elev gis:maximum-of elevation-dataset

  create-agents N
  [
    set shape "square"
```

```
    ifelse colonize? = TRUE [ ;unlike the previous models, this places agents in a clump at the center of the map
      let midpx round(max-pxcor / 2)
      let midpy round(max-pycor / 2)
      setxy midpx midpy
    ]
    [;else random placement, not used in article
      setxy round random-xcor round random-ycor
      while [ elevation <= 0 OR count agents-here > 1] [ setxy round random-xcor round random-ycor ]
    ]
    if N = 1 [setxy 50 50] ; runs in article always start with one agent at the map center (N = 1)
    ifelse randTrait? = false ;assign trait value from interface slider
    [
      if mode = "foresight" [set aforesight aforesight color-gradient aforesight]
      if mode = "info" OR mode = "infowave" [set acopyrate copyrate color-gradient acopyrate set shape "default"]
      if mode = "radius" [set fsdist 1 color-gradient ( fsdist / 2 )]
    ]
    [;else randTrait?
      if mode = "foresight" [set aforesight random-float 1 color-gradient aforesight]
      if mode = "info" OR mode = "infowave" [set acopyrate random-float 1 color-gradient acopyrate]
      if mode = "radius" [
        set fsdist 1 + plus-or-minus mutation-size
        if fsdist < 0 [set fsdist 0]
        color-gradient ( fsdist / 2 )
      ]
    ];close randTrait?
    set aforesight foresight
    set pop 1 ;group size variable of each agent, begins with 1
  ]; close agents

;  ask patches [set timestamp 0 set occfreq 0 set currentelev elevation ]
  ask patches [set cum-effit 0]
```

```
  reset-ticks
end

;GO CODE ##########################################

to go
  if (mode = "fswave") [go-fswave]
  if (mode = "infowave") [go-infowave]

  if not any? agents [stop]


  ;;;; mapping different variables, not used in article
  ;if maptype = "ticks" [display-ticks]
  ;if maptype = "fitness" [if one-of [hidden?] of agents = TRUE [display-elevation]]
  ;if maptype = "occfreq" [display-occfreq]
  ;if maptype = "effit" [display-effit]

  tick
end

to go-fswave
  ask agents
  [
    repeat pop
    [
      reproduce ;submodule below
      move-fswave ;submodule below
    ]

    if pop = 0 [ die ]
    set color scale-color green pop 0 110 ; misses just born agents (created inside this loop)
  ]
  exit-count ;submodule below
end

to go-infowave ;wave of advance by information sharing agents, removed from final version of article
  ask agents
  [
    repeat pop
    [
      reproduce ;submodule below
```

```
    ]
  ]

  ;;;; create a list of all individuals of all agents
  set poplist (list)
  ask agents [set poplist lput self poplist]
  foreach poplist [
    ask ?1 [repeat (pop - 1) [set poplist lput self poplist]]
  ]

  ask agents
  [
    repeat pop
    [
      move-infowave ;submodule below
      die-by-rate-wave ;submodule below
    ]
    if pop = 0 [ die ]
    set color scale-color green pop 0 100
  ]
  exit-count
end

to reproduce ;each individual in the group (agent) has birth-rate prob of increasing subject to current pop dens
  if (random-float 1 < (1 - (pop / elevation))); AND random-float 1 < birth-rate);decomment last section if birth-rate not 100%
    [
      set pop pop + 1
    ]
end

to move-fswave ;each i of pop moves to new cell subject to local pop dens
  let p patch 1 1 ;create temporary variable for holding a patch
  ifelse random-float 1 < foresight [set p max-one-of neighbors [elevation]][set p one-of neighbors] ; selects best or random patch based on foresight probability
```

```
  ifelse any? agents-on p ;if occupied move individual to that cell by increasing target pop and decreasing origin pop
    [
      if sum [pop] of agents-on p < [elevation] of p [ ; have to limit because foresighted movement can exceed carrying cacpacity
        ask agents-on p [ set pop pop + 1 ]
        set pop pop - 1
      ]
    ]
    [;else no agents-on p, move by creating new agent on target and decreasing origin pop
      hatch 1 [move-to p set pop 1 set color black]
      set pop pop - 1
    ]
end

to move-infowave
  let a one-of poplist
  while [is-agent? a = false][set a one-of poplist]
  let p one-of neighbors
  let move? true
  ifelse random-float 1 < copyrate
  [
    ifelse [elevation] of a > elevation [face a][set move? false] ;biased copying
  ]
  [;else non-copy
    face p
  ] ;face a is unbiased copying, except that its weighted by pop size
  if move? = true [ ;adjusted to stop movement in case a is worse
    set p patch-ahead 1
    ifelse any? agents-on p
    [
      if sum [pop] of agents-on p < [elevation] of p [ ; have to limit because foresighted movement can exceed carrying cacpacity
        ask agents-on p [ set pop pop + 1 ]
        set pop pop - 1
      ]
    ]
    [;else no agents-on p = 100% of moving
```

```
      hatch 1 [move-to p set pop 1]
      set pop pop - 1
    ]
  ]
end

to die-by-rate-wave ;not used in article, just adds noise
  if death-rate > 0 [
    if (random-float 1 < death-rate)
      [
        set pop pop - 1
        if pop = 0 [die]
      ]
  ];close death
end

to exit-count
  ask agents with [xcor = 0 OR xcor = 99 OR ycor = 0 OR ycor = 99] ;any agents on the outside edge of the map
  [
    die!-wave ;submodule below
  ]
end

to die!-wave ;record tick of first agent to reach map edge and output a screenshot
;  set exits exits + pop
;  set total-exits total-exits + pop
;  set total-exit-trait total-exit-trait + acopyrate * pop
  ifelse fmap = "cone" [
    if exit-first-tick = 0 AND behaviorspace-run-number > 0 [set exit-first-tick ticks export-view (word "exit/screenshots/waves/" foresight "_" fmap "_" run# "_" behaviorspace-run-number ".png")]
    if exit-first-tick = 0 [set exit-first-tick ticks export-view (word "exit/screenshots/waves/" foresight "_" fmap "_" run# "_" behaviorspace-run-number ".png")]
    ;if exit-first-tick = 0 AND behaviorspace-run-number > 0 [set exit-first-tick ticks export-view (word "exit/screenshots/wavescd/" copyrate "_" fmap "_" run# "_" behaviorspace-run-number ".png")]
```

```
  ][; else
    if exit-first-tick = 0 [set exit-first-tick ticks export-view (word "exit/screenshots/waves/" foresight "_" fmap "_" run# ".png")]
    ;if exit-first-tick = 0 [set exit-first-tick ticks export-view (word "exit/screenshots/wavescd/" copyrate "_" fmap "_" run# ".png")]
  ]
  die ;not really needed since runs end with the first exit
end

to patch-calcs [maxfit] ;not used in article
  let effit 0
  ask patches
  [
    if timestamp = 0 [if any? agents-here = TRUE [set timestamp ticks]]
    if timestamp > 0 AND any? agents-here = TRUE [set occfreq occfreq + count agents-here]
    let basefit ( elevation / maxfit * birth-rate)
    ifelse (count agents-on neighbors < 8) [set effit basefit][set effit 0]
    set cum-effit cum-effit + effit
  ]
end

to display-ticks
  ask agents [set hidden? true]
  ask patches
  [
    if (timestamp > 0)
    [
      set pcolor scale-color red timestamp 0 ticks
    ]
  ]
end

to display-occfreq
  let max-occfreq max [occfreq] of patches
  ask agents [set hidden? true]
  ask patches
  [
    if (occfreq > 0)
    [
```

```
      set pcolor scale-color red occfreq 0 max-occfreq
    ]
  ]
end

to display-elevation
  ; This is the preferred way of copying values from a raster dataset
  ; into a patch variable: in one step, using gis:apply-raster.
  ;gis:apply-raster elevation-dataset elevation
  ; Now, just to make sure it worked, we'll color each patch by its
  ; elevation value.
  let min-elevation gis:minimum-of elevation-dataset
  let max-elevation gis:maximum-of elevation-dataset
  ;let min-elevation min [elevation] of patches
  ;let max-elevation max [elevation] of patches

  ask patches
  [ ;
    set pcolor 99
    if (elevation > 0) [set pcolor scale-color black elevation min-elevation max-elevation ]
  ]
  ask agents [set hidden? false]
end

to export-map [folder]
  ;  ask patches
  ;  [
  ;    if any? agents-here
  ;    [
  ;      set agent-trait [trait] of one-of agents-here
  ;    ]
  ;  ]

  ;** Create raster dataset
  let occraster gis:create-raster world-width world-height gis:world-envelope
  ;** Transfer agent's trait value of each netlogo patch to the occraster layer
  set occraster gis:patch-dataset occfreq

  ;** At last store the data in file
```

```
  ;gis:store-dataset occraster (word "occraster/" nummap "_" run# "_f" round (foresight * 100) ".asc")
  ;  ifelse (mode = "infoshare")
  ;  [
  ;    gis:store-dataset occraster (word folder remove "f" fmap "_" run# "_cr" round (copyrate * 100) "_f" round (foresight * 100) ".asc")
  ;    gis:store-dataset occraster (word "infoshare/occraster/uh/" remove "f" fmap "_" run# "_cr" round (copyrate * 100) ".asc")
  ;    gis:store-dataset occraster (word "infoshare/occraster/br/" remove "f" fmap "_" run# "_cr" round (copyrate * 100) ".asc")
  ;  ]
  ;  [;else
  ;gis:store-dataset occraster (word "occraster/" remove "f" fmap "_" run# "_f" round (foresight * 100) ".asc")
  ;gis:store-dataset occraster (word folder "/" fmap "_" run# "m_" mutation-size ".asc")
  gis:store-dataset occraster (word folder "/" fmap "_" run# "br_" birth-rate ".asc")
  ;  ]
  ;  gis:store-dataset occraster (word "occraster/" fmap "_f" round (foresight * 100) ".asc")
  ;(word "occraster/" fmap "/" colonize? "/" "f" round (foresight * 100) ".png")
end


to color-gradient [number]
  ;ifelse (number < 0.5) [set color [255 ( number * 255) ( number * 255)]] [set color [( number * 255) ( number * 255) 255]]
  ifelse (number <= 0.5) [set color red + ( number * 9.99 )] [set color 114 - (number * 9.99) ]
end

to-report plus-or-minus [ value ]
  ; randomly reports either +value or -value
  report value * (((random 2) * 2) - 1)
  ; explanation of "(((random 2) * 2) - 1)"
  ; Operation:     Yields:
  ; random 2   -> 0            or 1
  ;       * 2  -> 0 * 2 =  0   or 1 * 2 = 2
```

```
  ;        - 1    -> 0 - 1 = -1  or 2 - 1 = 1
  ; thus, returns -1 or +1
end

to display-effit
  ;init set cum-effit 0 in setup
  ;add cum-effit to patches-own
  ;add to maptype chooser
  ;add display to go
  ;let effit 0
  ;let maxfit max [elevation] of agents + 1
  let max-cum-effit max [cum-effit] of patches
  ask agents [set hidden? true]
  ask patches
  [
    ;  let basefit ( elevation / maxfit )
    ;  ifelse (count agents-on neighbors < 8) [set effit basefit][set effit 0]
    ;  set cum-effit cum-effit + effit
    set pcolor scale-color green cum-effit 0 max-cum-effit
  ]
end
@#$#@#$#@
GRAPHICS-WINDOW
304
10
814
541
-1
-1
5.0
1
10
1
1
1
0
0
0
1
0
99
0
99
```

```
1
1
1
ticks
1000.0

BUTTON
15
9
78
42
setup
setup
NIL
1
T
OBSERVER
NIL
S
NIL
NIL
1

BUTTON
15
41
78
74
go
;ifelse ticks != 50000 [go][stop]\n;ifelse ticks != 499 [go][stop]\nifelse exit-first-tick = 0 [go][stop]\n;go\n
T
1
T
OBSERVER
NIL
G
NIL
NIL
1

BUTTON
15
74
```

```
78
107
step
go
NIL
1
T
OBSERVER
NIL
NIL
NIL
NIL
1

SLIDER
118
180
290
213
N
N
0
2000
1
100
1
NIL
HORIZONTAL

CHOOSER
118
12
281
57
mode
mode
"fswave" "infowave"
0

CHOOSER
118
57
256
102
fmap
```

```
fmap
"2.001" "2.20" "2.25" "2.40" "2.50" "2.60" "2.75" "2.80" "2.999" "cone" "i0" "i10" "i20" "i40" "i60" "i80" "i100"
9

SLIDER
118
213
290
246
foresight
foresight
0
1
0
.05
1
NIL
HORIZONTAL

CHOOSER
118
135
256
180
maptype
maptype
"fitness" "ticks" "occfreq" "effit"
0

SLIDER
118
102
256
135
run#
run#
1
100
9
1
1
NIL
HORIZONTAL
```

```

SLIDER
814
10
984
43
birth-rate
birth-rate
0
1
1
0.1
1
NIL
HORIZONTAL

SLIDER
814
43
984
76
death-rate
death-rate
0
birth-rate
0.25
0.01
1
NIL
HORIZONTAL

SWITCH
15
140
105
173
colonize?
colonize?
0
1
-1000

SLIDER
118
246
```

```
290
279
copyrate
copyrate
0
1
0
0.05
1
NIL
HORIZONTAL

PLOT
3
509
244
629
Pop
ticks
Pop
0.0
10.0
0.0
10.0
true
false
"" ";ask agents [measure-total-distance]"
PENS
"Default" 1.0 0 -16777216 true "" ";plotxy ticks count agents"
"pen-1" 1.0 0 -7500403 true "" ";plotxy ticks sum [pop] of agents"

PLOT
3
378
245
509
Trait
ticks
Trait
0.0
1.0
0.0
1.0
```

```
true
false
"" ""
PENS
"Median" 100.0 0 -16777216 true "" ";plotxy ticks mean [acopyrate] of agents"

MONITOR
245
378
295
423
MedC
median [acopyrate] of agents
2
1
11

SLIDER
118
279
290
312
mutation-size
mutation-size
0
.5
0
0.01
1
NIL
HORIZONTAL

BUTTON
250
103
305
136
rand
set run# random 100 + 1
NIL
1
T
OBSERVER
NIL
```

```
NIL
NIL
NIL
1

PLOT
304
541
504
691
Effective fitness
NIL
NIL
0.0
100.0
0.0
1.0
true
false
"" ""
PENS
"default" 1.0 0 -16777216 true "" "clear-plot\nif plots-on? = TRUE [\nlet env 0\nwhile [env <= 100 AND ticks > 0][\n  set env env + 1\n  let patch-env patch-set patches with [elevation = env]\n  if any? patch-env [ plotxy env mean [cum-effit] of patch-env ]\n  ]\n  ]"

SWITCH
15
206
105
239
randTrait?
randTrait?
1
1
-1000

SLIDER
118
311
290
344
mutation-rate
mutation-rate
```

```
0
.1
0
.001
1
NIL
HORIZONTAL

SWITCH
15
239
105
272
plots-on?
plots-on?
1
1
-1000

MONITOR
245
423
295
468
MedR
median [fsdist] of agents
2
1
11

PLOT
504
541
704
691
Dispersal
Ticks
Dispersal rate
0.0
100.0
0.0
0.01
true
false
"" ""
```

```
PENS
"default" 100.0 0 -16777216 true "" ";plotxy ticks exits"

BUTTON
831
154
906
187
profiler
;setup                    ;; set up the model\nprofiler:start          ;; start profiling\nrepeat 10 [ go ]        ;; run something you want to measure\nprofiler:stop           ;; stop profiling\nprint profiler:report   ;; view the results\n;print profiler:exclusive-time \"patch-calcs\"\nprofiler:reset          ;; clear the data
NIL
1
T
OBSERVER
NIL
NIL
NIL
NIL
1

PLOT
705
541
905
691
Wave
X axis
Pop
0.0
100.0
0.0
100.0
true
false
"" ""
PENS
```

```
"default" 1.0 0 -16777216 true "" "if waveplot-on? = true [\nclear-plot\nlet i 1\nwhile [i <= max-pxcor] \n[\n  plotxy i sum [pop] of agents-on patch i 50 \n  set i i + 1\n  ]\n]"

SLIDER
814
76
984
109
move-rate
move-rate
0
1
1
.1
1
NIL
HORIZONTAL

SWITCH
912
541
1051
574
waveplot-on?
waveplot-on?
1
1
-1000

MONITOR
244
509
301
554
Pop
count agents
0
1
11

MONITOR
244
553
```

```
301
598
Pop
sum [pop] of agents
0
1
11

@#$#@#$#@
## WHAT IS IT?

Agent-based model that measures the velocity of a Fisher (1937) wave of advance enhanced by hominin cognition. A related earlier model may be found here: http://www.openabm.org/model/3846/

Our proxy for cognition is the accuracy at which agents assess their resource environment.

## HOW IT WORKS

There are two variations of the model, "fswave" and "infowave". In each, agents have their own population of individuals and effectively the model runs on these sub-agents. Sub-agents reproduce and move to selected neighbouring cells. In fswave, sub-agents move to the highest resource cell in their neighbourhood at probability "foresight", or randomly otherwise.

In "infowave", sub-agents copy resource information from another random sub-agent, or move randomly otherwise according to probability copyrate. When copying, agents move one cell towards the target sub-agent if they occupy a higher resource cell.

## HOW TO USE IT

Maps are not generated by NetLogo. Download the map set as well which (includes a bash script for generating your own with GRASS GIS). Unzip the surfeq folder into the same folder as this nlogo file.

```

```
Choose a heterogeneity value from the "fmap" list running from 2.001 (least heterogeneous) to 2.999 (most heterogenous). Click rand to choose 1 of the 100 randomly generated surfaces at the selected heterogeneity level. Alternatively, choose "cone" and run# 1-8 for plains, corridors, gradients, and patches of resources. Optionally also adjust other initial parameters. Setup and Go to run.

See the BehaviourSpace dialog for the run sets used in the article.

Velocity may be calculated using exit-first-tick / 50.

## THINGS TO NOTICE

Wave velocity generally decreases with increased "foresight", resource assessment accuracy, or with increased "copyrate", probability of copying environmental resource knowledge. The fastest velocity occurs as a random walk.

## CREDITS AND REFERENCES

Colin D. Wren wrote this model as a part of his PhD dissertation at McGill University. An article stemming from the "fswave" model was submitted to a special issue of the Journal of Human Evolution under the title, Putting (hominin) thought into hominin dispersal.
@#$#@#$#@
default
true
0
Polygon -7500403 true true 150 5 40 250 150 205 260 250

airplane
true
0
Polygon -7500403 true true 150 0 135 15 120 60 120 105 15 165 15 195 120 180 135 240 105 270 120 285 150 270 180 285 210 270 165 240 180 180 285 195 285 165 180 105 180 60 165 15

arrow
```

```
true
0
Polygon -7500403 true true 150 0 0 150 105 150 105 293 195 293 195 150 300 150

box
false
0
Polygon -7500403 true true 150 285 285 225 285 75 150 135
Polygon -7500403 true true 150 135 15 75 150 15 285 75
Polygon -7500403 true true 15 75 15 225 150 285 150 135
Line -16777216 false 150 285 150 135
Line -16777216 false 150 135 15 75
Line -16777216 false 150 135 285 75

bug
true
0
Circle -7500403 true true 96 182 108
Circle -7500403 true true 110 127 80
Circle -7500403 true true 110 75 80
Line -7500403 true 150 100 80 30
Line -7500403 true 150 100 220 30

butterfly
true
0
Polygon -7500403 true true 150 165 209 199 225 225 225 255 195 270 165 255 150 240
Polygon -7500403 true true 150 165 89 198 75 225 75 255 105 270 135 255 150 240
Polygon -7500403 true true 139 148 100 105 55 90 25 90 10 105 10 135 25 180 40 195 85 194 139 163
Polygon -7500403 true true 162 150 200 105 245 90 275 90 290 105 290 135 275 180 260 195 215 195 162 165
Polygon -16777216 true false 150 255 135 225 120 150 135 120 150 105 165 120 180 150 165 225
Circle -16777216 true false 135 90 30
Line -16777216 false 150 105 195 60
Line -16777216 false 150 105 105 60

car
false
0
```

```
Polygon -7500403 true true 300 180 279 164 261 144 240 135 226 132 213 106 203 84 185 63 159 50 135 50 75 60 0 150 0 165 0 225 300 225 300 180
Circle -16777216 true false 180 180 90
Circle -16777216 true false 30 180 90
Polygon -16777216 true false 162 80 132 78 134 135 209 135 194 105 189 96 180 89
Circle -7500403 true true 47 195 58
Circle -7500403 true true 195 195 58

circle
false
0
Circle -7500403 true true 0 0 300

circle 2
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240

cow
false
0
Polygon -7500403 true true 200 193 197 249 179 249 177 196 166 187 140 189 93 191 78 179 72 211 49 209 48 181 37 149 25 120 25 89 45 72 103 84 179 75 198 76 252 64 272 81 293 103 285 121 255 121 242 118 224 167
Polygon -7500403 true true 73 210 86 251 62 249 48 208
Polygon -7500403 true true 25 114 16 195 9 204 23 213 25 200 39 123

cylinder
false
0
Circle -7500403 true true 0 0 300

dot
false
0
Circle -7500403 true true 90 90 120

face happy
false
0
```

```
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 255 90 239 62 213 47 191 67 179 90 203 109 218 150 225 192 218 210 203 227 181 251 194 236 217 212 240

face neutral
false
0
Circle -7500403 true true 8 7 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Rectangle -16777216 true false 60 195 240 225

face sad
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 168 90 184 62 210 47 232 67 244 90 220 109 205 150 198 192 205 210 220 227 242 251 229 236 206 212 183

fish
false
0
Polygon -1 true false 44 131 21 87 15 86 0 120 15 150 0 180 13 214 20 212 45 166
Polygon -1 true false 135 195 119 235 95 218 76 210 46 204 60 165
Polygon -1 true false 75 45 83 77 71 103 86 114 166 78 135 60
Polygon -7500403 true true 30 136 151 77 226 81 280 119 292 146 292 160 287 170 270 195 195 210 151 212 30 166
Circle -16777216 true false 215 106 30

flag
false
0
Rectangle -7500403 true true 60 15 75 300
Polygon -7500403 true true 90 150 270 90 90 30
Line -7500403 true 75 135 90 135
```

```
Line -7500403 true 75 45 90 45

flower
false
0
Polygon -10899396 true false 135 120 165 165 180 210 180 240 150 300 165 300 195 240 195 195 165 135
Circle -7500403 true true 85 132 38
Circle -7500403 true true 130 147 38
Circle -7500403 true true 192 85 38
Circle -7500403 true true 85 40 38
Circle -7500403 true true 177 40 38
Circle -7500403 true true 177 132 38
Circle -7500403 true true 70 85 38
Circle -7500403 true true 130 25 38
Circle -7500403 true true 96 51 108
Circle -16777216 true false 113 68 74
Polygon -10899396 true false 189 233 219 188 249 173 279 188 234 218
Polygon -10899396 true false 180 255 150 210 105 210 75 240 135 240

house
false
0
Rectangle -7500403 true true 45 120 255 285
Rectangle -16777216 true false 120 210 180 285
Polygon -7500403 true true 15 120 150 15 285 120
Line -16777216 false 30 120 270 120

leaf
false
0
Polygon -7500403 true true 150 210 135 195 120 210 60 210 30 195 60 180 60 165 15 135 30 120 15 105 40 104 45 90 60 90 90 105 105 120 120 120 105 60 120 60 135 30 150 15 165 30 180 60 195 60 180 120 195 120 210 105 240 90 255 90 263 104 285 105 270 120 285 135 240 165 240 180 270 195 240 210 180 210 165 195
Polygon -7500403 true true 135 195 135 240 120 255 105 255 105 285 135 285 165 240 165 195

line
true
0
```

```
Line -7500403 true 150 0 150 300

line half
true
0
Line -7500403 true 150 0 150 150

pentagon
false
0
Polygon -7500403 true true 150 15 15 120 60 285 240 285 285 120

person
false
0
Circle -7500403 true true 110 5 80
Polygon -7500403 true true 105 90 120 195 90 285 105 300 135 300 150 225 165 300 195 300 210 285 180 195 195 90
Rectangle -7500403 true true 127 79 172 94
Polygon -7500403 true true 195 90 240 150 225 180 165 105
Polygon -7500403 true true 105 90 60 150 75 180 135 105

plant
false
0
Rectangle -7500403 true true 135 90 165 300
Polygon -7500403 true true 135 255 90 210 45 195 75 255 135 285
Polygon -7500403 true true 165 255 210 210 255 195 225 255 165 285
Polygon -7500403 true true 135 180 90 135 45 120 75 180 135 210
Polygon -7500403 true true 165 180 165 210 225 180 255 120 210 135
Polygon -7500403 true true 135 105 90 60 45 45 75 105 135 135
Polygon -7500403 true true 165 105 165 135 225 105 255 45 210 60
Polygon -7500403 true true 135 90 120 45 150 15 180 45 165 90

sheep
```

```
false
0
Rectangle -7500403 true true 151 225 180 285
Rectangle -7500403 true true 47 225 75 285
Rectangle -7500403 true true 15 75 210 225
Circle -7500403 true true 135 75 150
Circle -16777216 true false 165 76 116

square
false
0
Rectangle -7500403 true true 30 30 270 270

square 2
false
0
Rectangle -7500403 true true 30 30 270 270
Rectangle -16777216 true false 60 60 240 240

star
false
0
Polygon -7500403 true true 151 1 185 108 298 108 207 175 242 282 151 216 59 282 94 175 3 108 116 108

target
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240
Circle -7500403 true true 60 60 180
Circle -16777216 true false 90 90 120
Circle -7500403 true true 120 120 60

tree
false
0
Circle -7500403 true true 118 3 94
Rectangle -6459832 true false 120 195 180 300
Circle -7500403 true true 65 21 108
Circle -7500403 true true 116 41 127
Circle -7500403 true true 45 90 120
Circle -7500403 true true 104 74 152

triangle
```

```
false
0
Polygon -7500403 true true 150 30 15 255 285 255

triangle 2
false
0
Polygon -7500403 true true 150 30 15 255 285 255
Polygon -16777216 true false 151 99 225 223 75 224

truck
false
0
Rectangle -7500403 true true 4 45 195 187
Polygon -7500403 true true 296 193 296 150 259 134 244 104 208 104 207 194
Rectangle -1 true false 195 60 195 105
Polygon -16777216 true false 238 112 252 141 219 141 218 112
Circle -16777216 true false 234 174 42
Rectangle -7500403 true true 181 185 214 194
Circle -16777216 true false 144 174 42
Circle -16777216 true false 24 174 42
Circle -7500403 false true 24 174 42
Circle -7500403 false true 144 174 42
Circle -7500403 false true 234 174 42

turtle
true
0
Polygon -10899396 true false 215 204 240 233 246 254 228 266 215 252 193 210
Polygon -10899396 true false 195 90 225 75 245 75 260 89 269 108 261 124 240 105 225 105 210 105
Polygon -10899396 true false 105 90 75 75 55 75 40 89 31 108 39 124 60 105 75 105 90 105
Polygon -10899396 true false 132 85 134 64 107 51 108 17 150 2 192 18 192 52 169 65 172 87
Polygon -10899396 true false 85 204 60 233 54 254 72 266 85 252 107 210
Polygon -7500403 true true 119 75 179 75 209 101 224 135 220 225 175 261 128 261 81 224 74 135 88 99

wheel
false
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Circle -16777216 true false 30 30 240
Line -7500403 true 150 285 150 15
Line -7500403 true 15 150 285 150
Circle -7500403 true true 120 120 60
Line -7500403 true 216 40 79 269
Line -7500403 true 40 84 269 221
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Line -7500403 true 84 40 221 269

x
false
0
Polygon -7500403 true true 270 75 225 30 30 225 75 270
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NetLogo 5.0
@#$#@#$#@
@#$#@#$#@
@#$#@#$#@
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display-effit
export-view (word "infoshare/screenshots/fp_ef" fmap "_" run# ".png")</final>
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    run# ".png")
display-effit
export-view (word "infoshare/screenshots/pp_ef" fmap "_"
      run# ".png")</final>
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display-elevation
export-view (word "fsdist/screenshots/pp" fmap "_" run#
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display-effit
export-view (word "fsdist/screenshots/pp_ef" fmap "_"
    run# ".png")</final>
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export-view (word "fsdist/screenshots/fp" fmap "_" run#
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display-effit
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    <metric>total-exits / ticks</metric>
    <metric>(word "screenshots/wavescd/" copyrate "_"
        fmap "_" run# "_" behaviorspace-run-number ".csv
        ")</metric>
    <metric>(word "screenshots/wavescd/" copyrate "_"
        fmap "_" run# "_" behaviorspace-run-number ".png
        ")</metric>
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      <value value="1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="maptype">
      <value value="&quot;fitness&quot;"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mode">
      <value value="&quot;infowave&quot;"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="run#">
      <value value="7"/>
      <value value="8"/>
      <value value="9"/>
      <value value="3"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="fmap">
      <value value="&quot;cone&quot;"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="colonize?">
      <value value="true"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="copyrate">
      <value value="0"/>
      <value value="0.25"/>
      <value value="0.5"/>
      <value value="0.75"/>
```

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      <value value="0.99"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="birth-rate">
      <value value="1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="death-rate">
      <value value="0.25"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="move-rate">
      <value value="1"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-size">
      <value value="0"/>
    </enumeratedValueSet>
    <enumeratedValueSet variable="mutation-rate">
      <value value="0"/>
    </enumeratedValueSet>
  </experiment>
</experiments>
@#$#@#$#@
@#$#@#$#@
default
0.0
-0.2 0 1.0 0.0
0.0 1 1.0 0.0
0.2 0 1.0 0.0
link direction
true
0
Line -7500403 true 150 150 90 180
Line -7500403 true 150 150 210 180

@#$#@#$#@
0
@#$#@#$#@
```