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Does Environmental Knowledge Inhibit Hominin Dispersal?

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Abstract

We investigate the relationship between the dispersal potential of a hominin population, its local scale foraging strategies, and the characteristics of the resource environment using an agent-based modeling approach. Wren et al. (2014) demonstrated that natural selection can favour a relatively low capacity for assessing and predicting the quality of the resource environment, especially when the distribution of resources is highly clustered. This also suggested that the more knowledge foraging populations had about their environment, the less likely they were to abandon the landscape they know and disperse into novel territory. The

present study gives agents new individual and social strategies for learning about their environment. For both individual and social learning, natural selection favours decreased levels of environmental knowledge, particularly in low heterogeneity environments. Social acquisition of detailed environmental knowledge results in crowding of agents, which reduces available reproductive space and relative fitness. Agents with less environmental knowledge move away from resource clusters and into areas with more space available for reproduction. These results suggest that rather than being a requirement for successful dispersal, environmental knowledge strengthens the ties to particular locations and significantly reduces the dispersal potential as a result. The evolved level of environmental knowledge in a population depends on the characteristics of the resource environment and affects the dispersal capacity of the population.

Understanding the causes of hominin dispersal events requires addressing multiple spatial and temporal scales. On one hand, the data we use to reconstruct particular events, palaeoenvironmental reconstructions (e.g., Palombo 2013, and the references therein) and the location and dating of hominin fossils and artefacts (Bar-Yosef and Belfer-Cohen 2013), needs to be at a very broad scale, sometimes even global. On the other, the processes driving dispersal occur at the most local spatial and temporal scales, individuals and groups moving in search of resources and reproducing over days, years, and generations. It is also important to note that dispersal is not inevitable but a fairly uncommon result of particular local scale behavioural adaptations within a specific environmental context. The approach advocated in this paper attempts to bridge the scalar gap by evaluating the aggregated result of local scale decisions at a broad scale, within different environmental patterns. Previous approaches to modeling dispersal, including those by Ammerman and Cavalli-Sforza (1971), Steele et al. (1998), and Hughes

et al. (2007), have also characterized dispersal processes with local scale mechanisms. However, the novelty of our approach is the focus on the decision making process at the local scale and whether environmental knowledge helps or hinders the dispersal potential of a population. With this approach we explore the relationship between population dispersibility and the environment.

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 often non-intuitive. Using an agent-based modeling approach where foraging groups tried to repeatedly move in order to maximize foraging returns, Wren et al. (2014) experimented with a heritable trait which determined the group's ability to accurately assess their environment for quality resource patches. They showed that cognitively sophisticated agents may accurately evaluate the resource potential of the landscape at a local scale, but have lower dispersibility than agents that select new foraging areas at random. Being able to accurately concentrate on certain resource patches restricted the exploration of unknown parts of the landscape. Natural selection of heritable accuracy in resource assessment, referred to as spatial foresight, resulted in the evolution of very low levels of accuracy and high dispersibility for environments with relatively low heterogeneity. This occurred as the more accurate agents crowded onto resource patches in a way that restricted their reproductive potential, leaving the somewhat less accurate agents with a reproductive advantage. 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 results from local scale mobility decisions.

This paper builds on the findings of Wren et al. (2014) by extending the ways in which groups acquire knowledge of the current state of their environment before making mobility

decisions. Two methods are tested in the simulation. The first model varies the resource assessment radius of the agents, giving them knowledge of a variable proportion of the environment, to see if this would improve their ability to navigate a heterogeneous resource landscape. The second model allows agents to learn about the resource landscape through social interactions instead of direct observation, allowing them to make use of their social networks to acquire environmental knowledge, and to capitalize on the success of the population as a whole. We narrowly define environmental knowledge as knowledge of the resource value of a cell, where increasing that knowledge either increases the number of cells being evaluated (model 1), or increases the frequency at which environmental knowledge is used as the basis of the mobility decision rather than random movement (model 2). Through random changes during group fissioning, each model allows levels of environmental knowledge to increase or decrease, and then evaluates how the heterogeneity of the resource distribution affects the natural selection of environmental knowledge. This allows us to evaluate the impact of environmental knowledge on population dispersibility.

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: population growth, temporal environmental change, and local resource depletion (Rockman 2003; Johnson and Gaines 1990; Matthysen 2012; Bowler and Benton 2005). The most often cited in human dispersals 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 2006). We

therefore add a small degree of population growth to the previous two models to evaluate its effect on mobility strategies. The other possible push factors were not included in the models but will be addressed briefly in the discussion. The current paper only considers the natural selection of the level of environmental knowledge, first in terms of the assessment area and then in terms of the frequency of cultural transmission, and its effect on dispersibility. A future paper will consider other model results, such as the quantification of dispersal rates under different behavioral and environmental conditions.

Materials and Methods

We used the NetLogo toolkit (Wilensky 1999) to program the models. They are available for download from <https://www.openabm.org/model/4176/>. 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 denoting habitat quality ranging from 0 to 100%. We imagine this value to represent the sum of all subsistence resources necessary for survival. We generated resource landscapes with different degrees of spatial heterogeneity using a fractal algorithm and varying the fractal dimension from 2.001 to 2.999 in 0.2 increments (GRASS Development Team 2012). This results in continuously varying landscapes with spatially auto-correlated resource values such that low heterogeneity landscapes have a few large resource patches, and high heterogeneity landscapes have many small patches (Figure 1). 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. To ensure spatial heterogeneity was the only varying environmental characteristic, we scaled the cell values of each raster landscape to have an approximately equal cell count of each resource value and the same summed resource abundance.

Figure 1. *Example simulated resource landscapes with different spatial heterogeneity values. Note that as spatial heterogeneity increases, there are more resource patches but they are smaller in size.*

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 each agent's relative fitness, a ratio of their currently occupied cell's resources, s , to the maximum resource value of the cells currently occupied by the agents (Equation 1). An important additional constraint is that reproduction requires an empty neighboring cell (8-cell Moore neighborhood) for the group to fission into. The fissioning event fails if there is no neighboring cell available and the offspring agent is

removed from the simulation. A change in each agent's trait value, which determines the level of environmental knowledge they have access to (see details of each model), occurs by random 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 model of Wren et al. (2014), for which mutation occurred in every offspring with a uniform random probability 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 amplitude, a process more akin to a selective sweep of a trait under positive selection (Richerson et al. 2010; Premo and Hublin 2009).

$$r_a = \frac{s}{\max(s)} \cdot r_b \quad (1)$$

Each model 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 1). In all models, the probability of removal, or death, of an agent is equal for all agents, irrespective of their resource value. In this way, the agent's fitness relative to other agents is determined solely by their currently occupied resource value's impact on their adjusted reproductive rate (Equation 1), and the availability of an empty cell for the fissioned group to occupy.

The models only vary by the number of cells the agents have access to, determined by their trait value. In each case the optimal trait value emerges as the run progresses. Small mutations in trait value lead to a reproductive advantage or disadvantage for the agents, and over time the population converges on the optimal trait value. In effect, the model lets natural

selection act as an optimizer, incrementally adjusting the trait value with random changes until it provides the optimal solution for the population. This is similar to evolutionary algorithms, where a set of algorithms are iteratively altered via a random process and where only the best performing versions are kept, until the best version of the algorithm is found.

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_a	Assessment accuracy	0.25	0.25	0.25	n/a	n/a	n/a
		0.75	0.75	0.75	n/a	n/a	n/a
Env	Range of heterogeneities in run-set	All	2.001 only	All	All	2.001 only	All
Steps	Number of time steps for each run						100 000

Table 1: *Parameters used to initialize model runs.*

Model 1: Assessment Radius

The first model tests whether increasing the assessment radius [beyond the 8-cell Moore neighborhood used in Wren et al. (2014)] would improve the ability of agents to navigate

through a complex resource landscape, 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 2).

Figure 2. *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.*

Lima and Zollner (1996) review ecological models of perceptual range, an equivalent concept to what we refer to as assessment radius. They suggest that increased perceptual range could increase dispersal since search time and risk of mortality would be reduced, but note that empirical data supporting their model is lacking (see also Zollner and Lima 1999). More broadly, there is a large body of literature evaluating the utility of information available to foragers in

variable environments (Dall et al. 2005; Stephens 1989, 1987). Within the optimal foraging theory framework there is a trade-off between the time spent searching for quality patches and time spent foraging in possibly sub-optimal patches particularly when the presence or quality of a resource is unknown until after the movement decision has been made. The optimal strategy pertains to the frequency at which the animal samples the environment and how they respond when they find desired or undesired food items. Unlike the present model where many groups are competing for resources and space, these models typically consider the optimal strategy of one forager in isolation or possibly the impact of local population density on probability of emigration from a cell (e.g., Stephens 1989), the implications of this will be discussed further below.

Binford (2001) notes that the distance between residential moves of hunter-gatherer groups varies depending on resource base and subsistence strategy. This, and many ethnographic accounts, confirms the intuitive assumption that resource distribution is the primary factor in mobility decisions (for other factors, see Whallon 2006). Coddington and Jones (2013) argue that the pattern of human occupation density is roughly based on the underlying environmental productivity, and predicts that the top ranked environments should always be occupied first, a pattern that broadly conforms to the ecological concept of the ideal free distribution which assumes complete knowledge of the environment and unrestricted movement. Similar conclusions are found by O'Connell and Allen (2012) in their model of the colonization of Sahul along the highly profitable coastal environments. These studies assume that environmental perturbations or local depletion would continuously drive local movements, and do not explicitly model any particular spatial range of environmental knowledge. However, in each of these cases, linear and fairly uniform features like coasts and river valleys were the most profitable

environments and thus continuously channeled movement without the need for detailed environmental knowledge. 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 2011:48).

Model Description

Model 1 evaluates the natural selection of assessment radius by making radius a heritable trait subject to small random increases or decreases. Agents begin each run with an assessment radius of $1 \pm m_s$. Each run lasts for 100,000 time steps, a duration initial experiments deemed more than sufficient to reach a stable trait value. Since the baseline model (Wren et al. 2014) demonstrated that foraging accuracy varies with environmental heterogeneity, the model holds foraging accuracy constant. Foraging accuracy, f_a (called foresight in Wren et al. 2014) is the probability that the agent will select the highest resource cell in their radius, with $1 - f_a$ being the probability of selecting a random neighboring cell instead. The model runs through all 600 landscapes twice, once with low foraging accuracy ($f_a = 0.25$) and once with high foraging accuracy ($f_a = 0.75$). The model output includes the median assessment radius and currently occupied cell value of all surviving agents at the end of each run (See Table 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. 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 move to a random unoccupied neighboring cell (8-cell Moore neighborhood).
 - 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_a , target the highest resource cell within their inherited radius f_r (correct assessment), or target a random cell otherwise (incorrect assessment).
 - a. Attempt to move one cell directly towards the targeted cell.
 - b. Stay if another agent blocks the move.
 3. Pop. growth only: be removed with probability, d .

Since foraging accuracy is always below one, agent mobility over time is a combination of randomly directed steps and steps toward high resource cells, with the proportion of each being determined by f_a . While agents forget their target cell after each time step, they will (with probability f_a) re-select the same cell during each subsequent time step unless a higher valued cell comes into range.

Results

The model shows that there is strong selection to keep assessment radius at low levels in all landscapes (Figure 3). Evolved median assessment radius ranged between 0.5 and 1.2 for high foraging accuracy runs and between 1.5 and 2.7 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, essentially equivalent to a random walk. A

radius between 1 and 1.41 represents a 5-cell von Neumann neighborhood, while a radius between 1.42 and 2 represents the 9-cell Moore neighborhood used in (Wren et al. 2014).

(a) Fixed population size

(b) Variable population size

Figure 3. *Natural selection favors 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 neighborhood (M), a 5-cell von Neumann (vN), and only the current cell (O) .*

Repeating model 1 with a variable population size resulted in lower median radii than with fixed populations, and reduced variance between the various surfaces of equal heterogeneity (Figure 3b). In these runs the population size 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 4).

Figure 4. *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 the hypothesis that the population size simply increases crowding, or population density, we re-ran the model with different initial population sizes and the same

resource heterogeneity (Figure 5). As expected, increasing the fixed population size decreases the value and variance of assessment radius.

Figure 5. *As the landscape remains the same size, increasing the fixed population size increases crowding. As a result, natural selection further decreases assessment radius.*

Mechanisms of Selection.

The strong selection against increased assessment radius is a counter-intuitive result. It seems logical that 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, especially on the higher heterogeneity landscapes. This poses a significant fitness risk relative to other agents, through a lowered reproductive rate, that may not be compensated by the potential fitness advantage of the distant patch.

Second, the model suggests that the relative fitness of foraging strategies is strongly affected by population density, not in terms of the number of individuals in a cell, but in terms of the number of groups competing on the landscape. If groups have access to environmental information over a wide area (high assessment radius), they tend to make similar decisions about where to forage, and this reduces their fitness relative to groups with less environmental knowledge. This results in lower radius mutations being positively selected as those agents have more access to reproductive space. 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 high 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 (Wren et al., 2014), 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 6). In the assessment radius model, the most advantageous strategy is to keep assessment radius to the immediately accessible surroundings (9-cell neighborhood), 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. This is especially true at higher radii, as there is increased likelihood that the same patch will be selected by a large number of agents. Similarly, there is little likelihood that the intermediate patches will be available to pass through. This is supported by Figure 4 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.

Figure 6. *Example simulation run on a single resource patch where the center had the highest cell value and cell values decreased linearly to away from the center. Shade represents the cumulative reproductive potential over the course of a run where brighter shades represent higher likelihood of successfully placing offspring agents, small triangles are agents. Note that the crowded center area which has the most abundant resources, has a relatively low reproductive potential due to increased crowding. Natural selection via increased reproductive success is therefore driven by those agents at the edges of the population cluster. To produce this figure for illustrative purposes, this run had radius fixed at 1.5 and mutation rate set to 0.*

Unlike the baseline model (Wren et al. 2014), the heterogeneity of the environment does not greatly affect the natural selection of assessment radius. While crowding is reduced on a highly heterogeneous surface, and assessment radius increases slightly, 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 likely explains the slight reversal of the trend of increasing assessment radius in Figure 3a for the low assessment accuracy run ($f_a = 0.25$) when the inter-peak distance was greatest (i.e., an environmental heterogeneity of 2.99). This aspect remains somewhat speculative. To interrogate this further, we would need to develop a new type of resource surface where the size and inter-peak distance of clusters varied independently.

We attempted to model population growth to simulate a push factor for dispersal by including a remove probability slightly lower than the base reproductive probability (i.e., $d < b_r$, see Table 1). However, since the resource landscape is bounded and the probability of reproduction is a product of available resources, the population stopped growing once all the cells with an adjusted reproductive probability greater than the removal probability were occupied (Eq. 1). On average, this caused the population to grow to a higher population size than the fixed runs, but then to stabilize. 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.

Model 2: Information Sharing

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 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). Our second model changes the source of agent's experience of cell values 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, any occupied cell is now observable. In a review of information use in evolutionary ecology, Dall et al. (2005) calls this "inadvertent social information" to emphasize that it is not through purposeful signaling by the more successful group, which would only draw unwanted attention to the beneficial location, but through the less successful animals picking up on cues suggesting success in others (e.g. being seen eating is a signal to others that food is available). As before, the optimal foraging theory approach is to estimate the trade off between spending time trying to observe the success of others, and foraging for yourself.

Cultural transmission is a 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 neighboring 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 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 modeling the mechanisms of cultural transmission. This work originated with Boyd and Richerson (1985) and was later expanded and 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 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.

	Individual or group	Description
Learning mechanism		
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 2: *Mechanisms of cultural transmission. Adapted and expanded from Mesoudi and Lycett (2009).*

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 2008:8). 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), having every group learn about the same, already occupied, location is obviously a maladaptive strategy. Dall et al. (2005) notes that this type of complete public

information dissemination will favor the cohesion of a larger population of animals which will have some advantages such as defense and synchronized departure of a depleted resource patch (neither of which are modeled here), but will also have disadvantages if too many are relying on public information instead of generating information through individual observation [i.e., an unbalanced producer-scrouter game (Barnard and Sibly 1981)]. Our model uses a spatial equivalent of success bias by allowing a group to copy information about the current cell value of one randomly selected group at a time. This models the chance acquisition of a piece of information through a dense social network, and through natural selection will find the optimal copy probability, c at which it is adaptive to act upon that information by moving towards that location.

Like the baseline model (Wren et al. 2014), this model assumes movement is random with respect to the resource distribution when groups are not copying from others ($1 - c$). 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.

Model Description

Model 2 evaluates the natural selection of cultural transmission of resource information using a simple form of mobility behavior, which is based on the observed cell values 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. Agents begin each run with $c = 0$, and each run lasts for 100,000 time steps, a duration initial experiments deemed sufficient to reach a stable trait value. 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 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. 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.
 - b. If target has less or another agent blocks the movement, the agent stays.
3. Pop. growth only: be removed with probability, d .

As in model 1, since the probability of cultural transmission is generally below one, agent mobility during a run is a combination of randomly directed steps and steps toward successful agents, with the proportion of each being determined by c . Agents forget their target agent after

each time step but will probabilistically move towards the center of occupied resource clusters since they will only move towards agents with more resources than they currently possess.

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 7). 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 7b).

(a)

(b)

Figure 7. 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 in selecting against copy probability. Constant and variable population sizes for $\text{env} = 2.001$ are shown.

As with model 1, 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 and 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 8a).

(a)

(b)

Figure 8. *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*

Mechanisms of Selection

The mechanism behind the natural selection of copy probability is the same as in the baseline model. The availability of reproductive space around an agent is more important than the resource value at their current location. The fitness of a trait value is determined by its ability to produce offspring, which is not only related to acquiring resources. Considered from another perspective, the effective reproductive probability, or fitness, is determined by a combination of adjusted reproductive rate and the probability of finding an unoccupied neighboring 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 9).

(a) $c = 0.75$

(b) $c = 0.25$

Figure 9. *Spatial distribution of cumulative frequency of successfully placing an offspring on a cone shaped resource landscape where lighter shades represent higher frequency. The center area has the most abundant resources, but has lower probability of agents finding reproductive space a) with high copy probability versus b) low copy probability, than the lighter ring towards the outside of each population cluster. These example runs held copy probability constant.*

Given this model of crowding, the agent that consistently has available reproductive space has higher relative fitness. If the population's mean copy probability is above the optimal, 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 and are out-competed by agents that copy enough to occupy a higher cell value. The copy probability of the population stabilizes when the effective reproductive probability is relatively constant over space (i.e., some agents have slightly higher reproductive space with lower adjusted reproductive rate, while others have slightly higher adjusted reproductive rate and lower reproductive space), although this occurs at different levels depending on the spatial heterogeneity of the environment (Figure 9b).

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 10). 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.

Figure 10. *Illustration of the clustering effect of cultural transmission. Image produced by asking each agent to face towards the mean of all other agents' locations.*

A variety of other programming choices could change the way resource information (cell values) is copied within the model. Agents could have access to information about the whole population or all agents within a limited 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 [except perhaps frequency-dependent trimming (Mesoudi and Lycett 2009)], namely one large cluster of agents would form and stick closely together.

In this sense, the dispersal potential of the population is inversely related to copy probability, and dispersal is generally unlikely to occur for a population that bases its mobility on socially 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. As found by Wren et al. (2014), less heterogeneous landscapes could evolve a population that could radiate outwards to a certain extent. However, given the tight grouping behavior driven by copying, the dispersibility of even low copy probability agents would be much lower than agents with low individual foraging bias 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.

Discussion

We modelled environmental knowledge narrowly in terms of the ability to accurately assess the current state of the resource environment over a wide area (whether through direct observation or indirectly through cultural transmission). However, the model dynamics illustrate a seemingly general pattern that it is better to know less, but more than nothing, about the spatial distribution of a resource landscape. This is a counter-intuitive result as it runs contrary to the common hypothesis that increased cognitive capacity, at least in the form of foraging accuracy or cultural transmission, gave hominins a unique ability to disperse rapidly into novel landscapes (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). Our results do not reject these hypotheses as these factors may affect other traits important for dispersal such as increased population growth, but we argue that there may be adaptive limits to environmental knowledge acquisition. Although the mechanism is different, this result is in line with conclusions in evolutionary ecology which indicate that there are costs to acquiring information about the resource distribution, and the potential advantage of information may not be great enough to pay that cost (Dall et al. 2005; Stephens 1989).

Our results demonstrate that natural selection of traits that maximize foraging returns tend to reduce the dispersibility of a population, since when these traits (e.g., foraging accuracy, assessment radius, and cultural transmission) are adaptive, they bias movement towards valued resource patches instead of outwards into unknown areas. The antithesis to foraging based mobility decisions 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 the lack of knowledge of the landscape would increase dispersal since no location, including the currently occupied place, is particularly well known in a novel landscape. 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). In a crowded landscape, which should occur under normal assumptions of population growth towards a carrying capacity, we find that natural selection should favor traits that continue to enable

successful reproduction, but that reproduction is determined by available resources, including space. In low heterogeneity landscapes with a small number of large smooth resource patches, the degree and selective effect of crowding is very strong. This reduces the reproductive advantage of accurate foraging, larger radii of assessment, and frequent 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 as groups are better able to focus on known resource patches without a reproductive cost.

In most archaeological dispersal models, such as those based on the wave of advance, density-dependence is assumed in terms of the rate of local population growth, but not in terms of mobility (Steele et al. 1998; Fort 2015). A more recent approach to dispersal has been to use the assumptions of the ideal free distribution (or a variant known as the ideal despotic distribution), where a dispersing population is assumed to evaluate the local population density compared to the carrying capacity to find the location with the most available resources (e.g., Coddington and Jones 2013; O'Connell and Allen 2012; Kennett and Winterhalder 2008). This is assumed to drive dispersal along profitable corridors or coastlines as the population size increases, although this process has not been explicitly modeled in these papers (for an exception, see Crema 2013). In an upcoming paper we will evaluate these perceptive assumptions, just environment or local population and environment, within corridors and heterogeneous landscapes to evaluate their effect on dispersal velocity and on the dispersing wave front (for an early version of that work, see Wren 2014: Ch. 3).

Highly heterogeneous landscapes typically decrease dispersal of plants and animals since neighboring locations are likely lower in resources (Johnson and Gaines 1990). Since crowding

is reduced in heterogeneous landscapes, and this favors 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 our previous work is therefore a robust result as the pattern is repeated under several different mobility strategies. This further strengthens the prediction in Wren et al. (2014), that low heterogeneity resource distributions should characterize the period leading up to major dispersal events (for a discussion of temporal heterogeneity, see Grove 2015).

Our experiments with population growth as a stimulus for dispersal resulted in some unexpected conclusions. The results do show a strong effect of population size on the natural selection of traits since increased population size is linked to crowding. However, since the model landscape was bounded to simulate the evolution of dispersal capacity in a population, 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, although the outcome on an unbounded landscape is simple to predict from the observed model dynamics. If the landscape's edges were porous, the agents with less knowledge of the resource distribution would have higher probability of dispersing. This would also leave behind a population with greater environmental knowledge but low dispersibility. Similarly, Bowler and Benton (2005) notes that animals in lower quality marginal habitats, or at patch edges, have the most to gain from dispersing into novel areas. They also note that since these areas should have lower population density due to lower carrying capacity, dispersal should be generally selected against when habitat varies spatially.

Assessment radius 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. 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 (Reid, 1899). Rather, rare but long distance dispersals (e.g., carried by a storm or animal) were a necessary component of the explanatory model (Clark 1998). Isern et al. (2008) have adapted the wave of advance model to include a variable dispersal distance function and show that it does have a significant effect on dispersal velocity although their model is based on a random walk for mobility.

Note on Temporal Change and Depletion. The introduction noted that resource depletion and temporal environmental change would not be modeled in this paper as our focus was on the role of knowledge of the spatial resource distribution. Since we have demonstrated that increasing environmental knowledge tends to lead to decreased dispersal, future models should investigate these other factors in more depth for their role in dispersing a cognitively sophisticated agent. For example, perhaps accurate environmental assessment would be advantageous when the environment is continuously being depleted or the distribution of quality resource patches are shifting in position over time. In preliminary experiments, we have found that foraging accuracy is of limited utility in these cases as well. If the environment is changing

too quickly, the agents are unable to track the environment no matter their accuracy. If the environment is changing slowly, then the same issues of crowding highlighted in this paper occur. A more thorough evaluation is required to identify if there is a limited intermediate rate of change at which foraging accuracy is adaptive. In a recent paper, Grove (2014) shows that long periods of highly variable temporal climate change may lead to the evolution of behavioral plasticity, and that this plasticity may enable dispersal when the climate stabilizes. Grove (2015) then uses an East African palaeoclimate reconstruction to show that there were specific periods of high climatic variability preceding hominin dispersal events.

Note on Memory. One component seemingly missing from the above models is the ability to remember the location of high value resource cells. 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 favorable or available. While mobility strategies like increased foraging accuracy, greater assessment radius, cultural transmission, and memory seem like they would be highly adaptive for a small

group isolated in unknown territory (which also begs the question of how they ended up there), their use in a crowded landscape is greatly constrained.

Note on Resource Landscapes. This article has only explored one characteristic of landscapes, namely the spatial distribution or heterogeneity of resources assuming actual differences in the heterogeneity of the physical environment. The ABM technique could also enable a new approach to understanding and modeling other hypotheses of hominin-environment interaction. For example, within the same bio-geographic landscape, a generalist's perception of that landscape would look less heterogeneous (since resources have different distributions) and have lower resource 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 reproductive success and dispersibility of populations. Changes in technology have already been suggested to increase dispersal (Mellars 2004, 2006), and our results suggest a new way to evaluate that hypothesis. These ideas will be explored further in future work.

Perspectives

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 cognitive capacity. Second, since dispersibility is higher in low heterogeneity environments, high heterogeneity environments should have greater population densities. 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 (Wren et al. 2014; Grove 2014). In fact, we should expect that dispersal corridors should be relatively low heterogeneity as well, although this will be explicitly modelled in a forthcoming article. 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).

We would like to stress that our conclusions depend on the model assumptions. Different assumptions could lead to different results. For example, in our model agents find high-resource patches attractive even if crowding makes reproduction difficult in them. Until some sort of evidence is found, we cannot know whether this assumption is realistic for hominins or not. Even if this assumption were not realistic, our model would be useful as a first step. In the future it could be extended into more complicated models taking this point into account. In such models, the foraging accuracy (or the spatial foresight in Wren et al. 2014) would no longer be the probability to select the highest resource cell, but the probability to select the highest resource cell of those in which the population density (or the number of occupied neighbors) is below some threshold. Above this threshold, the chances to reproduce are so low that the cell becomes unattractive for the agents (even if the cell has many resources). Moreover, in the future the

parameter values of the model (Table 1) should be estimated from empirical data. As mentioned in our previous paper (Wren et al. 2014), demic front speeds (or, equivalently, hominin arrival times in several regions) obtained from our models (with population growth) could be compared to those from other models.

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 explicitly evaluate how they are thought to interact using a computational 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. 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. In a forthcoming article, we examine the change in the rate and pattern of dispersing population waves under different cognitive and environmental conditions.

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Literature Cited

- Ammerman, A. J., and L. L. Cavalli-Sforza. 1971. Measuring the rate of spread of early farming in Europe. *Man* 6:674–688.
- Anderson, D. G., and J. C. Gillam. 2000. Paleoindian colonization of the Americas: Implications from an examination of physiography, demography, and artifact distribution. *Am. Antiquity* 65:43–66.
- Anthony, D. W. 1990. Migration in archeology: The baby and the bathwater. *Am. Anthropol.* 92:895–914.
- Bar-Yosef, O., and A. Belfer-Cohen. 2013. Following pleistocene road signs of human dispersals across Eurasia. *Quatern. Int.* 285:30–43.
- Barnard, C. J., and R. M. Sibly. 1981. Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Anim. Behav.* 29:543–550.
- Barton, C. M., and J. Riel-Salvatore. 2012. Agents of change: modeling biocultural evolution in upper Pleistocene western Eurasia. *Adv. Complex Syst.* 15:1150003.
- Barton, C. M., S. Schmich, and S. R. James. 2004. The ecology of human colonization in pristine landscapes. In *The Settlement of the American Continents: A Multidisciplinary Approach to Human Biogeography*, C. M. Barton, G. A. Clark, D. R. Yesner et al., eds. Tucson: University of Arizona Press, 138–161.
- Binford, L. R. 2001. Constructing frames of reference: An analytical method for archaeological theory building using hunter-gatherer and environmental data sets. Berkeley: University of California Press.
- Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. *Biol. Rev.* 80:205–225.
- Boyd, R., and P. J. Richerson. 1985. *Culture and the Evolutionary Process*. University of Chicago Press.
- Clark, J. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *Am. Nat.* 152:204–224.
- Codding, B. F., and T. L. Jones. 2013. Environmental productivity predicts migration, demographic, and linguistic patterns in prehistoric California. *PNAS* 110:14569–14573.
- Crema, E. R. 2013. A simulation model of Fission–Fusion dynamics and long-term settlement change. *J. Archaeol. Method Th.* 21:385–404.
- Dall, S. R. X., L.-A. Giraldeau, O. Olsson et al. 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* 20:187–193.
- Dunbar, R. I. M. 1998. The social brain hypothesis. *Evol. Anthropol.* 6:178–190.

- Fiedel, S. J., and D. W. Anthony. 2003. Deerslayers, pathfinders, and icemen: Origins of the European Neolithic as seen from the frontier. In *Colonization of Unfamiliar Landscapes: The Archaeology of Adaptation*, M. Rockman and J. Steele, eds. London: Routledge, 144–168.
- Fitzhugh, B., S. C. Phillips, and E. Gjesfjeld. 2011. Modeling variability in hunter-gatherer information networks: An archaeological case study from the Kuril Islands. In *Information and its role in hunter-gatherer bands*, R. Whallon, W. A. Lovis, and R. K. Hitchcock, eds. Los Angeles: UCLA/Cotsen Institute of Archaeology Press, 85–115.
- Fort, J. 2015. Demic and cultural diffusion propagated the Neolithic transition across different regions of Europe. *J. Roy. Soc. Interface* 12:20150166.
- Funk, C. 2011. Yup'ik Eskimo gendered information storage patterns. In *Information and its role in hunter-gatherer bands*, R. Whallon, W. A. Lovis, and R. K. Hitchcock, eds. Los Angeles: UCLA/Cotsen Institute of Archaeology Press, 29–58.
- Gamble, C., W. Davies, P. Pettitt et al. 2004. Climate change and evolving human diversity in Europe during the last glacial. *Phil. Trans. R. Soc. Lond. B* 359:243–254.
- GRASS Development Team. 2012. Geographic Resources Analysis Support System (GRASS GIS) Software. Open Source Geospatial Foundation.
- Grove, M. 2014. Evolution and dispersal under climatic instability: A simple evolutionary algorithm. *Adap. Behav.* 22:235–254.
- Grove, M. 2015. Palaeoclimates, plasticity, and the early dispersal of *Homo sapiens*. *Quatern. Int.* 369:17–37.
- Grove, M., E. Pearce, and R. Dunbar. 2012. Fission-fusion and the evolution of hominin social systems. *J. Hum. Evol.* 62:191–200.
- Henrich, J., and R. McElreath. 2003. The evolution of cultural evolution. *Evol. Anthropol.* 12:123–135.
- Hughes, J. K., A. Haywood, S. Mithen et al. 2007. Investigating early hominin dispersal patterns: Developing a framework for climate data integration. *J. Hum. Evol.* 53:465–474.
- Isern, N., J. Fort, and J. Pérez-Losada. 2008. Realistic dispersion kernels applied to cohabitation reaction–dispersion equations. *J. Stat. Mech.* 2008:P10012.
- Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. *Annu. Rev. Ecol. Syst.* 21:449–480.
- Kennett, D. J., and B. Winterhalder. 2008. Demographic expansion, despotism and the colonisation of east and south Polynesia. In *Islands of Inquiry: Colonisation, Seafaring and the Archaeology of Maritime Landscapes* (Terra Australis 29). Canberra: Australia National University Press, 87–96.
- Lake, M. W. 2000. MAGICAL computer simulation of Mesolithic foraging. In *Dynamics in Human and Primate Societies: Agent-Based Modeling of Social and Spatial Processes*, T. Kohler and G. Gumerman, eds. New York: Oxford University Press, 107–143.

- Lake, M. W. 2001. The use of pedestrian modelling in archaeology, with an example from the study of cultural learning. *Environ. Plann. B*. 28:385–404.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* 11:131–135.
- Matthysen, E. 2012. Multicausality of dispersal: A review. In *Dispersal Ecology and Evolution*. Oxford: Oxford University Press, 3–18.
- McElreath, R., M. Lubell, P. J. Richerson et al. 2005. Applying evolutionary models to the laboratory study of social learning. *Evol. Hum. Behav.* 26:483–508.
- Mellars, P. 2004. Neanderthals and the modern human colonization of Europe. *Nature* 432:461–465.
- Mellars, P. 2006. Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. *PNAS* 103:9381–9386.
- Mesoudi, A. 2008. An experimental simulation of the “copy-successful-individuals” cultural learning strategy: Adaptive landscapes, producer–scrounger dynamics, and informational access costs. *Evol. Hum. Behav.* 29:350–363.
- Mesoudi, A., and S. J. Lycett. 2009. Random copying, frequency-dependent copying and culture change. *Evol. Hum. Behav.* 30:41–48.
- Mesoudi, A., and M. J. O’Brien. 2008. The cultural transmission of great basin projectile-point technology I: An experimental simulation. *Am. Antiquity* 73:3–28.
- . 2008. The cultural transmission of great basin projectile point technology II: An agent-based computer simulation. *Am. Antiquity* 73:627–644.
- Mithen, S. J. 1990. *Thoughtful Foragers: A Study of Prehistoric Decision Making*. Cambridge: Cambridge University Press.
- Müller, U. C., J. Pross, P. Tzedakis et al. 2011. The role of climate in the spread of modern humans into Europe. *Quaternary Sci. Rev.* 30:273–279.
- O’Connell, J. F., and J. Allen. 2012. The restaurant at the end of the universe: Modelling the colonisation of Sahul. *Aust. Archaeol.* 74:5–17.
- Palombo, M. R. 2013. What about causal mechanisms promoting early hominin dispersal in Eurasia? A research agenda for answering a hotly debated question. *Quatern. Int.* 295:13–27.
- Potts, R. 1998. Variability selection in hominid evolution. *Evol. Anthropol.* 7:81–96.
- Potts, R. 2002. Complexity and adaptability in human evolution. In *Probing Human Origins*, M. Goodman and A. S. Moffat, eds. Cambridge: American Academy of Arts and Sciences, 33–57.
- Premo, L. S., and J.-J. Hublin. 2009. Culture, population structure, and low genetic diversity in Pleistocene hominins. *PNAS* 106:33–37.
- Ray, C., and A. Hastings. 1996. Density dependence: Are we searching at the wrong spatial scale? *J. Anim. Ecol.* 65:556–566.

- Reid, C. 1899. *The Origin of the British Flora*. London: Dulau & Company.
- Richerson, P. J., R. Boyd, and J. Henrich. 2010. Gene-culture coevolution in the age of genomics. *PNAS* 107:8985–8992.
- Rockman, M. 2003. Knowledge and learning in the archaeology of colonization. In *Colonization of Unfamiliar Landscapes: The Archaeology of Adaptation*, M. Rockman and J. Steele, eds. London: Routledge, 3–24.
- Rockman, M., and J. Steele. 2003. *Colonization of Unfamiliar Landscapes: The Archaeology of Adaptation*. London: Routledge.
- Steele, J., J. Adams, and T. Slutkin 1998. Modelling paleoindian dispersals. *World Archaeol.* 30:286–305.
- Stephens, D. W. 1987. On economically tracking a variable environment. *Theor. Popul. Biol.* 32:15–25.
- Stephens, D. W. 1989. Variance and the value of information. *Am. Natur.* 134:128–140.
- Stewart, J. R., and C. B. Stringer. 2012. Human evolution out of Africa: The role of refugia and climate change. *Science* 335:1317–1321.
- Veth, P., N. Stern, J. MacDonald et al. 2011. The role of information exchange in the colonization of Sahul. In *Information and Its Role in Hunter-Gatherer Bands*, R. Whallon, W. A. Lovis, and R. K. Hitchcock, eds. Los Angeles: UCLA/Cotsen Institute of Archaeology Press, 203–220.
- Whallon, R. 2006. Social networks and information: Non-“utilitarian” mobility among hunter-gatherers. *J. Anthropol. Archaeol.* 25:259–270.
- Whallon, R., W. A. Lovis, and R. K. Hitchcock. 2011. Information and its role in hunter-gatherer bands. Los Angeles: UCLA/Cotsen Institute of Archaeology Press.
- Wilensky, U. 1999. NetLogo. Evanston: Center for Connected Learning and Computer-Based Modeling, Northwestern University.
- Winder, I. C., G. C. King, M. Deves et al. 2013. Complex topography and human evolution: The missing link. *Antiquity* 87:333–349.
- Wren, C. D. 2014. The effect of spatial environmental heterogeneity on hominin dispersal events and the evolution of complex cognition. PhD thesis. Montreal: McGill University.
- Wren, C. D., J. Z. Xue, A. Costopoulos et al. 2014. The role of spatial foresight in models of hominin dispersal. *J. Hum. Evol.* 69:70–78.
- Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030.