Population density, mobility, and cultural transmission

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Abstract

Prompted by the results of a series of recently published simulation models, there is an increasing tendency for archaeologists to invoke demographic variables as explanations for changes in the sophistication or complexity of material culture. Whilst these models are undoubtedly valuable, this paper draws attention to persistent failings in the interpretation and application of these models by archaeologists. Despite having quite different effects, variables such as population size and population density are often used interchangeably; and whilst increasing mobility has an effect broadly equivalent to that of increasing population density, it is rarely given sufficient weight in archaeological explanations of cultural change. The analyses reported here develop a series of new simulations based on the ideal gas model, allowing for an explicit prediction of the encounter rate – the variable for which population density and mobility are proxies, and which ultimately governs the rate of cultural transmission. This model supports the predictions of earlier studies on the effects of population density and mobility, but suggests that population size will have no effect on rates of cultural transmission. These simulations are coupled with analyses that demonstrate a reciprocal correlation between population density and mobility in a large hunter-gatherer dataset. Given this correlation, it is argued that archaeological inferences about cultural transmission based on just one of these variables are unlikely to be valid. These findings are discussed in the context of previous research, and it is suggested that future studies would gain greater explanatory power by focusing explicitly on the social network structures likely to have characterised a particular archaeological population.

Keywords: Population density; population size; mobility; encounter rate; cultural transmission; hunter-gatherer; simulation.

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1. Introduction

Over the past 15 years, an increasing number of archaeologists have invoked variables such as population density or population size as explanations for changes in material culture. Increases in these variables, it is argued, will lead to greater sophistication or complexity in toolkits, in individual tools, or in methods of tool manufacture (e.g. Shennan 2001; Henrich 2004; James and Petraglia 2005; Zilhão 2007; Powell et al. 2009; Langley et al. 2011). The current trend can be traced to the fall of the 'human revolution' model, and in particular to the failure of the associated theory that the fluorescence of artistic and symbolic expression during the Upper Palaeolithic of Europe could be attributed to a sudden and dramatic increase in cognitive abilities (e.g. Klein, 2000). Given that *Homo sapiens* appears shortly after 200 ka, the sporadic appearance (and disappearance) of apparently 'modern' technologies prior to c.60 ka requires a set of candidate explanations that are extrinsic to the biology of our species; demographic variables are rapidly colonising this niche, to the extent that Palaeolithic archaeology appears to be approaching a new orthodoxy (see Collard et al. 2013; French, 2015).

Citations demonstrate that three papers have been instrumental in influencing archaeological thought on the relationship between cultural change and demography in recent years: those of Shennan (2001), Henrich (2004), and Powell and colleagues (2009). Shennan (2001) adapted a genetic model of the evolution of sex (Peck et al. 1997), allowing oblique transmission (i.e. transmission of cultural information from an elder who is not necessarily a genetic parent) to influence the 'fitness' of a series of cultural traits. Varying the effective population size – taken in this model to be the subset of the overall population that are likely to act as 'cultural parents' – and running the models until they reached stationary distributions, Shennan (2001) found that the geometric mean fitness taken across all traits was higher in larger populations. This relationship is approximately logarithmic, with the greatest increases in fitness occurring when very small populations increase in size. Despite the potential archaeological salience of Shennan's (2001) model, subsequent research has focused on overall skill levels rather than multiple cultural traits. Shennan's (2001) explicit assumption that cultural change is an evolutionary process, however, remains implicit in more recent work.

Henrich (2004) develops a model in which each individual attempts to copy the most skilful member of the population in each iteration. Although the model assumes that the most skilful individual is always accurately identified, copying is subject to error, and more complex skills are harder to copy. By analogy with the genetic process most copying errors are detrimental, but occasionally "through a combination of imperfect imitation, experiments, errors, bad memories and ill fortune" (Henrich 2004:200) an individual will produce a copy that is better than the original. Given an original skill value z, the possible outcomes of copying are given by a Gumbel (extreme value) distribution with location parameter $z - \alpha$ and scale parameter β. The complexity of a skill – how hard it is to imitate – is thus measured by α, whilst the extent to which the skill is subject to copying error is governed by β. (For those unfamiliar with the Gumbel distribution, the most relevant description for the purposes of Henrich's (2004) model is that it is the distribution created by repeatedly choosing the highest value (the 'extreme value') from a series of normally distributed random numbers; if one

were to generate 100 random numbers from a normal distribution, then discard all but the single highest number among them, and repeat this process multiple times, the numbers retained would follow a Gumbel distribution.) Using a simplified but accurate approximation of the Gumbel distribution, Henrich (2004:202) demonstrates that $\Delta\bar{z} = -\alpha + \beta(\varepsilon + \ln(N))$, where $\Delta\bar{z}$ is the average change in skill level per iteration, N is population size, and ε is the Euler-Mascheroni constant. Skill level thus increases logarithmically with increasing population size. This result is remarkably close to that of Shennan (2001) despite the considerable differences between the two models.

Powell and colleagues (2009) introduced a stochastic meta-population simulation analogous to Henrich's (2004) analytical model. This simulation employs a series of equally sized subpopulations and examines the effects of variation in the number and density of subpopulations and the extent of migratory activity between them. Three particularly important results arise from this simulation. Firstly, increasing the number of subpopulations only causes increases in skill level whilst the number of subpopulations is less than approximately 50, indicating that "the accumulation, or maintenance, of culturally inherited skill is not dependent on the absolute meta-population size" (Powell et al. 2009:1300). Whilst 'cultural fitness' increases approximately logarithmically with population size in Shennan's (2001) model, and skill level increases exactly logarithmically with population size in Henrich's (2004) model, Powell and colleagues (2009) demonstrate that in a structured meta-population skill level approaches an asymptote relatively quickly, and is unaffected by further increases in population size.

Secondly, Powell and colleagues (2009) demonstrate that sub-population density has a far more consistent effect on the accumulation of skill than does meta-population size; skill levels in high density areas were consistently higher in these simulations, regardless of the values of the parameters α and β. Thirdly, and perhaps most importantly for archaeological interpretation, these authors find that greater migratory activity also leads to higher skill levels, and that this effect is particularly pronounced when the skill being copied is of greater complexity (i.e. when α is higher). These simulations thus provide a series of insights that are of vital importance to archaeological interpretation, and they have, accordingly, been widely utilised.

A number of researchers have identified problems with the models of Shennan (2001), Henrich (2004), and Powell and colleagues (2009); broadly speaking, these problems can be divided into the theoretical and the empirical. From a theoretical perspective, Vaesen (2012) has noted a series of mathematical issues with the performance of the Henrich (2004) equation. Several authors have also noted that none of these models make reference to the underlying ecology (Vegvari and Foley 2014, Collard et al. 2013). Empirically, Collard and colleagues (2013; Vaesen et al. in press) note that, of the studies examining both demographic variables and variables indexing material culture complexity in extant hunter-gatherer populations, few have found positive correlations between the two. Whilst these problems merit further attention, the purpose of the current paper is to draw attention to a further issue which stems from the interpretation and application of the models by archaeologists rather than from the models themselves. This issue arises from the neglect of migration (or, on a smaller scale, mobility) in the vast majority of archaeological analyses that have made use of the results of these models.

In the most comprehensive model published to date, Powell and colleagues (2009:1300) make it abundantly clear that "migratory activity among a set of subpopulations can have the same effect on skill accumulation as increasing the size of a single population". These authors are also explicit about the limited effect of overall population size. Yet archaeological analyses seeking explanations for cultural change focus primarily on population size, secondarily on population density, and rarely, if at all, discuss mobility (e.g. Zilhão 2007; Langley et al. 2011). While there are some more nuanced applications in the archaeological literature – Riede (2008), for example, stresses the sudden decrease in connectedness following the Lacher See eruption of 12,920 BP, and Hopkinson (2011; Hopkinson et al. 2013) focuses on the spatial interaction of locally and regionally separated populations – the majority of studies opt for population size *or* density (often inter-changeably) as the sole explanation. As the analyses reported below demonstrate, population *density* and mobility must be considered as joint, interacting factors in any valid explanation of cultural change.

2. Deriving predictions

The hypothesis that high population densities will increase rates of cultural transmission has a clear intuitive appeal: when population densities are high, individuals will encounter one another more often, with each encounter affording an opportunity to transmit cultural information. The same logic underlies the related hypothesis that high mobility rates will increase rates of cultural transmission. Both population density and mobility, therefore, are proxies for the individual encounter rate: it is this latter variable that actually controls the rate of cultural transmission. Following similar logic, although population size is not a direct proxy for an individual's encounter rate, it might affect the number of encounters that occur at the *population level* per unit time. Encounter rates can be modelled directly via the ideal gas model (IGM) developed originally by particle physicists but employed routinely by primatologists (e.g. Waser 1976; Dunbar 1995; Harcourt and Greenberg 2001; Gursky 2005) and increasingly by anthropologists (e.g. Grove 2010; Grove et al. 2012; Pearce 2014). The IGM is used here to derive predictions about the relationships between population density, mobility, and population size on the one hand, and encounter rates and rates of cultural transmission on the other.

The gas model states that an individual's encounter rate is $E_{ind} = \frac{8\rho D v}{\pi}$, where ρ is density, v velocity and D is the radius within which the individual can detect other individuals. For current purposes, the constants 8 and π are ignored, and we replace detection distance and velocity with a single mobility parameter $M = Dv$. In this simplified form, $E_{ind} \propto \rho M$, the IGM provides a very basic but useful prediction:

1. Individual encounter rate has positive, linear relationships with both density and mobility ($E_{ind} \propto \rho, E_{ind} \propto M$);

Modifying the Henrich (2004) equation such that the average change in skill level per iteration is related to encounter rate rather than population size gives $\Delta\bar{z} = -\alpha + \beta(\varepsilon + \ln(\rho M))$. This form is henceforth referred to as the Modified Henrich Equation (MHE), and yields a pair of predictions for the scaling of average change in skill level with population density and mobility:

2. Average change in skill level per iteration has positive, logarithmic relationships with both density and mobility ($E_{ind} \propto \beta \ln(\rho)$, $E_{ind} \propto \beta \ln(M)$).

(More fully, $E_{ind} = \underbrace{\beta \ln(\rho)}_{Slope} + \underbrace{\beta(\varepsilon + \ln(M)) - \alpha}_{Constant}$ and $E_{ind} = \underbrace{\beta \ln(M)}_{Slope} + \underbrace{\beta(\varepsilon + \ln(\rho)) - \alpha}_{Constant}$, but it is really the generic scaling relationships that are of interest here).

The basic IGM does not include a term for population size. However, the number of individuals inhabiting an area A at density ρ will be ρA. The total number of encounters that occur between individuals in this area per unit time will therefore be the individual encounter rate multiplied by ρA. Maintaining the above simplifications, this gives the total number of encounters per unit time at the population level as $E_{pop} \propto A\rho \cdot \rho M$. The average number of encounters experienced by an individual, however, is E_{pop} divided by population size, $E_{ind} \propto \frac{A\rho \cdot \rho M}{A\rho} = \rho M$; the population size term thus falls out of the equation governing individual encounter rate, as above. The IGM therefore suggests that, whilst the overall rate of encounters within the population increases with increasing population size, the individual encounter rate does not. Since it is the individual encounter rate that determines changes in skill level, this leads to a third prediction:

3. Individual encounter rate, and thus average change in skill level per iteration, will have no relationship with population size.

Finally, in order to explore this framework using the abundant data on hunter-gatherer population density and mobility, a direct relationship between these two variables is derived. There is considerable variation in both population density and mobility among hunter-gatherer groups, but if encounter rates are important for the maintenance of skill levels, it is to be expected that these will be relatively invariant between groups. Following Henrich (2004), it is considered that a lowering of skill levels could be highly detrimental; it is therefore hypothesized that population density and mobility will covary so as to maintain relatively consistent encounter rates among hunter-gatherers. The simplified IGM shows that encounter rate is the product of population density and mobility. To maintain a constant encounter rate when one of these variables changes, the other variable must scale reciprocally. This yields a fourth prediction to be tested via hunter-gatherer data:

4. To maintain a constant encounter rate, the relationship between density and mobility must be reciprocal ($\rho \propto M^{-1}$, or, equivalently, $M \propto \rho^{-1}$).

Figure 1 plots this relationship, demonstrating that high density, low mobility populations can experience encounter rates identical to those of low density, high mobility populations. Predictions 1-4 are tested below via a combination of simulations and empirical analyses.

3. Methods

3.1. Simulations

n individuals were placed randomly in a square grid with the density of individuals in the upper half of the grid being ten times that in the lower half (following Powell et al. 2009). Each individual interacts only with the neighbours falling within its mobility radius, r. In terms of the hunter-gatherer system, most of these individuals are likely to be kin by blood or marriage, since the degree of kinship will be higher between geographically proximate individuals. Although it does not affect the results of the model, a pattern of isolation by distance as proposed theoretically by Wright (1943; see also Malécot 1969) and confirmed empirically among numerous hunter-gatherer groups

by Morton and colleagues (e.g. Morton 1969; Lalouel and Morton 1973; see also Relethford 2004) is assumed. To avoid edge effects, the grid is represented as a torus. Each iteration, each individual copies the skill value, z^*, of the most skilled individual within its radius, obtaining a new value drawn from a Gumbel distribution with location parameter $z^* - \alpha$ and scale parameter β. This is an exact implementation of the model of skill transmission and accumulation described in detail by Henrich (2004).

In **Simulation 1**, r is equal for all individuals, irrespective of population density. In **Simulation 2**, the mobility radius in the low density area is set such that the mobility *area* is ten times greater than that in the high density area. This ensures that, on average, individuals in the low and high density areas will have the same number of neighbours from which to copy. **Simulation 3** replicates **Simulation 1**, but with a population four times as large. To maintain population densities identical to those of **Simulation 1**, the increase in population size is achieved by simply increasing the area of the simulation grid (and therefore the number of individuals) by a factor of four. All individuals begin with a skill level of zero, and each simulation is run for 100 iterations. As noted by Powell and colleagues (2009), a duration of 100 iterations is sufficient to yield stable and representative output, and is not prohibitive in terms of computation time.

Changes in skill level were recorded for each individual in each iteration, together with the skill level of each individual after 100 iterations. To ensure that comparisons between high and low density areas were not affected by individuals in low density areas who had neighbours in high density areas (or vice versa), individuals that were located at distances less than the mobility radius from the edge of their respective density area were excluded. Statistical analyses were then performed on simulation output so as to test the following predictions of the above listed hypotheses.

A significantly higher skill level in the high density area than in the low density area in **Simulation 1** would be consistent with the hypothesis that increasing population density increases rates of cultural transmission. If this first result is confirmed, lack of a significant difference between skill levels of the high and low density areas in **Simulation 2** would be consistent with the hypothesis that increasing mobility increases rates of cultural transmission, negating the differences caused by population density. A lack of significant differences in skill levels between the high population density areas in **Simulations 1** and **3** *and* between the low population density areas in **Simulations 1** and **3** would be consistent with the hypothesis that increasing population size has no effect on rates of cultural transmission, regardless of variation in population density.

As expected from the use of Henrich's (2004) model, the skill levels of individuals in both high and low density areas throughout all simulations were Gumbel-distributed; as such, non-parametric statistics were used to test the above predictions. Running multiple simulations in parallel and performing Wilcoxon Rank-Sum tests on high and low density populations after each iteration demonstrated that relative skill levels were prone to considerable stochastic variance. When running **Simulation 2**, for example, it was not unusual for the individuals in the high density area to have significantly higher skill levels in one iteration, but to have significantly *lower* skill levels a few iterations later (or vice versa), leading to both positive and negative Z-values in the output of the Rank-Sum tests over the course of a simulation. To ensure the statistical analyses tested long-term trends rather than short-term variance, the following procedure was adopted:

1. A Wilcoxon Rank-Sum test for each of the comparisons listed above was performed after each of the 100 iterations of each simulation;

2. The *Z*-values resulting from the Rank-Sum tests were then aggregated for each comparison and subjected to one-sample Sign tests;

3. If the stochastic variance of a given model during a given iteration was equally likely to lead to a positive or a negative *Z*-value, the Sign test should fail to reject the null hypothesis that the median of the aggregated *Z*-values is zero;

4. If there is a genuine long-term difference between skill levels in any given comparison, by contrast, the Sign test should significantly reject this null hypothesis.

Finally, to complement the above pair-wise comparisons of particular population density, mobility, and population size values detailed above, an extensive set of simulations were carried out in which each parameter was varied independently, over a wider set of parameter values. With the other parameters at constant values, population density was varied between 0.1 and 4 individuals per unit square in increments of 0.1, the mobility area between 0.1 and 4 units squared in increments of 0.1, and population size between 100 and 2000 individuals in increments of 50. These analyses were used to test the wider validity of the findings of the pair-wise analyses, and to provide more robust tests of Predictions 1-3. All simulations were programmed in Matlab; code is freely available from the author. Statistical analyses were carried out in SPSS 22.1.

3.2. Ethnographic analyses

Ethnographic data on population density and mobility were taken from Binford's *Frames of Reference* database (2001:118-129). This database collates a vast amount of information on hunter-gatherer ecology, subsistence, and sociality, encompassing elements of many earlier databases and publications. Binford's DENSITY variable records the number of individuals per 100km^2; this was converted to individuals per km^2 prior to analysis. Binford's (2001) DISMOV variable records the distance moved per year in miles; these measurements were converted to kilometres prior to analysis. Only cases in which groups were fully mobile (Binford's GRPPAT=1) and had DISMOV values >0 were used, yielding a sample of 175 groups. To test the hypothesis that $M \propto \rho^{-1}$ (or vice versa), the two variables were logarithmically transformed and $\ln(M)$ was regressed on $\ln(\rho)$. The slope of the resulting linear regression equation (the unstandardized B value) thus equates to the exponent of a power law fitted to the raw data, and can be evaluated against the theoretical prediction. The data were considered to be consistent with the theoretical predictions if the predicted exponents fall within the 95% confidence intervals of the empirical, unstandardized B values. As before, statistical analyses were carried out in SPSS 22.1.

4. Results

4.1. Simulations

For consistency, all plots and statistics are given for simulations in which α = 4 and β = 2. Repeated simulations with α and β values in the range 2-5 (i.e. with $\frac{\alpha}{\beta}$ values ranging from 0.4 to 2.5) did not affect the directionality or significance of the results presented below. In Figures 2-4, panel A shows the locations and skill levels of all individuals after 100 iterations, whilst panel B shows the

distributions of changes in skill level per individual per iteration separately for the high and low density areas.

Figure 2 shows a representative result of **Simulation 1**. Figure 5A shows the distribution of *Z*-values resulting from the Wilcoxon Rank-Sum tests performed after each of the 100 iterations of the simulation. A Sign test performed on this distribution indicates that the median is significantly different from zero ($Z = -9.38$, $p < 0.001$), confirming the prediction that skill levels are lower in the low density area. Figure 3 shows a representative result of **Simulation 2**. Figure 5B shows the distribution of *Z*-values resulting from the Wilcoxon Rank-Sum tests. The Sign test demonstrates that the median of this distribution is not significantly different from zero ($Z = 1.16$, $p = 0.25$), confirming the prediction that higher levels of mobility can negate the effects of low population density and lead to equal skill levels in the high and low density areas.

Figure 4 shows a representative result of **Simulation 3**. Figure 5C shows the distribution of *Z*-values resulting from the Wilcoxon Rank-Sum tests comparing the low density area in **Simulation 1** to the low density area in **Simulation 3**; Figure 5D shows a similar plot comparing the two high density areas. Sign tests performed on these distributions indicate that in neither case is the median significantly different from zero (low densities $Z = -0.95$, $p = 0.34$; high densities $Z = -0.32$, $p = 0.75$). This result is consistent with the prediction that skill levels are not affected by population size. Figure 6A explicitly compares the distributions of change in skill level per individual per iteration for the low density areas of Simulation 1 and Simulation 3; Figure 6B fulfils a similar function for the high density areas. Figure 6 lends clear visual support to the statistical finding that population size does not affect skill levels in these simulations.

Figure 7 expands the pairwise comparisons discussed above to examine wider ranging differences in population density, mobility, and population size, thus testing Predictions 1-3 over a wider range of parameter values. Figures 7a and 7b show linear increases in encounter rate with increasing population density and mobility respectively, confirming Prediction 1. Figures 7d and 7e show logarithmic increases in skill level with increasing population density and mobility respectively, confirming Prediction 2. Note however that in both Figures 7d and 7e the simulation results depart from the theoretical expectation at very low values; possible reasons for this discrepancy are discussed further below. Figures 7c and 7f show that population size does not affect either encounter rate or skill level, confirming Prediction 3.

4.2. Ethnographic analyses

The gas model suggests that distance moved per year should scale with the reciprocal of population density. Figure 8 plots the relationship between these two variables for the 175 hunter-gatherer groups employed in the analysis. The regression of distance moved per year on population density (performed as a linear regression on logarithmically transformed data) is significant ($\beta=-.794$, $t(173)=-17.184$, $p<.001$), explaining 63.1% of the variance ($R^2=.631$, $F(1,173)=295.284$, $p<.001$). As predicted, the relationship is a power law with a negative exponent; however, the exponent is approximately half the predicted value of -1 (unstandardized $B=-.461$, 95% confidence interval [-.514, -.408]). Possible reasons for this discrepancy are discussed below.

5. Discussion

The above results are consistent with Predictions 1-3; there is qualitative but not quantitative support for Prediction 4 (see Table 1 for a summary of predictions and results). Accordingly, the section below discusses potential reasons for this quantitative discrepancy. Following sections discuss the implications of the analyses presented here for archaeological interpretation and highlight micro-scale deviations from expectations of the MHE that should inform future research.

5.1. Sociality, subsistence, and mobility in hunter-gatherers

The result shown in Figure 8 suggests that mobility scales with population density as $M \propto \rho^{\sim -0.5}$, a significant departure from the prediction of $M \propto \rho^{-1}$. A possible explanation for this departure stems from a discrepancy in the way mobility is measured between the IGM and the empirical data. Binford's (2001) DISMOV variable is a measure of the *distance* covered, whereas mobility in the IGM is ideally defined as an *area* covered. If DISMOV is converted to an area variable by simply squaring it, the regression of LN(DISMOV^2) on LN(Population Density) yields the same statistics as above (β=-.794, t(173)=-17.184, p<.001; R^2=.631, F(1,173)=295.284, p<.001), but with a unstandardized B value that includes -1 within its 95% confidence interval (unstandardized B=-0.921, 95% CI [-0.815, -1.027]). This adjustment therefore supports Prediction 4. Simply squaring DISMOV, however, is unlikely to provide a particularly reasonable estimate of the area covered by a foraging group (and although Binford (2001) gives an AREA estimate, this is the total area inhabited by the whole population).

Rather than attempting to convert the DISMOV variable into an area, a more useful approach involves converting the population density estimate into a distance between groups. Thompson (1956) demonstrated that the mean distance D to the nth nearest neighbour in a randomly distributed population at density ρ is $D(n) = \frac{1}{\sqrt{\rho}} \cdot \frac{n \cdot (2n)!}{(2^n \cdot n!)^2}$. Hubbell and colleagues (2008) showed that qualitatively similar patterns hold even when distributions are non-random. The important feature of this equation is that the value of n simply provides a constant to be multiplied by $\frac{1}{\sqrt{\rho}}$; verbally, the distance to any of n neighbouring groups is related linearly to the reciprocal of the square root of population density (henceforth RSPD). Regressing LN(DISMOV) on LN(RSPD) for the hunter-gatherer dataset yields identical statistics again, with the exception that the β, t, and B values are now positive (β=.794, t(173)=17.184, p<.001; R^2=.631, F(1,173)=295.284, p<.001). As such, the unstandardized B value now includes 1 within its 95% confidence interval (unstandardized B=0.921, 95% CI [0.815, 1.027]).

That the B value of a linear regression on logarithmically transformed variables is close to 1 suggests that the relationship may be better characterised by a linear regression on the raw (untransformed) data. This regression should pass through the origin, since if $\ln(\mathrm{DISMOV}) = 1 \times \ln(\mathrm{RSPD}) + \ln(\delta)$, then $\mathrm{DISMOV} = \delta \times \mathrm{RSPD}^1 = \delta \times \mathrm{RSPD}$; there is no constant in this equation. Such a relationship would suggest that DISMOV is a simple multiple of RSPD and that, accordingly, hunter-gatherers adjust the distances they move in direct proportion to the distances to neighbouring groups. Regressing DISMOV on RSPD and forcing the line through the origin produces a significant relationship (β=.922, t(174)=31.456, p<.001), explaining 85% of the variance in DISMOV (R^2=.850, F(1,174)=989.463, p<.001). This relationship is plotted in Figure 9.

Prediction 4 was predicated upon the hypothesis that hunter-gatherers might adjust their population densities and mobility strategies so as to maintain a given number of encounters per unit time. Converting DISMOV into an area metric or, more realistically, converting Population Density into a distance metric, provides a result that is consistent with this hypothesis. Although regression analyses do not permit assessment of causality, the most realistic explanation for this result is that population densities (and hence neighbour distances) are determined by the distribution of resources, with mobility strategies adjusted so as to ensure a sufficient number of encounters with neighbouring groups. However, a further hypothesis – not tested here – must also be considered. It remains possible that both population densities *and* mobility strategies are determined by resource densities, with the relationship between them arising purely from this common dependence. This latter hypothesis has a certain intuitive appeal: when resources are at low density, foragers dependent on those resources should also exist at low density; furthermore, with resources at low density a forager must cover a greater area in order to satisfy a given energetic requirement (e.g. Grove 2009, 2010). Equivalently, when resources are at high density we might expect high population densities and low mobility. Further analyses will be required to determine whether hunter-gatherer mobility is constrained by sociality, subsistence, or some combination thereof.

Although the annual distance moved (DISMOV) is the metric most appropriate for use with the ideal gas model, it may also in future be possible to build the number of residential moves per annum (Binford's (2001) NOMOV variable) into models of this kind. Whilst a higher frequency of residential moves would not necessarily impact directly upon the number of encounters an individual experiences (in the current model, two individuals can encounter each other on numerous occasions), it might be expected to increase the number of *different* individuals that a given individual encounters per unit time. This could have interesting additional effects on the speed with which cultural variants spread through a population. Given that there is a positive correlation between DISMOV and NOMOV, at least within the sample employed above, inclusion of this variable in future models would likely accentuate the positive effect of high mobility on rates of cultural transmission described above.

5.2. Implications of results for archaeological analyses

Regardless of its ultimate causes, the result that there exists a reciprocal correlation between population density and mobility among extant hunter-gatherers has serious consequences for archaeological interpretation. This result leads to a conclusion that can be stated in strong or weak forms. The weak form states that archaeological analyses that consider only population density *or* mobility as proxies for rates of cultural transmission are invalid; only joint consideration of these variables can lead to informed analyses. The strong form states that since population density and mobility covary so as to equalise encounter rates, neither is a useful proxy for rates of cultural transmission. The weak form of the conclusion is fully supported by the analyses reported above; the strong form is also supported by these analyses, but it should be noted that the results highlight only a general pattern. The scatters around the regression lines in Figures 8 and 9 demonstrate that there does exist some variation in encounter rates, and that as such population density and mobility may retain some explanatory power in certain specific contexts.

The simulation results reported above demonstrate the independent effects of population density, mobility, and population size on rates of cultural transmission. These results are in broad agreement

with those of Powell and colleagues (2009), despite the fact that these authors consider subgroups interacting within a meta-population structure, whereas the model presented above considers individuals interacting within a single continuous population. The broad agreement between the two models is therefore reassuring, and suggests that when fine-grained differences in encounter rates between archaeological societies can be discerned their consequences can be reliably inferred.

The results reported here do, however, differ markedly from those of Shennan (2001) and Henrich (2004) in terms of the effects of population size. The disparity between the above results and those of Henrich (2004) is in fact more apparent than real, and can be easily resolved. It is established above that population density and mobility are simply proxies for the encounter rate, with the latter being the actual determinant of rates of cultural transmission. Population size is not a proxy for encounter rate simply because an individual does not encounter all other members of her population on a timescale relevant to cultural transmission, if ever. Instead, the cultural influence of distant members of a population occurs via diffusion, and does not depend on the adopter of an idea coming into direct contact with its originator. Henrich's (2004) equation does, however, have the potential to provide a very useful method for examining the combined effects of encounter rate and imperfect copying. By replacing 'population size' with 'encounter rate', in what is referred to above as the MHE, the benefits of this model can be maintained and strengthened.

The disparity between the above results and those of Shennan (2001) is more complex. Whilst the central problem is again the assumption that an individual will interact with all members of her population, the structure of Shennan's (2001) model is quite different in that it considers the 'fitness' of multiple cultural traits rather than a broad measure of skill. As outlined above, the IGM suggests that the size of the population will affect the number of encounters that occur at the population level per unit time for given population density and mobility combinations, even though it will not affect the individual encounter rate. This implies that when a given innovation appears it may spread to a greater *number* of individuals per unit time in a larger population, but that the *proportion* of the population that the innovation spreads to per unit time is unaffected by population size. If the rapid spread of an innovation to a large number of people is important to that innovation's longer-term survival, therefore, it remains possible that innovations occurring in larger populations will be more likely to survive. If it is also assumed that there is a per capita innovation rate, and therefore that innovations are more likely per unit time in larger populations, it is possible that population size could influence rates of cultural innovation and transmission in subtle ways not accounted for in the model presented here.

5.3. Networks and higher-order effects

The results of the simulations presented here are largely consistent with the predictions of the MHE as regards the relationship between encounter rate and skill level. There are some discrepancies, however, and these are most notable towards the ends of simulations that compare high and low density or high and low mobility groups. Figure 10 plots the number of neighbours an individual has against skill level after 1, 10, and 100 iterations of a single run of **Simulation 1**. Unlike Figure 2, in which individuals were discounted if they were positioned within a mobility radius of the boundary of their respective high or low density area, Figure 10 plots all 1100 individuals regardless of location. Figure 10a shows that the MHE is a good model for skill level after a single iteration; Figures 10b and 10c, however, show that the MHE is less effective at predicting skill level as the simulations

progress. Two observations concerning Figure 10c are particularly important: firstly, some individuals with just one neighbour have a skill level as high as those with as many as 19 neighbours; secondly, the median skill level is relatively constant for individuals with ≥4 neighbours.

Both these observations are explained by the higher-order effects of skill diffusion along networks of individuals in the simulation. Although an individual can only copy her neighbours, her neighbours can copy their neighbours, and so on throughout the population. This leads to a diffusion of higher skill levels throughout the population which is beyond the scope of either Henrich's (2004) original equation or the MHE presented here. To give an example, with $\alpha = 4$ and $\beta = 2$, an individual (A) with just one neighbour (B) should have a change in skill after one iteration of $z_A = -4 + 2(\varepsilon + \ln(2)) \approx -1.46$ (an individual with one neighbour has two possible models, herself and her neighbour). This negative number amounts to a maladaptive loss of skill in Henrich's (2004) terminology. If her one neighbour (B) has four neighbours, B's change in skill after one iteration should be $z_B = -4 + 2(\varepsilon + \ln(5)) \approx 0.37$; that is, B experiences an adaptive gain in skill. Assuming that none of B's neighbours has more than four neighbours, B's skill level will continue to grow at a rate of ≈ 0.37 per iteration. Since B will always have a skill level higher than A, A will simply be trying to copy B from iteration 2 onwards; her skill level in subsequent iterations will be $z_A(t) = z_B(t-1) - \alpha + \beta\varepsilon$. This demonstrates that A's skill level will become positive when $z_B(t-1) + \beta\varepsilon > \alpha$; in the example above, this occurs in the fifth iteration. Thus an individual with just one neighbour, and who is predicted by the MHE to have a steadily decreasing skill level, will in fact have a positive skill level after just five iterations due to the presence of a well connected neighbour.

Higher-order effects such as this will be common in continuous populations, with high skill levels diffusing further through populations over larger numbers of iterations. Generalising further, if you are connected to a neighbour n vertices away who has a skill level in the current iteration that is greater than $n(-\alpha + \beta\varepsilon)$, your skill level in the next iteration will be positive, regardless of the number of immediate (first-order) neighbours you have. This effect explains the majority of the discrepancies between the MHE and the simulation results shown in Figures 10b and 10c. It also explains the fact that simulated skill levels are higher than those predicted by the MHE at low population densities in Figure 7d and at low mobility values in Figure 7e.

There is, however, another effect to be considered at the opposite end of the 'connectedness' spectrum. Whilst those individuals with the fewest neighbours will often be copying their best connected neighbour, those with the most neighbours will often be copying themselves. This effect occurs because in a given iteration the individual with the most neighbours will have the greatest number of models from whom to select; in the subsequent iteration, that individual will inevitably be among the best possible models herself. A clear analogy comes from the work of Pulliam (1988) on 'sources' and 'sinks' in population regulation. In Pulliam's (1988) terms, source areas demonstrate higher birth rates than death rates and thus add to the regional population, whereas in sink areas the reverse is true. In the current model, well-connected individuals act as sources of skill, with their advances radiating out towards less-connected individuals; these less-connected individuals act as sinks, because they absorb these advances but rarely produce any of their own. A necessary corollary is that such well connected 'source' individuals will not be buoyed by their neighbours in the way that 'sink' individuals are; hence the MHE remains a relatively good model for those individuals who have the greatest number of neighbours, even after many iterations (see Figures 10b and 10c). The particular source-sink effects that occur will depend on the topology of the

network, and future research into demographic effects on cultural transmission in archaeology would benefit from studies that explicitly compare different network structures (see Cowan and Jonard 2004; Allen et al. 2013).

6. Conclusions

The analyses reported above demonstrate that population density and mobility have independent, equivalent effects on individual encounter rates, and therefore on rates of cultural transmission; conversely, population size has no effect on either of these variables. Population density and mobility are reciprocally correlated in extant hunter-gatherers, suggesting that archaeological inferences about cultural transmission based on just one of these variables are unlikely to be valid. Future research should redress the imbalance caused by a tendency to postulate population density as the sole explanation for variation in the rate of cultural change; mobility should be viewed as an equal partner in this relationship, with the ultimate goal being the explicit characterisation of the network structures characteristic of particular archaeological populations. This endeavour will be of particular importance in future analyses of the emergence and spread of particularly innovative behaviours such as those thought to characterise 'behaviourally modern' *Homo sapiens*. Accurately provenanced raw materials act as ideal markers of archaeological mobility (e.g. Pearce and Moutsiou 2014), whilst commonalities between assemblages give potential insights into the social connections between groups and how these relate to patterns of geographic separation (e.g. Coward 2013). Consideration of the archaeological proxies for mobility and network structure alongside those for population density will considerably advance our understanding of this critical phase in human evolution.

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Table Caption:

Table 1. Summary of the hypotheses and results, with references to the relevant figures. Accompanying statistics are given in the text. *Hypothesis 4 is supported only after conversion of the original distance metric to an area metric; see Section 5.1.

Figure Captions:

Figure 1. The relationship between population density, mobility, and encounter rate as predicted by the ideal gas model (IGM). The diagonals are encounter rate isoclines. Individual A is a member of a low population density, high mobility population, whilst individual B is a member of a high population density, low mobility population. The two individuals have identical encounter rates.

Figure 2. Results of Simulation 1. Skill levels after 100 iterations (A) and changes in skill per iteration (B) are significantly higher in the high population density area.

Figure 3. Results of Simulation 2. With mobility increased so as to equate the average number of neighbours an individual interacts with in the high and low density areas, skill levels after 100 iterations (A) and changes in skill per iteration (B) are no longer significantly different.

Figure 4. Results of Simulation 3. Skill levels after 100 iterations (A) and changes in skill per iteration (B) are significantly higher in the high population density area. Population size is four times that depicted in Figure 2.

Figure 5. Distributions of Z values from Wilcoxon rank-sum tests performed after each of the 100 iterations of Simulations 1-3. (A) compares the low and high density areas of Simulation 1, and (B) the low and high density areas of Simulation 2; (C) compares the low density areas of Simulations 1 and 3, and (D) compares the high density areas of these two simulations.

Figure 6. Comparison of change in skill level per iteration between the small population of Simulation 1 and the large population of Simulation 3. (A) compares the low density areas, (B) the high density areas.

Figure 7. Results of further simulations demonstrating the wider relationships between population density, mobility, and population size and encounter rates and skill levels. All simulations conform to the expectations of the modified Henrich equation (MHE) with the exception of the relationships between skill level and very low population density (D) and very low mobility (E). Simulation results are shown as median ± median absolute deviation.

Figure 8. The relationship between population density (individuals per km^2) and mobility (km / year) for the 175 groups in the hunter-gatherer dataset. The inset shows the same relationship on logarithmic axes. Data from Binford (2001: 118-129).

Figure 9. The relationship between the reciprocal of the square root of population density (km) and mobility (km / year) for the 175 groups in the hunter-gatherer dataset. The regression line show is forced through the origin. Data from Binford (2001: 118-129).

Figure 10. Skill levels after (A) 1, (B) 10, and (C) 100 iterations of Simulation 1. The red ellipse in (C) highlights individuals with only one neighbour who have skill levels indistinguishable from those with as many as 19 neighbours.

Tables

Table 1

	Hypothesis	Supported?	Figures
1	Encounter rate has a positive, linear relationship with population density	Yes	7a
	Encounter rate has a positive, linear relationship with mobility	Yes	7b
2	Average change in skill level has a positive, logarithmic relationship with population density	Yes	2, 4, 7d
	Average change in skill level has a positive, logarithmic relationship with mobility	Yes	3, 7e
3	Encounter rate has no relationship with population size	Yes	7c
	Average change in skill level has no relationship with population size	Yes	5, 6, 7f
4	To maintain constant encounter rate, population density and mobility must scale reciprocally	Yes*	8, 9

Figures

Figure 1

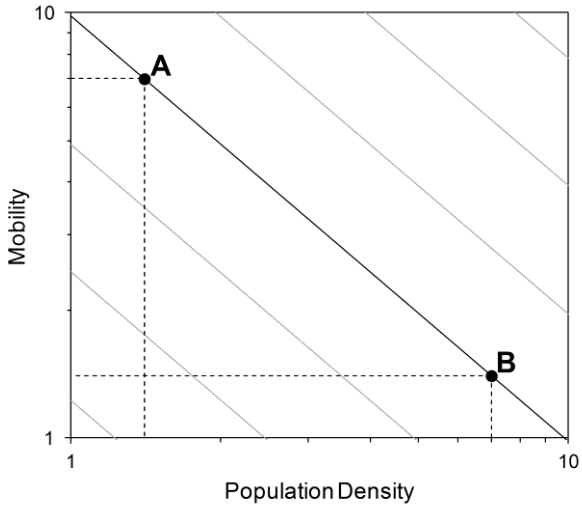

Figure 2

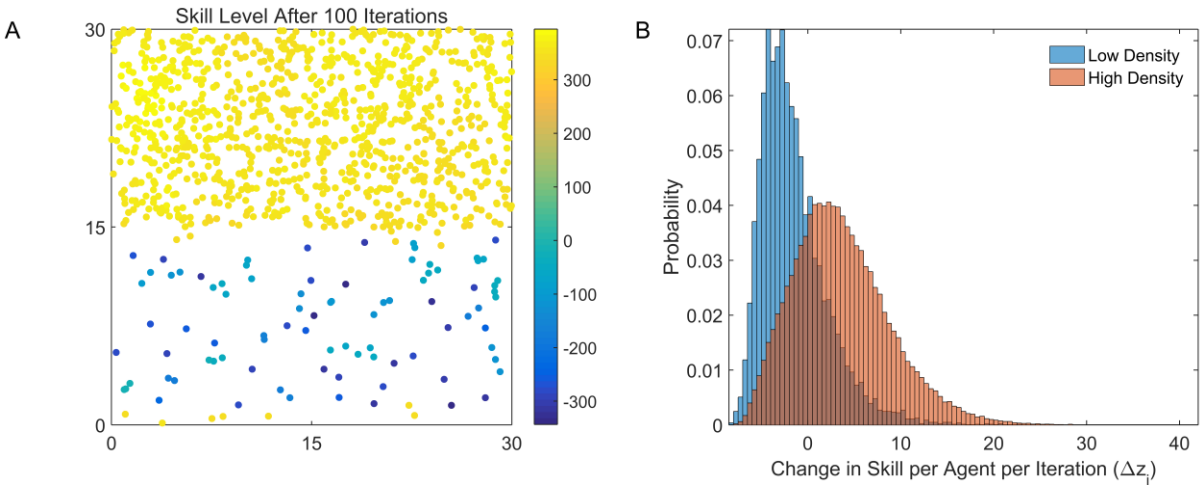

Figure 3

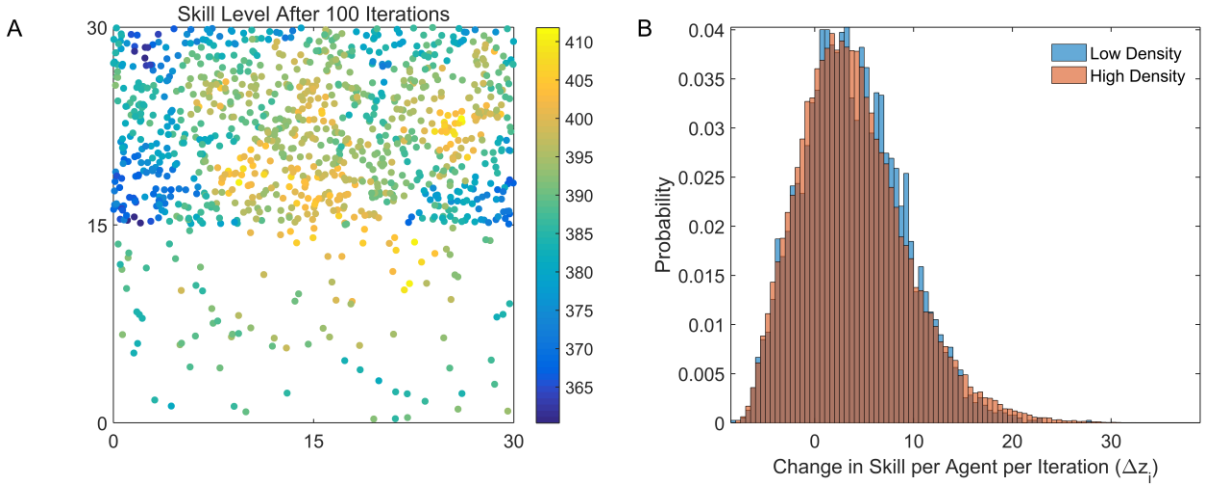

Figure 4

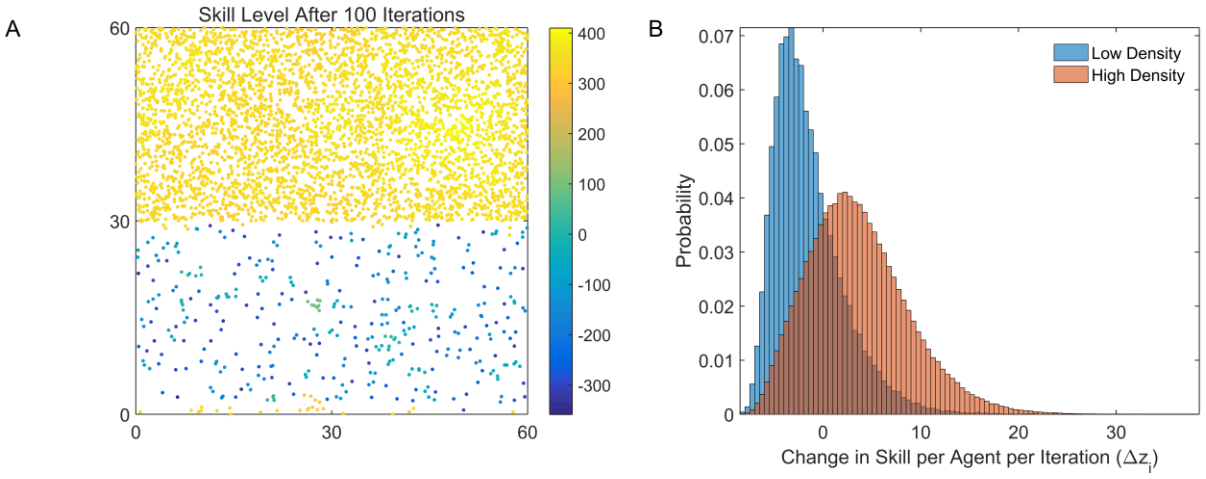

Figure 5

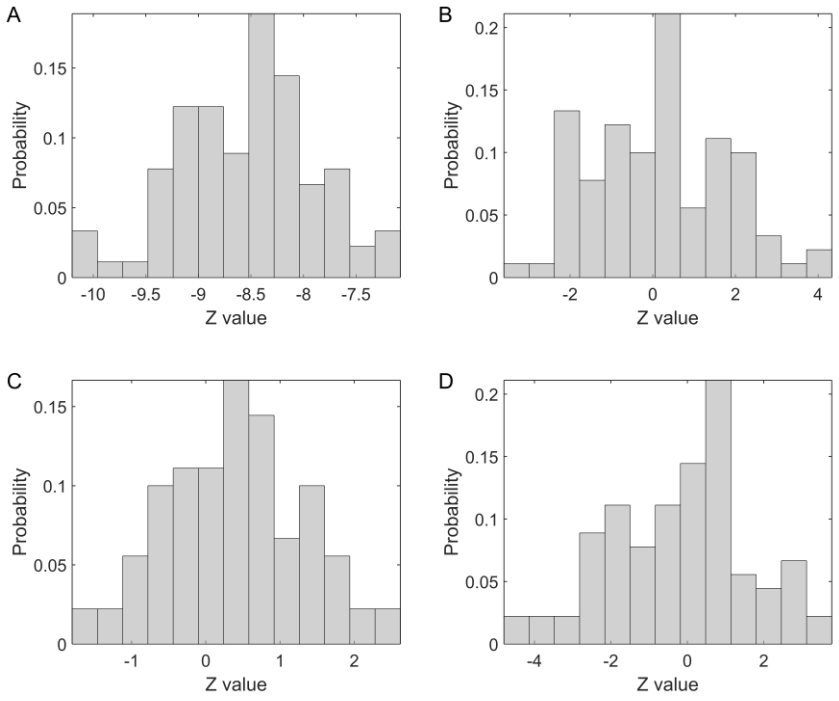

Figure 6

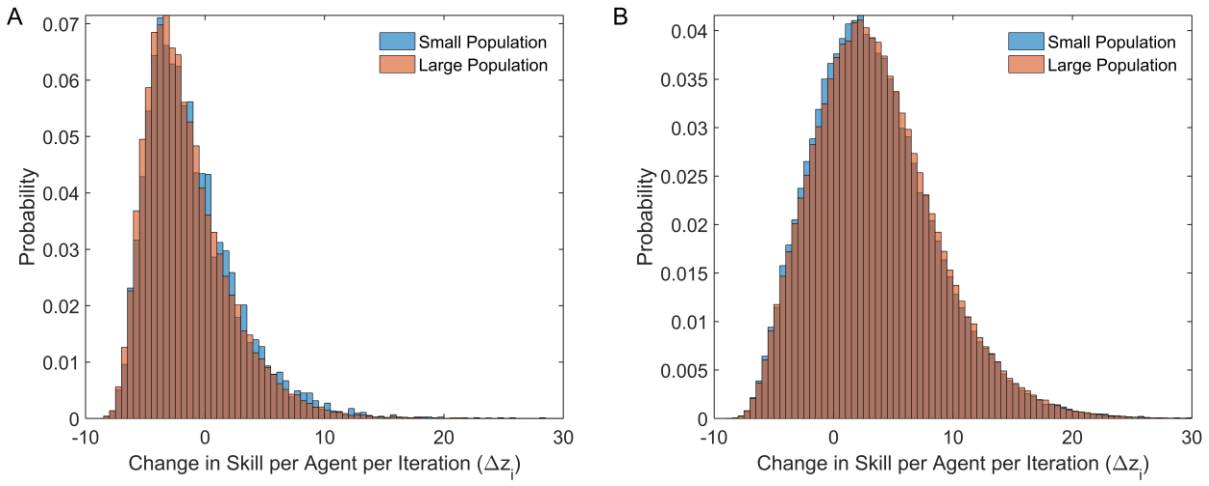

Figure 7

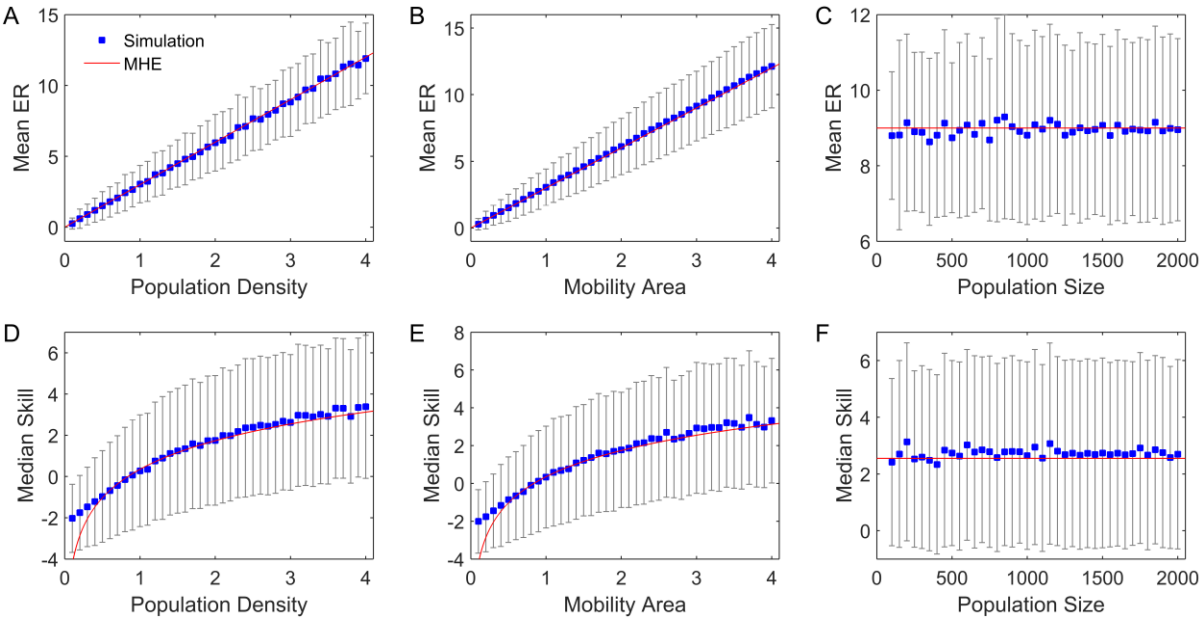

Figure 8

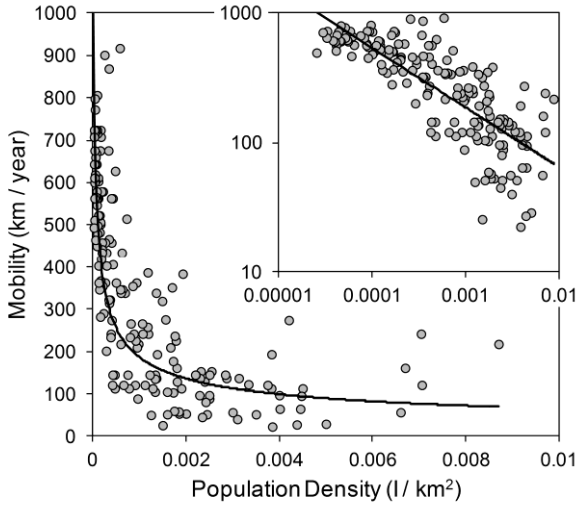

Figure 9

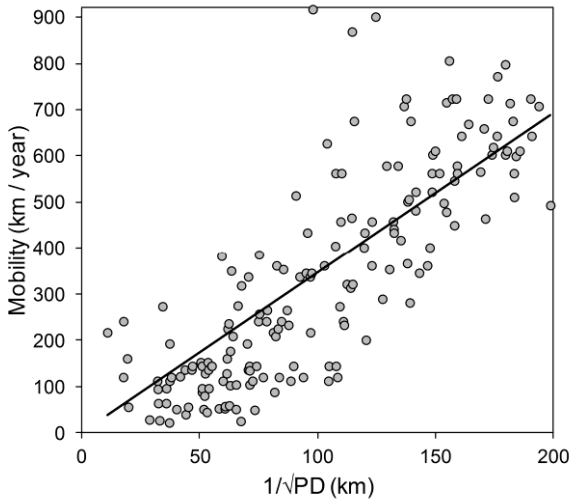

Figure 10