Human Biology

Volume 81
Issue 2 *Special Issue on Demography and Cultural Macroevolution*
Article 2

2009

Human Dispersals: Mathematical Models and the Archaeological Record

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Recommended Citation

Steele, James (2009) "Human Dispersals: Mathematical Models and the Archaeological Record," Human Biology: Vol. 81: Iss. 2-3, Article 2. Available at: http://digitalcommons.wayne.edu/humbiol/vol81/iss2/2

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Abstract

The theoretical literature on human population dispersal processes at the large time and space scale is reviewed, including references to and discussions of relevant empirical data. The basic Fisher-KPP reaction-diffusion system is summarized for the single population situation, and developments relating to the Allee effect, density-dependent dispersal, time delay, advection, spatial and temporal heterogeneity, and anomalous and stratified diffusion are reviewed. Two- and three-population competitive reaction-diffusion systems of Lotka-Volterra type are also reviewed, as are dynamic approaches to carrying capacity that incorporate predator-prey instabilities, ecosystem engineering, and gene-culture coevolution.

Keywords

Fisher-KPP reaction-diffusion system, Lotka-Volterra system, Allee effect, density-dependent dispersal, time delay, advection, spatial and temporal heterogeneity, anomalous and stratified diffusion, biological invasions, human population dispersal, Paleolithic, Neolithic, radiocarbon dating, carrying capacity.

Cover Page Footnote

I am very grateful to Anne Kandler and Tim Sluckin for clarifying my understanding of these systems and to Anne and two anonymous referees for commenting on an earlier draft.

Human Dispersals: Mathematical Models and the Archaeological Record

JAMES STEELE[1]

Abstract The theoretical literature on human population dispersal processes at the large time and space scale is reviewed, including references to and discussions of relevant empirical data. The basic Fisher-KPP reaction-diffusion system is summarized for the single population situation, and developments relating to the Allee effect, density-dependent dispersal, time delay, advection, spatial and temporal heterogeneity, and anomalous and stratified diffusion are reviewed. Two- and three-population competitive reaction-diffusion systems of Lotka-Volterra type are also reviewed, as are dynamic approaches to carrying capacity that incorporate predator-prey instabilities, ecosystem engineering, and gene-culture coevolution.

Dispersal Models and Case Studies: Fisher-Skellam-KPP

In this paper I review mathematical models of population dispersals and consider some archaeological applications. The focus is on deterministic approaches using differential equations. These have the virtue of enabling a good understanding of the behavior of a model system and are reasonable approximations for large-population situations. In such cases, systematic empirical deviations from the expectations of the modeled system can be taken as indicating the need for an additional parameter or for some alternative treatment of an existing parameter. Note, however, that where the process being studied involves only small numbers of individuals, it may be more difficult to distinguish such situations from ones in which the observed deviations are merely the result of chance effects of sampling from among the possible individual trajectories.

Understanding large-scale human dispersals requires us to model two components: a population growth process and a spatial spreading process (when more than one population is involved, we must also consider the nature of the interaction). In population ecology the standard model of the nonlinear dynamics of

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Human Biology, April–June 2009, v. 81, nos. 2–3, pp. 121–140.

KEY WORDS: FISHER-KPP REACTION-DIFFUSION SYSTEM, LOTKA-VOLTERRA SYSTEM, ALLEE EFFECT, DENSITY-DEPENDENT DISPERSAL, TIME DELAY, ADVECTION, SPATIAL AND TEMPORAL HETEROGENEITY, ANOMALOUS AND STRATIFIED DIFFUSION, BIOLOGICAL INVASIONS, HUMAN POPULATION DISPERSAL, PALEOLITHIC, NEOLITHIC, RADIOCARBON DATING, CARRYING CAPACITY.

such processes is the reaction-diffusion system defined by R. A. Fisher (1937) and applied to population expansion by J. G. Skellam (1951); the system was also investigated simultaneously to Fisher's paper by Kolmogorov, Petrovsky, and Piskunov (1937), with somewhat greater mathematical detail. Thus in ecology the usual references are to the Fisher equation or the Fisher-Skellam model, whereas in mathematics the usual reference is to Fisher-KPP or KPP-Fisher or simply the KPP equation. In the present paper, I use the term Fisher-Skellam. The basic system is

$$\frac{\partial n}{\partial t} = f(n,\alpha,K) + D\nabla^2 n, \tag{1}$$

where $n(\mathbf{r}, t)$ denotes the population density at time t and at position $\mathbf{r} = (x, y)$. This system has two components: a nonlinear population growth (or reaction) term and a linear population dispersal (or diffusion) term. $f(n, \alpha, K)$ is the population growth function, which in the Fisher-KPP equation follows the logistic growth law proposed by Verhulst (1838) and widely used in theoretical population biology (Murray 1993). This function describes a self-limiting density-dependent population increase and is given by

$$f(n,\alpha,K) = \alpha n\left(1 - \frac{n}{K}\right), \tag{2}$$

where α is the intrinsic maximum population growth rate and K is the carrying capacity, which is related to local environmental factors. D is a diffusion constant that specifies the mean spatial dispersal rate of individuals between birth and reproduction, and ∇^2 is the Laplacian operator that redistributes the population from regions of higher density into those of lower density (for simplicity I use the Laplacian operator in the equations in this paper; however, many recent investigators use an integral formulation that allows variably shaped dispersal kernels). In general, individuals move from their birthplace a distance λ during their generation time τ. The square of this distance is, in general, proportional to the time available (this is a standard random walk result); the constant of proportionality is the diffusion constant $D = \lambda^2/2d\tau$, where d is the number of dimensions in the system being modeled, typically 1 or 2 (Einstein 1905). The width of the wave front region, over which the population changes from a high to a low density, can be shown to depend on D and α and to have an intrinsic spatial scale $\xi \sim (D/\alpha)^{1/2}$. The speed v at which this wave front travels is also related to D and α, tending asymptotically to approach $v = 2(D\alpha)^{1/2}$ (Fisher 1937; Kolmogorov et al. 1937).

Prehistoric and Historical Human Population Dispersals

It is no trivial matter to resolve the detailed demographic processes involved in prehistoric dispersals. Much effort has been expended on estimating speeds of spatial population expansion, because the relation between the speed v and the product $D\alpha$ implies that speed is determined by population growth and diffusion rates. Archaeologists have found that radiocarbon dating can be used to obtain sufficiently precise estimates of the age of cultural events at different spatial locations for this purpose, although there are many subsidiary methodological and sampling issues that need to be addressed before the results can bear close examination. With the advancement of radiocarbon measurement and calibration techniques, we are seeing the application of accurate and precise dating to increasingly remote episodes of human dispersal during and subsequent to the last ice age.

For hunter-gatherer dispersals, early applications of the Fisher-Skellam model to Paleolithic dispersal problems include the studies of Young and Bettinger (1995) and Steele et al. (1996, 1998), none of which focus specifically on front speeds (partly because of limits on the accuracy and precision of available archaeological dates). Studies focused on front propagation speed include Mellars's (2006) attempts to estimate the speed of spread of anatomically modern humans into Europe before the last glacial maximum; Housley et al.'s (1997) and Fort et al.'s (2004) studies of the rate of subsequent late glacial recolonization of northern Europe as the ice receded; and Hamilton and Buchanan's (2007) study of the diffusion of Clovis spear point technology in late glacial North America. For agricultural dispersals several studies have been conducted on the chronology of the European Neolithic transition, and a more limited number of studies have been made on the Lapita period colonization of Polynesia; a more recent event studied from a Fisher-Skellam perspective but using historical records as a source of empirical control is the European colonization of the American West.

Mellars's (2006) study illustrates the potential and pitfalls of using radiocarbon dates to estimate dispersal velocities. Mellars collated radiocarbon dates from sites in Europe and the Near East associated with stone tool technology of Emiran, Ahmarian, Bacho-Kirian, Bohunician, Proto-Aurignacian, and Aurignacian technologies, all of which are believed to be the products of anatomically modern humans. He took the oldest dates from each region, on the assumption that these samples were, by virtue of their greater age, the least likely to have been contaminated by more recent carbon, and calibrated them using a mean best-fitted line for a comparison curve that summarizes a number of data sets extending beyond the range of the IntCal04 calibration curve (for which the upper bound is 26,000 cal. BP). Mellars then commented that the obtained results indicated a significantly faster rate of spread of anatomically modern humans into Europe than that previously estimated. Specifically, he suggested that the dispersal of anatomically modern humans from southeast Europe into central and western Europe now seems to have taken 5,000 calibrated years (rather than 7,000 uncalibrated radiocarbon years) and that this implies a spread speed of 0.4 km/yr rather than 0.3 km/yr (this velocity calculation is inexact; the distances from Mellars's only plotted southeast European site with a date, Bacho-Kiro in Bulgaria, to the most distant dated sites in Spain and France are of the order of 2,500 km, which implies a mean spreading velocity of 0.5 km/yr).

Mellars's calibration arguments were the object of justified criticism by Turney et al. (2006), but the greater significance of his results for the demographic models considered here is their confirmation of a rather slow asymptotic front speed for anatomically modern humans advancing into Europe. In terms of the Fisher-Skellam model, we might therefore ask whether there is need for an additional term in the model—either an expansion of the system as a Lotka-Volterra two-species competition model that takes account of Neanderthal presence in the region, or a temporal heterogeneity in the environmental parameters affecting the migration of the anatomically modern human population front.

Some light has been shed on this problem through a series of studies of the radiocarbon record of hunter-gatherer recolonization of northern Europe as the ice receded after the last glacial maximum (which was of course by anatomically modern humans, the Neanderthals having by then become extinct). Fort et al. (2004) fitted a slightly modified version of the Fisher-Skellam model to this spread episode, as documented archaeologically by a series of radiocarbon dates obtained by Housley et al. (1997). Fort et al. (2004) estimated D and α from modern ethnographic cases and obtained a maximum rate of increase α in the range 0.017–0.027 per year, or 1.7–2.7%, and a mean dispersal rate D of 1,400–3,900 km^2/generation (with mean generation time estimated as 27 years) based on observations of marriage distances among Aka and Bofi-Aka African pygmies (Hewlett et al. 1986). From these estimates they predict an asymptotic population front speed of between 0.7 and 1.4 km/yr, which is consistent with the range estimated from the archaeological data by linear regression (0.4–1.1 km/yr). They therefore concluded that no additional term (such as temporal heterogeneity in the environmental parameters affecting the migration of the recolonization front) was needed to explain the spread rates observed. If these arguments are correct, then they also indicate the potential scale of any retardation of the front speed for anatomically modern humans in Mellars's (2006) study for which an additional term might be necessary.

However, the territory sizes (which give a length scale to the distribution of marriage distances) of high-latitude Ice Age hunter-gatherers should probably be estimated from an Inuit ethnographic analogy: High-latitude hunters typically have much larger territories than equatorial foragers (e.g., Binford 2001; Kelly 1995), which has implications for the expected recolonization rate if there really was no delay induced by the deglaciation process. A further note of caution is that the empirical front speed estimates of Fort et al. (2004) are based on the mean values of a small sample of uncalibrated radiocarbon dates, whereas Mellars's estimates were based on his own attempt at calibration; indeed, Mellars's (2006) main claim of a faster than expected spreading rate is based on a comparison of the dispersal chronologies obtained with and without calibration. There is therefore scope for further useful work on resolving front speeds from a purely archaeological science perspective (see Steele 2009).

A recent study by Hamilton and Buchanan (2007), much along the lines of Fort et al.'s (2004) analysis, addresses the dated Clovis sites of late glacial North America. Waters and Stafford (2007) had suggested that there was no discernible spatial gradient in the ages of reliably dated early Paleo-Indian sites in the Western

Hemisphere, but Hamilton and Buchanan (having supplemented Waters and Stafford's Paleo-Indian data set with a small number of additional sites taken from the literature) found a statistically significant trend for the North American Clovis culture sites to become younger with distance from a postulated origin at the southern end of the ice-free corridor. Their regression analysis indicated a front speed in the range 5–8 km/yr, which is much faster than that expected from the demographic parameters of Fort et al.'s (2004) hunter-gatherer model. Hamilton and Buchanan explain this as an effect of selective dispersal by Clovis hunters along favorable habitat corridors. Whether or not they are right about the Clovis spread dynamic (see Steele 2009), it is clear from our own work that humans reached southern South America much earlier than can be explained by a front traveling at that speed and originating in Alberta at about 13,380 cal. BP [95% CI: 12,900–13,870 cal. BP, as estimated by Hamilton and Buchanan (2007); see Steele and Politis (2009)]. Once again there is scope for archaeological science to contribute further empirical observations before the demographic questions can be satisfactorily resolved.

For the spread of farming, the classic study is the work of Ammerman and Cavalli-Sforza (1984); their study introduced the Fisher-Skellam system to archaeologists, who typically now refer to this variant as the wave-of-advance model. Ammerman and Cavalli-Sforza fitted a linear regression curve to dates and distances from Jericho, finding a mean rate of spread of about 1 km/yr and finding this to be consistent with the spreading speed predicted for a Fisher-Skellam system with ethnographically derived values for the demographic terms.

More recently, the radiocarbon record has been revisited by Gkiasta et al. (2003) and Pinhasi et al. (2005). Gkiasta et al. (2003) fitted a linear regression curve to dates from a set of 510 archaeological sites in Neolithic Europe and explored other line-fitting and visualization techniques. Pinhasi et al. (2005) fitted a linear regression curve to dates from a set of 735 archaeological sites in Europe and the Near East using various origins and two possible distance measures and found an average rate of spread for the Neolithic transition in the range of 0.6–1.3 km/yr. Pinhasi et al. (2005) found that this spread rate was consistent with predictions from a slightly modified Fisher-Skellam model of demic diffusion, taking anthropological estimates of 2.9–3.5% annually for α and a mean dispersal rate $D = 1{,}400\text{–}3{,}900\ \text{km}^2/\text{generation}$, with 29–35 years for the generation time τ. They noted that although these archaeological data might in principle be consistent with a wave of adoption-diffusion of an economic innovation without population turnover, the interpretation of the process as a demographic expansion was supported by the fact that to their knowledge, no cultural diffusion model to date has been able to derive a speed compatible with the observed range for this case study (0.6–1.3 km/yr).

Fort (2004) has also attempted to fit the Fisher-Skellam model to the colonization of Austronesia by using a regression analysis of dates and distances from Mussau. He found from the oldest site in his data set that the Lapita phase spread with a velocity of at least 8 km/yr. Fort suggests that for this episode a maximum growth rate $\alpha = 0.032 \pm 0.003$ per year, a generation time $\tau = 25 \pm 5$ years, and a mean dispersal rate D of 3.6×10^3 to 3.0×10^5 km^2/generation (the higher rate reflecting the greater distances of transfers between islands) would yield spreading rates in the observed range, but he also acknowledges the limited resolution of the existing archaeological chronology.

Finally, Campos et al. (2006) attempted to model the westward expansion of European American settlers during the period 1790–1910, for which an average front speed of 13.5 ± 0.8 km/yr was estimated from a historical atlas. With $\alpha = 0.031$ per year, a generation time $\tau = 25$ years, and a mean individual dispersal distance in the east-west axis of $\lambda = 810 \pm 93$ km (based on a sample of historical records), the Fisher-Skellam system predicts a one-dimensional front speed of about 40 km/yr, which is more than twice the observed rate. Campos et al. (2006) therefore introduced an additional argument about the spatial delay introduced when dispersal is along fractal river networks, with side branches being the equivalent of wrong turns; the mathematical arguments and the use of historical demographic records are creative and interesting, and this case study would repay further work with closer attention being given to the empirical dispersal distance distributions and population front characteristics. A subsequent model of the same process (colonization of the United States in the 19th century) by Fort and Pujol (2007) argues that the spread rate might be more simply explained by anisotropic diffusion (i.e., a higher probability to back-migrate eastward rather than westward), without any need to assume that any properties of fractal networks apply to this process.

Further Considerations in Modeling Dispersal Processes

Having considered the basic Fisher-Skellam system and some applications to the study of human dispersals, I now turn to some further modeling considerations. It is worth emphasizing that in considering alternative treatments of basic parameters in the Fisher-Skellam system, my intention is not to open up a large menu of options that can be selected to optimize the fit of the model to an empirical data set based on no other considerations. This would introduce many additional degrees of freedom into the model, thereby reducing its ability to generate useful explanations. However, if the assumptions of the basic Fisher-Skellam system can be seen to be at odds with observed behavior of the system being modeled or to be in some important way unphysical, then it is useful to explore the effects of alternative and more realistic treatments of these elements of the model system to see whether or not the discrepancy matters (e.g., for the prediction of front speeds). If one can estimate the relevant parameters independently, then there is no loss of explanatory power but there is a gain in realism from incorporating one's findings into the modeled system. Hastings et al. (2005) give a useful brief overview.

Allee Effect. At low densities, local populations are at greater risk of extinction because of sampling and group size effects on fertility and survivorship (imbalanced sex ratios, asynchronous reproductive timing among potential mates, inbreeding depression, reduced efficiency in cooperative foraging and in predator avoidance, etc.). W. C. Allee (1938) focused attention on situations in which population density has a positive effect on some fitness-related characteristic. Where that characteristic is a demographic one, namely, the rate of reproductive increase, then the effect may be strong (or critical) (meaning that below a certain density threshold the population experiences negative growth) or weak (noncritical) (meaning that the rate of growth below that threshold is depressed but remains positive). For invading species, local populations at the front are susceptible to Allee effects of this kind. Taylor and Hastings (2005) give an excellent review.

For primates (including humans), social structure has a major influence on the existence and strength of the Allee effect at low population densities. If the population is subdivided into autonomous foraging groups and if those groups are of uniform size, then the risks are much greater than if group sizes vary with a substantial fraction of the whole population concentrated in the largest groups (Dobson and Lyles 1989). This is because with variable group sizes and a small number of large groups, the average number of potential partners available to each reproductively fertile individual is much greater than in a uniform distribution (for a constant total population size). Human hunter-gatherers in seasonal environments are generally thought to solve these kinds of problems in part by varying their group sizes over time, with periodic seasonal aggregation into large groups (e.g., Kelly 1995).

In the Fisher-Skellam system, a strong or critical Allee effect can be represented by an additional term A:

$$\frac{\partial u}{\partial t} = ku(1-u)(u-A) + D\nabla^2 u, \tag{3}$$

where population size n is normalized to the interval $0 < u \leq 1$, $0 < A \leq 1$, and k is a normalized growth rate constant [if maximum per capita growth rate is 1, then $k = 4/(1 - A)^2$] (Lewis and Kareiva 1993). In this system, where population size is below a critical fraction A of the carrying capacity, a strong Allee effect applies and local population growth is negative.

Lewis and Kareiva (1993) showed that the consequence of this for front speed is to decelerate the front proportional to the magnitude of the threshold A: $v = (2Dk)^{1/2}\left(1/2 - A\right)$. For a successful invasion with positive front speed, it follows that A must be less than 0.5. With $A = 0.3$, the front is decelerated to less than half of the speed expected from the basic Fisher-Skellam system. Lewis and Kareiva (1993) also commented that habitat geometry plays a role in determining invasion success; a front that extends on a finger of colonized habitat surrounded by uncolonized area will be more susceptible to extinction as a result of Allee effects than the converse situation, because of the imbalance between the sizes of the source and adjacent sink locations, which are the recipients of local density-dependent diffusion.

Density-Dependent Dispersal. As previously noted by Steele et al. (1998), the assumption of symmetry in the distribution of dispersal distances in two dimensions can also be called into question. Symmetry is a feature of the logistic model of density-dependent growth such that as a population approaches carrying capacity, there is a linear decline in the net rate of increase. Consequently, if we assume a colonizing population of fitness maximizers seeking to maximize their individual reproductive rate, then we will predict that people will disperse preferentially into those areas of adjacent habitat in which human occupancy is furthest from carrying capacity.

However, positive density-dependent dispersal may not in itself imply accelerated rates of range expansion. Newman (1980) [for more recent considerations of this topic, see also Petrovskii and Li (2003) and Lutscher (2008)] found that when the diffusion coefficient has the density-dependent form $D(n/K)^b$, the velocity of range expansion can be expressed in the form $u(2D\alpha)^{1/2}$, with u a function of b. When $b = 0$, $u = 2^{1/2}$, consistent with the standard Fisher-Skellam model solution. When $b > 0$ and people move further as the population approaches carrying capacity, then it seems that $u \approx (b + 1)^{-1}$. It follows that if $b = 1$, then individual dispersal distances when $n = K$ (and dispersal distance is assumed to be greatest due to crowding) must be at least three times the value taken for mean lifetime dispersal distance in the standard model in order for range expansion to be faster and not slower than in the standard model.

By contrast, when $b < 0$ (such that dispersal distances are greatest at low densities, as a result of, for instance, mate searching), Newman (1980) found that u assumes any value. We might then expect that density-dependent dispersal will accelerate range expansion when it is negatively density dependent and driven by mate searching and when α is low, such that at a given location, n is slow to approach K. This theoretically possible dynamic was explored mathematically by King and McCabe (2003). Behaviorally, however, the underlying process here is conspecific mate attraction, the importance of which for demographic survival has been emphasized in animal ecology (Wells et al. 1998). Because the greatest density of potential mates will be found behind the front, negative density-dependent dispersal driven by mate search would be expected to lead to anisotropic dispersal with a bias against the direction of migration of the expanding front, which would have a decelerating effect.

Time Delay. The basic Fisher-Skellam system assumes continuous random movement and a constant likelihood of reproduction by individuals in a population, but empirical estimates of human dispersal distances are usually obtained from marriage transfers, which represent one-off movements at or shortly before the time of first reproduction. Ecologists have considered the effects of age- and sex-structured dispersal on front speeds (e.g., Van den Bosch et al. 1990, 1992), but Fort and colleagues (e.g., Fort and Mendez 1999, 2002; Ortega-Cejas et al. 2004) have considered in greatest detail the implications for Fisher-Skellam systems of a time delay between birth and dispersal. They showed that a time-delayed reaction-diffusion system that is otherwise of Fisher-Skellam type leads to a front speed that is lower than the classical Fisher-Skellam result and that the effect is related to the size of the delay: $v = [2(D\alpha)^{1/2}]/(1 + \alpha\tau/2)$, with τ representing the delay time between birth and dispersal (estimated as the generation time, to a first approximation). For the demographic values typically used for human dispersals, $\alpha\tau \sim 0.03(25)$ implies that front speed in the time-delayed model will be approximately $0.73v$, where v is the speed estimated from the classical Fisher-Skellam relation $v = 2(D\alpha)^{1/2}$. The front speeds estimated by Fort and co-workers and by Hamilton and Buchanan (2007) and discussed in a previous section, were derived using this formula for time-delayed dispersal. It would seem to be a sensible correction to apply when estimating front speeds for agricultural dispersals; the relevance for highly mobile hunter-gatherer populations is perhaps less obvious (cf. Surovell 2000).

Spatial and Temporal Heterogeneity. A number of investigators have considered the effects of environmental heterogeneity on dispersal dynamics, both in space and over time. This is the situation in which parameters of the Fisher-Skellam model (D, α, K) vary with location and/or with time as a result of external factors. Such variation in space and time is intuitively more realistic as an approximation of the geographic conditions that affected dispersing human populations, given that humans are generalists in overall distribution but are specialized in their local adaptations. The problem with incorporating heterogeneity into a model is that it improves the realism of the representation of a given situation but at the expense of generality: What works in describing observed dynamics of one highly parameterized case may not apply to another case that is parameterized differently (Hastings 2005). However, some work has been done on generalizable aspects of environmental heterogeneity.

Shigesada et al. (1986, 1987) have shown that a front traveling through randomly distributed (isotropic) patches of favorable and unfavorable habitat, each with its own values for D and α, will propagate with locally varying rates but nonetheless at an overall mean speed $v = 2(D\alpha)^{1/2}$, with D estimated as the harmonic mean and α as the arithmetic mean of the values over the space being invaded. Kinezaki et al. (2003) considered the same problem in a somewhat more complex two-dimensional space, and Kinezaki et al. (2006) considered front speed dynamics in sinusoidally varying environments. Neubert et al. (2000) meanwhile considered the complementary case in which there is periodic or random environmentally driven variation in the values of D and α over time, as might also occur as a result of predator-prey interaction instabilities.

In archaeology, Young and Bettinger (1995) modeled the first global dispersals of anatomically modern human hunter-gatherers using two sets of values for D and α, one for low and one for higher latitude environments. Steele et al. (1996) demonstrated the consequences for front contours in two dimensions when the front propagates at varying speeds at the ecoregion scale, and Steele et al. (1998) considered the consequences of spatial and temporal heterogeneity in K at the same scale in a highly parameterized model of the first peopling of North America. In their 1998 paper, Steele and co-workers found that the archaeological response variable was not first arrival time but the cumulative occupancy signature when the archaeological signal is the time-averaged density of discarded artifacts. Hazelwood and Steele (2004) considered this more generally, showing that where an invading population travels up a gradient of carrying capacity, the initial density gradient in cumulative occupancy will point to the origin of the dispersal but that subsequently this will be washed out by the effect of the greater carrying capacity at locations distal to the entry point. Spatial heterogeneity is also a feature of recent models of the European Neolithic transition by Davison et al. (2006) and Ackland et al. (2007).

Advection. The basic Fisher-Skellam system assumes that dispersal is isotropic; that is, movement is equally likely in all directions and serves to redistribute population to achieve uniform densities, regardless of local variation in the concentrations of resources. In many biological systems at a range of scales, movement is anisotropic at the population level and there is preferential migration up resource concentration gradients. Incorporation of this leads to a reaction-advection-diffusion system with (if we take the concentration gradient to be in units of K, the spatially varying carrying capacity) an additional term $\chi(K)\nabla K$:

$$\frac{\partial n}{\partial t} = \alpha n\left(1 - \frac{n}{K}\right) + D\Delta n - \chi(K)\nabla K \nabla n, \tag{4}$$

where ∇K denotes the concentration gradient and $\chi(K)$ is a sensitization parameter that denotes the magnitude of the response to that gradient (Hazelwood et al. 2008). This system is not immediately susceptible to a general analytical solution for front speeds in different directions relative to the concentration gradient. However, one can readily observe that this system has two spatial components, namely, conventional diffusion plus the advection term (purely advective spread would have the disadvantageous consequence of confining the population on a local concentration peak). In the reaction-advection-diffusion system, the advection component will accelerate spread up gradients of concentration and retard invasion of less attractive regions; as a rough rule of thumb, the advection component will be the predominant influence on the spread dynamic where concentration gradients are steep enough to double on the diffusion length scale λ (Hazelwood et al. 2008). Advection was considered a component by Cohen (1992) in a model of front dynamics for the European Neolithic transition and by Davison et al. (2006) in a model with localized advective spread toward the Danube River corridor.

Anomalous and Stratified Diffusion. The standard treatment of diffusion in the Fisher-Skellam system uses the value of the average (root mean square) dispersal distance of individuals in a population. This single value permits a good approximation of the effects on front width and propagation speed of a random distribution of dispersal distances where that distribution is approximately Gaussian in shape. This restriction is appropriate for a conventional random walk process if all individuals are broadly comparable in their dispersal characteristics. However, in many empirical instances of both animal and human movement, it seems that the distribution of individual displacements may be more leptokurtic than in a Gaussian distribution (with higher frequencies of both short-distance and long-distance movements). The implications of such fat-tailed distributions have received particular attention, where the probability that any individual's straight-line dispersal distance is of length L in a given time interval decays slower than exponentially with increasing L. In such cases, the average (root mean square) distance is no longer adequate to approximate the effects on the front dynamics of the full dispersal distribution (or kernel).

The effect of fat-tailed kernels (e.g., power-law kernels) on Fisher-Skellam dynamics is to accelerate front speeds, and there may no longer be any stabilization at an asymptotic front speed—in the continuum limit, the front will accelerate indefinitely (e.g., Kot et al. 1996). In reality, however, the probability of individuals moving exceptionally long distances is low, even for the power-law distribution, and a cutoff is necessary for the modeled reaction term to ensure that no growth occurs where $n(x, t)$ is of subinteger value; the effect of this is to stabilize the front at a constant asymptotic speed that scales with the carrying capacity of the locally interacting population but that is still likely to be fast (Brockmann and Hufnagel 2007; cf. Clark et al. 2001).

Stochastic factors are likely to be influential in the evolution of a front driven by dispersal behavior of this kind, and the consequence may be a chaotic-seeming series of outbreaks of secondary dispersal foci ahead of the main front. This process is obviously antagonistic to the Allee effect, and the interaction of the two processes might well cancel out most of the effect of leptokurtic movement distributions on front speeds for species with small carrying capacities and low reproductive rates.

Finally, Shigesada et al. (1995) considered the related situation in which dispersal is strongly bimodal, with most dispersers moving short distances (neighborhood diffusion, producing a constant front speed) but with a small number of dispersers successfully relocating over long distances. They showed that the long-distance dispersal by a small group causes the effective radius of the total population range to expand at an accelerating rate, although the geometry of the range boundary will be more complex with multiple secondary foci ahead of the main front. The implications of fat-tailed distributions for human population expansions have been considered (albeit only briefly and qualitatively) by Brown et al. (2007) for early Paleo-Indians and by Lilley (2008) for the Lapita phenomenon in the Pacific.

Two- and Three-Population Models

Having now considered the basic Fisher-Skellam system for a single population undergoing an episode of expansion, I now consider the more complex case in which the invading population comes into contact with (and perhaps into competition with) a second preexisting population that already occupies the invaded region. I deal here with only n population extensions of the Fisher-Skellam reaction-diffusion system; for other approaches as applied to human prehistory, see Ray and Excoffier (2009) (this issue) and Currat and Excoffier (2004). The basic equations here are for a Lotka-Volterra competition system:

$$\frac{\partial n_1}{\partial t} = \alpha_1 n_1 \left(1 - \frac{n_1}{K_1} - c_1 \frac{n_2}{K_2}\right), \tag{5a}$$

$$\frac{\partial n_2}{\partial t} = \alpha_2 n_2 \left(1 - \frac{n_2}{K_2} - c_2 \frac{n_1}{K_2}\right), \tag{5b}$$

where the subscript denotes one or the other of the two populations and c_i is a competition coefficient that represents the influence of its competitor on the growth of each population *i*. The outcomes of this competition are determined by the carrying capacities and competition terms (Neuhauser 2001): The coexistence condition occurs when $c_1 < K_1/K_2$ and $c_2 < K_2/K_1$, and the competitive exclusion condition occurs when $c_j > K_j/K_i$ and $c_i < K_i/K_j$ (with population *j* going extinct). If both $c_1 > K_1/K_2$ and $c_2 > K_2/K_1$, then eventually one population will go extinct, but which one depends on the initial densities.

Addition of an isotropic diffusion term (e.g., Okubo et al. 1989) produces the reaction-diffusion system

$$\frac{\partial n_1}{\partial t} = D_1 \nabla^2 n_1 + \alpha_1 n_1 \left(1 - \frac{n_1}{K_1} - c_1 \frac{n_2}{K_1}\right), \tag{6a}$$

$$\frac{\partial n_2}{\partial t} = D_2 \nabla^2 n_2 + \alpha_2 n_2 \left(1 - \frac{n_2}{K_2} - c_2 \frac{n_1}{K_2}\right). \tag{6b}$$

This system has been used in archaeology by Young and Bettinger (1992) to model competition between populations speaking Numic and pre-Numic languages in the American Great Basin in the second millennium AD.

A similar system has been studied for the European Neolithic transition by Fort et al. (2008), but with the sign of the interaction term changed for one of the populations (so that the interaction takes the form of one-way conversion rather than mutual competition-interference):

$$\frac{\partial n_1}{\partial t} = D_1 \nabla^2 n_1 + \alpha_1 n_1 \left(1 - \frac{n_1}{K_1}\right) + \Gamma n_1 n_2, \tag{7a}$$

$$\frac{\partial n_2}{\partial t} = D_2 \nabla^2 n_2 + \alpha_2 n_2 \left(1 - \frac{n_2}{K_2}\right) - \Gamma n_1 n_2, \tag{7b}$$

where population 1 represents the Neolithic farmers and population 2 represents the Mesolithic hunter-gatherers. The interaction term Γ now represents a switching term, so that the loss to the Mesolithic population is balanced by a symmetric gain to the Neolithic population. Fort et al. (2008) analyzed the determinants of front speed for the spread of the Neolithic population in this system [with time delay, not shown in Eqs. (7)] and also determined the coexistence time for the two populations. Fort (personal communication, 2009) reports that this system produces a stable long-term coexistence condition if the fertility of hunter-gatherers is sufficient to compensate for the loss from switching to farming, which is fairly intuitive. This system has been considered in detail in a slightly different context by Kandler and Steele (2008), who also showed, however, that enforcing a single carrying capacity for both populations will inevitably lead to the extinction of the population that is the net source of switchers.

An interesting three-population dynamic is considered by Aoki et al. (1996) for the system

$$\frac{\partial n_F}{\partial t} = D_F \nabla^2 n_F + \alpha_F n_F \left(1 - \frac{n_F + n_C}{K_{F+C}}\right), \tag{8a}$$

$$\frac{\partial n_C}{\partial t} = D_C \nabla^2 n_C + \alpha_C n_C \left(1 - \frac{n_F + n_C}{K_{F+C}}\right) + \Gamma(n_F + n_C) n_H, \tag{8b}$$

$$\frac{\partial n_H}{\partial t} = D_H \nabla^2 n_H + \alpha_H n_H \left(1 - \frac{n_H}{K_H}\right) - \Gamma(n_F + n_C) n_H, \tag{8c}$$

where the populations of descendants of initial farmers, converted farmers, and hunter-gatherers are denoted by the subscripts *F*, *C*, and *H*, respectively. This system enables the composition of the expanding farming population to be monitored in terms of the two original source populations, which is of value for genetic arguments. Once again, a coexistence condition exists if the fertility of hunter-gatherers is sufficient to compensate for the loss from switching to farming. When the conversion rate is sufficient to drive the hunter-gatherer population to extinction, the final farming population will be composed mainly or entirely of the descendants of converted hunter-gatherers if the combined rates of influx and subsequent reproduction of switchers exceed the maximum intrinsic rate of increase of descendants of the initial farming population. Any frequency clines observed are due to diffusive mixing of the two farmer populations after the passage of the front. However, the final farming population will be composed mainly of the descendants of the initial farming population if the reverse situation applies. Note, however, that this system retains the assumption of separate and stable carrying capacities for the two economic strategies, with no competitive reduction of the resource base of hunter-gatherers as a result of the growth of the farming population. In addition, the assumptions of the three-population model break down if the mechanism of conversion is intermarriage, because the rates of increase of the descendants of initial farmers and converted hunter-gatherers would then be undifferentiated.

A model in which recruitment of converted hunter-gatherers is sex biased (e.g., fertile females only) would be interesting, with consideration of both the implications for the mtDNA and Y-chromosomal composition of the final farming population and the effects of sex- and age-structured conversion rates on extinction times for the hunter-gatherer population. This would correspond to a staged population-interaction wave-of-advance model, as outlined by Renfrew (2001), and a first modeling attempt using a reaction-diffusion framework can be found in Steele and Kandler (2010).

Finally, Ackland et al. (2007) considered a version of the Aoki et al. (1996) three-population model in which farmers can also switch between membership of the two cultural populations n_F and n_C according to a local majority rule (the local minority being the net source of switchers). The purpose of this is to model the fates in the farming population of cultural traditions that are adaptively neutral with respect to the economic strategy itself (e.g., the languages spoken), one set being derived from the initial farmers and the other from the original hunting and gathering culture of the converted farmers; the shift dynamic involves a simple positive frequency-dependent bias. The key alteration to the three-population model [Eqs. (8)] is the introduction of a cultural shift parameter λ (denoting the strength of the majority bias) into the equations governing the evolution of the size of the two farming (sub)populations:

$$\frac{\partial n_F}{\partial t} = D_F \nabla^2 n_F + \alpha_F n_F \left(1 - \frac{n_F + n_C}{K_{F+C}}\right) + \lambda n_F n_C (n_F - n_C), \tag{9a}$$

$$\frac{\partial n_C}{\partial t} = D_C \nabla^2 n_C + \alpha_C n_C \left(1 - \frac{n_F + n_C}{K_{F+C}}\right) + \Gamma (n_F + n_C) n_H - \lambda n_F n_C (n_F - n_C). \tag{9b}$$

The main result would seem to be that a parameterization of the Aoki et al. (1996) model leading to a cline of decreasing frequencies of initial farmers' genes in the final farming population with distance from the origin of the dispersal will, in the Ackland et al. (2007) model, also give rise to an abrupt cultural transition between areas characterized by "neutral" cultural traditions of the initial farmers and by those of the converted hunter-gatherers, with the boundary occurring near the point at which the genes of the converted hunter-gatherers start to make up the majority of the genes in the final farming population. An additional feature of the Ackland et al. (2007) model, not shown in Eqs. (9), is that local diffusion rates are supplemented by an advective term that responds to local gradients in carrying capacity.

Dynamic Carrying Capacity and Its Consequences

Predator-Prey Interactions and Population Instability. The systems discussed in previous sections have all assumed a stable value for the local population carrying capacity *K*, representing the density at which births are balanced by deaths and at which the local population is no longer growing. For human groups (typically subsisting at the uppermost trophic level in a culturally engineered ecosystem), this is equivalent to assuming that during the early settlement phase any effects of periodic predator-prey oscillations are of sufficiently low amplitude to allow their effects to be assimilated by taking *K* as an average value (and by assuming that there were no irreversible prey population crashes). In most models of initial human hunter-gatherer or agricultural dispersals, demographic parameters such as K, D, and α are also usually estimated by using a modern ethnographic analogy as though the cumulative ratcheting of cultural knowledge responsible for the modern systems can be ignored—or assumed to have occurred instantaneously on the time scale of the modeled processes. Each of these assumptions is useful as a first approximation, but they are all also surely rather naïve. Elsewhere we have considered in a qualitative way some aspects of the ratcheting of cultural knowledge that is required to enable local adaptations by pioneer human populations (Rockman and Steele 2003). In this section I consider briefly some aspects of such processes as they affect the dynamics of model systems of the Fisher-Skellam and similar types.

Numerous attempts have been made to model predator-prey interactions during the late Pleistocene human colonization of the Americas, with the particular objective of explaining the human contribution to megafaunal extinctions. A recent study by Alroy (2001) modeled Paleo-Indian dispersal in a spatially explicit Fisher-Skellam-type system using the same values for D and for α (and the same location for the invasion origin) as Steele et al. (1998) but with local population growth rates limited not by a fixed K but by per capita hunting yields. These yields were based on a variable hunting efficiency parameter, with local multispecies megafauna prey densities estimated independently from body mass and geographic range data for each species. Prey existed initially at carrying capacity and, once subject to hunting pressure, regenerated by logistic growth with the intrinsic maximum growth rates scaled inversely to adult body mass (again, based on empirical regularities in extant species). Prey population growth rates were also subject to variable levels of mutual interference competition. The main result was that human population growth and hunting activity almost always led to a major mass extinction of the prey species. For the human population the associated boom-and-bust cycle led (in the empirically best-fitting scenario) to a halving of the density of the final population compared with the maximum density achieved during the overhunting phase. From an archaeological viewpoint there is good evidence of a concentration of dated Clovis period events in a relatively short two- or three-century interval immediately before the onset of the Younger Dryas, followed by a remarkable dearth of dated events in subsequent centuries (Steele 2009). This may well reflect a human population crash, although the causes are less easily resolved empirically because the crash also coincides with a major rapid-onset episode of climatic deterioration.

Ecosystem Engineering. Comparatively little work has been done on ecosystem engineering effects, in which the activity of invading organisms causes lasting changes to the abiotic environment that then feed back to increase local values of demographic parameters such as K and α (Cuddington and Hastings 2004). An interesting step in this direction is a recent study by Fedotov et al. (2008), who introduced a system designed to model front propagation and (more importantly) the nonlinear dynamics of settlement formation and abandonment behind the front, evaluated against the empirical case of early agricultural settlements of the

Cucuteni-Triploye culture in the forest-steppe region of the East European Plain. This culture was perhaps the first European culture to produce large-scale (even proto-urban) settlements.

Fedotov et al.'s (2008) system has two populations: sedentary farmers, whose population grows logistically and is limited by local per capita crop production levels; and migrants, who are recruited from the farming population as local per capita crop productivity declines below a critical threshold and who migrate in jumps of intermediate length relative to the overall dimension of the domain. In turn, the migrants convert back to sedentary farming as local per capita crop productivity increases above that critical threshold. Thus the mechanism of diffusive spread of farming is by the transient conversion of farmers to migrants (semisedentary foragers), with farming being resumed once these migrants relocate to a region with sufficiently high potential per capita crop yields. The crucial variables in this system are those determining per capita crop productivity, which decreases as a function of population size and of time (because of cumulative soil degradation), and those determining the rate of movement by migrants. The main results are, first, that the farming population front propagates at a rate proportional to the migrants' jump probability and to the rate of population-pressure-induced soil degradation (which affects the rate of conversion of farmers to migrants). Second, in this system the population behind the front aggregates into clusters (because farmers are sedentary, experience local logistic growth, and do not jump-migrate until per capita crop yields have been depressed below a critical level), with the clusters or settlements separated by distances proportional to the migrants' minimum jump length. Third, in this system the soil degradation term also produces a subsequent traveling wave of local population decline or extinction, which persists during the time required for the soil to regenerate by natural mechanisms. It is interesting in this context to note that a boom-and-bust cycle has recently been proposed for the Linear Pottery Culture (LBK) and the post-LBK settlement of central Europe, based on changing frequencies of radiocarbon dates, for which no obvious extrinsic cause (such as a climatic extreme event) has been adduced (Shennan and Edinborough 2007).

Gene-Culture Coevolution. Finally, although it is not so directly relevant to population fronts, Aoki (1987) has considered the case of the coupled spatial spread of a culture trait and of a gene that increases the fitness of individuals adopting that cultural trait (e.g., the coevolution in space of dairying practices and of the gene for adult lactase persistence). The system for modeling changing frequencies of the cultural and genetic traits y and p, whose advantages may depend on whether or not both traits are present in the same individual, is

$$\frac{\partial y}{\partial T} = \frac{\partial^2 y}{\partial X^2} + y(1-y)[(\gamma + 2\sigma)p + \delta], \tag{10a}$$

$$\frac{\partial p}{\partial T} = \frac{\partial^2 p}{\partial X^2} + p(1-p)(\sigma y + \rho), \tag{10b}$$

where γ and δ are measures of the rate of cultural transmission of the new cultural trait as a function of its transmitter's genotype and ρ and σ are measures of the rate of genetic transmission of the new genetic trait as a function of its transmitter's cultural state. This system models the rate of spread of an advantageous gene through an established population in the sense originally considered by Fisher (1937) but for the special situation in which the advantage depends on parallel changes in subsistence practices.

Conclusions

Reaction-diffusion models of Fisher-Skellam type are now well established in archaeology and continue to be used to estimate the demographic processes involved in major human dispersal episodes. Two- and three-population models are increasingly being used to explore interactions during major economic transitions, and work is also under way on predator-prey interactions and population instabilities. The most obvious need is for a fuller exploration of cultural change processes when these are driven by underlying demographic factors. Ackland et al.'s (2007) work on cultural hitchhiking is one initial indicator of where this could go for neutral cultural traits, and Aoki's (1987) model of gene-culture coevolution illustrates the situation in which genetic fitness and cultural attributes are in some way functionally coupled. For language competition Kandler (2009) has explored the shift dynamic in considerable detail. Kandler and Steele (2009) have also extended Henrich's (2001) consideration of innovation adoption dynamics by adding a diffusion term to his modified-logistic reaction term, and we have also considered the implications of heterogeneity in adoption thresholds (somewhat analogous to susceptibility threshold heterogeneity in spatial epidemic models of disease spread); the result is a Fisher equation applied to the spread of an advantageous cultural innovation where the population of heterogeneous adopters is assumed to be at demographic equilibrium, but this last feature could easily be changed to create some kind of dynamic interaction.

Acknowledgments I am very grateful to Anne Kandler and Tim Sluckin for clarifying my understanding of these systems and to Anne and two anonymous referees for commenting on an earlier draft.

Received 13 January 2009; revision accepted for publication 9 April 2009.

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