Traveling waves with dispersive variability and time delay

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We first determine an approximate traveling wave profile for the Cook model [J. Murray, *Mathematical Biology I: An Introduction* (Springer, New York, 2002), pp. 471–478] for the case in which the number of dispersers is small relative to the number of nondispersers. The results are consistent with the previous linearized wavefront analysis that predicts, counterintuitively, that relatively few dispersers can drive the population expansion wave with a wavespeed not too different from that for the case of a single dispersing population as described by the Fisher equation. The method of solution differs from that used in the latter case since here the dimensionless wavespeed is close to unity. We next generalize the Cook model to include time-delay effects. While the Cook model, like the Fisher equation, does not adequately describe the wave of advance during the Neolithic transition in Europe, we show that the generalized Cook model provides a close agreement with the historical record.

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I. INTRODUCTION

The paradigm for describing the expansion of a colonizing or invading species is the Fisher equation (FE) [1–4]. Traveling wave solutions (TWS's) of this equation and a variety of generalizations [5–10] have been studied and applied in a number of ecological contexts. Despite considerable attention, even the basic FE has resisted efforts to obtain an exact analytic solution with the single exception of the special solution found [2] for dimensionless wavespeed $c=5/\sqrt{6}$, which is greater than the minimum speed $c_{\rm min}=2$ [11]. A great deal of success has been found with respect to the determination of qualitative properties of TWS's for the FE beginning with the seminal work of Kolmogoroff *et al.* [5] and a surprisingly good perturbation solution has also been found [10] using the inverse of the square of the dimensionless wavespeed, c^{-2}, as the parameter of smallness.

In the FE description the variability of the population with regard to its dispersal can be accounted for by using a diffusion coefficient taken as an average computed from the dispersal probability-versus-distance distribution [see, e.g., Eq. (8) in [7]]. This implies that in a population composed of dispersers and nondispersers the relative proportions of each of these subpopulations is space- and time-independent. A different approach was taken by Cook [2] to account for dispersive variability by considering a model in which the proportion of dispersers is greatest at the wavefront. In this model the population explicitly consists of distinct subpopulations consisting of dispersers and nondispersers, each having different birth rates. The resulting model has been studied in some detail [2] and like the FE many of its qualitative properties have been determined. In particular, the minimum wavespeed of a TWS, $c_{\rm min}=1+p^{1/2}$, with $p\leqslant 1$ the probability that a newborn is a disperser, follows from an analysis of the wavefront behavior that is more complicated than required for the corresponding FE result [2]. For large allowable values of p, it has been pointed out [2] that approximate TWS's can be obtained by the same method used by Canosa for the FE [10]; this is straightforward and does not lead to any surprises. We briefly present some of these results in the Appendix since they are relevant here for comparative purposes and do not appear to have been presented elsewhere. Conversely, the results for small p, i.e., when the population consists of relatively few dispersers, do provide unexpected results.

When p is small, the wavespeed is still slightly more than half the value of that for a population composed solely of dispersers and not the very small value that would be intuitively expected. In Sec. II, we describe the Cook model and then in Sec. III we obtain a TWS solution for the case of small p where the Canosa perturbation solution is not applicable (the parameter of smallness would be close to unity). In Sec. IV, we generalize the Cook model by taking into account time-delay effects [6,7] and use this model to obtain the speed describing the wave of population advance during the Neolithic transition in Europe. It has been shown previously [6,7] that including such effects in the FE model leads to good agreement with historical evidence for the wave of population advance during the Neolithic transition in Europe. We conclude in Sec. V by showing that the result for the wavespeed found here for the generalized Cook model also agrees well with the historical record in describing the Neolithic expansion in Europe.

II. COOK MODEL

The Cook model and many of its qualitative properties are discussed in the monograph by Murray [12] so we only briefly summarize the results we require here. The population is assumed to be composed of two distinct subpopulations, dispersers with density $u(x,t)$ and nondispersers with density $v(x,t)$. These densities are described by FE's with distinct birth rates, r_u, r_v, and no disperser diffusion. In dimensionless units

$$x\to x'\left[\frac{D}{r_u+r_v}\right]^{1/2}, t\to t'\left[\frac{1}{r_u+r_v}\right], u,v\to Ku',Kv',$$

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where D is the diffusion coefficient for the dispersers, K is the population carrying capacity, and $p \equiv [r_u/(r_u+r_v)]$, these FE's are

$$u_t = u_{xx} + p(u+v)[1-(u+v)], \tag{1a}$$

$$v_t = (1-p)(u+v)[1-(u+v)], \tag{1b}$$

where we have now dropped the primes for convenience. For a TWS we take $z = x - ct$ with c the dimensionless wavespeed and look for solutions $u(x,t), v(x,t) \to u(z), v(z)$ so that Eqs. (1) become

$$0 = cu_z + u_{zz} + p(u+v)[1-(u+v)], \tag{2a}$$

$$0 = cv_z + (1-p)(u+v)[1-(u+v)]. \tag{2b}$$

As mentioned above, a detailed analysis of the linearized wavefront equations [2] indicates that the wave speed is bounded below by $c_{\min} = 1 + p^{1/2}$. For large values of $p \leqslant 1$, the waveform solution of Eqs. (2) in terms of the transformed wave variable $y = c^{-1}z$ and the expansion of u and v in the small parameter c^{-2} in the manner of Canosa [10] can be found as suggested by Murray [2]. This is straightforward, and since the results do not appear to have been presented elsewhere, we briefly consider this in the Appendix. For small values of p, i.e., when the disperser population is small, this approach is not suitable, and this is the case we will consider below.

III. SMALL *p* WAVEFORM SOLUTION

The success of the Canossa [10,13] approach to finding TWS's of the FE is due to the fact that the nonlinear term vanishes at both boundaries, $z = \pm\infty$, allowing an apparent singular perturbation problem to be solved by regular perturbation methods. Fortunately, we are able to exploit this aspect of Eqs. (2) here, in a more direct manner not requiring a wave variable transformation. If we directly expand u and v in the small parameter $p^{1/2}$ so that

$$u = u_0 + p^{1/2}u_1 + pu_2 + \cdots,$$

$$v = v_0 + p^{1/2}v_1 + pv_2 + \cdots, \tag{3}$$

then equations for u_i, v_i follow from Eqs. (2). Since we must have $u_0, u_1 = 0$ [14], these determine the boundary condition $v_0(-\infty) = 1$; in addition we require $v_0(\infty) = 0$ and $u_0 v_i = 0$ for all $i > 0$ at the boundaries (as just noted, $u_1 = 0$ for all z). Because the nonvanishing solution for u is of second order in the small parameter, the waveform can be well described by v_0 and v_1; nevertheless, we will also determine $u_2 \neq 0$ to show that the procedure we are using leads to a nontrivial solution.

The equations for u_0, v_0 follow after substitution of Eq. (3) into Eqs. (2). For the former we find $u_{0zz} + u_{0z} = 0$ so that u_0 must be zero (this is the equation that would result for the equation of diffusion, which is a linear parabolic equation and does not admit a TWS); as noted above, this is consistent with the requirement that $u = O(p)$. For v_0, we have $v_{0z} + v_0(1-v_0) = 0$, the identical zeroth-order equation satisfied by the density in the Canosa expansion of the FE. The solution, which satisfies both boundary conditions despite the order of the equation, is

$$v_0 = [1 + \exp z]^{-1}, \tag{4}$$

where we have arbitrarily set $v_0(0) = \frac{1}{2}$. Moving to the first-order terms, u_1 satisfies the same equation as u_0 so this also vanishes, while the equation for v_1 is

$$v_{1z} + v_{oz} + v_1(1 - 2v_0) = 0 \tag{5}$$

so that, setting $v_1(0) = 0$,

$$v_1 = \frac{ze^z}{(1+e^z)^2}, \tag{6}$$

which differs from the first-order term in the Canosa solution. For small p, as we consider here, v_0 and v_1 provide a good approximation to the waveform (except, as for the Canosa FE solution, near $z \to \infty$, where both are close to zero). Therefore, we only consider the second-order term u_2, which we do only to show that the procedure we have followed leads to nontrivial results for the disperser density. Proceeding as before, we find that the equation for this quantity is

$$u_{2zz} + u_{2z} + v_0(1 - v_0) = 0 \tag{7}$$

and we can anticipate that the homogeneous solution will vanish if the particular solution satisfies the boundary conditions as we expect because of the inhomogeneous term. The homogeneous solution is the same as the solution for u_0 and u_1, $u_{2H} = a + be^{-z}$, where a and b are constants while the particular solution is $u_{2P} = e^{-z}\ln(1+e^z)$ so that $a = b = 0$ and $u_2 = u_{2P}$. Since this term is of $O(p)$, we will not consider it further.

The above results clearly illustrate that a very small number of dispersers, with density $u = O(p)$, can still drive a population wave with velocity $c = 1 + p^{1/2}$ when $p \ll 1$. The population waveform is solely due to the nondispersing population through $O(p^{1/2})$. In Fig. 1, we show the wave-

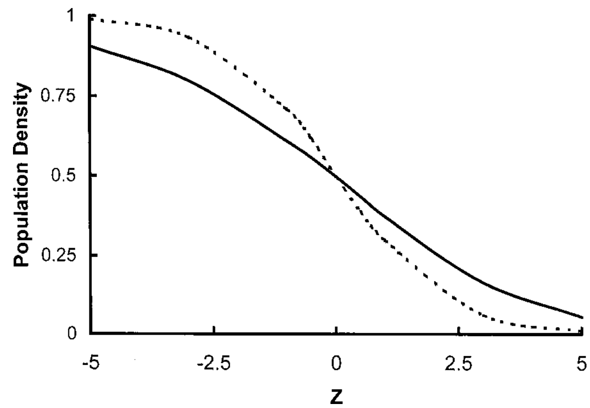

FIG. 1. Population as a function of wave variable z. (----) $n_0 + p^{1/2}n_1 = v_0 + p^{1/2}v_1$ for $p = 0.01$; (——) $n_0 + c_{\min}^{-2}n_1$ for $p = 0.9$. In both cases $c_{\min} = 1 + p^{1/2}$.

form for $p^{1/2}=0.1$, as found above, and compare it with that for $p^{1/2}=0.95$ as found in the Appendix using the Canosa approximation. The former is much steeper. The point of inflection of both is at the origin, and the absolute value of the slope there (the steepness) in the former case is $0.30+O(p)$ and in the latter case is $1/4c+O(1/c^5)\approx 0.13$. As would be expected, when there are fewer dispersers the population towards the front of the wave ($z>0$) is decreased while that behind the wave ($z<0$) is increased.

IV. GENERALIZED COOK MODEL

We now consider a specific example that indicates the need to extend the basic Cook model. Archeological data [15] regarding the expansion of agriculture into Europe indicate that the speed of the expansion wave was $C=1\pm 0.2$ km/yr, considerably below the FE prediction of $C_{\rm FE}=1.41$ km/yr [6,7,15] found using values of D and the population growth rate based on anthropological studies [6,7]. (Note, we are using dimensional values here.) For the Cook model, $C=1$ km/yr requires $p\approx 0.175$ for the same values of the above parameters. As discussed in the next section, this is far below plausible estimates for p.

For the FE, generalization to include time-delay effects [6,7] leads to results for the expansion wavespeed describing the Neolithic transition that are in close agreement with the historical record. This approach can also be used to extend the Cook model. The complete time-delayed model involves space and time derivatives to all orders, but analytical results for the approximation that only retains second derivatives have been shown [6] to agree well with numerical results for the former. We will use the latter approximation here as well.

In proceeding, as noted above, it is convenient to use dimensional variables. Following Refs. [6], [7], we generalize Eqs. (1) as

$$U_t+(\tau/2)U_{tt}=DU_{xx}+p[F(U,V)+(\tau/2)F_t(U,V)], \quad (8a)$$

$$V_t=(1-p)F(U,V), \quad (8b)$$

where $F(U,V)=a(U+V)[1+(U+V)]$. The densities U, describing dispersers, and V have been normalized to the carrying capacity, a is the population growth rate, τ is twice the delay time, and the wave of advance is along the x axis. We will also use $R_1=ap$ and $R_2=a(1-p)$ below.

To find the speed of the advancing wave, C, we look for solutions $U=U(x-Ct)=U(z)$, $V=V(z)$, and require that near the leading edge where both U and V are small we have $U,V\propto \exp \lambda z$. Substituting into Eqs. (8), with z now the sole dependent variable, we obtain the dispersion relation

$$\lambda^2[DC-C^3(\tau/2)]+\lambda[C^2+R_2D-a\tau^2C/2]+aC=0. \quad (9)$$

Stability requires that $\lambda<0$ and real so that it follows that the minimum speed is

$$C^2=[1+(a\tau/2)]^{-2}\{2aD+R_2D[(a\tau/2)-1]+a^{1/2}D(4R_1+2\tau R_1R_2)^{1/2}\} \quad (10)$$

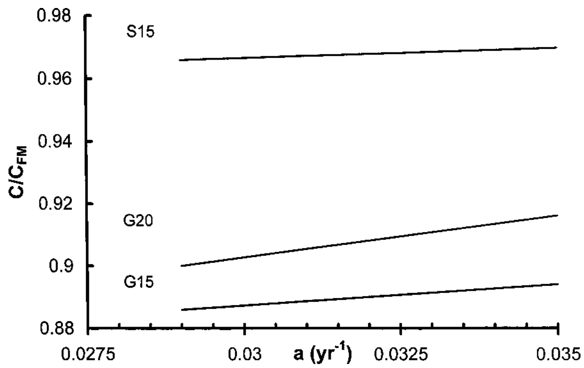

FIG. 2. C/C_{FM} as a function of a for S(15), $p=0.81$; G(15), $p=0.46$; and G(20), $p=0.52$ and $\tau=25$ yr as used in [6,7]. Note that C/C_{FM} is independent of D.

with $D-C^2\tau/2>0$. The plus sign preceding the square root in the above equation has been selected so that this result reduces to the proper limits when $\tau\rightarrow 0$ and when $R_2\rightarrow 0$. In the latter case we recover Eq. (24) of Ref. [6]. The requirement that these limiting results are recovered allows us to eliminate much of the complicated analysis of Ref. [2] in selecting the proper branches of the dispersion relation.

V. COMPARISON WITH THE HISTORICAL RECORD

We next examine how well Eq. (10) compares with the historical record. Values of the parameters a and τ have been discussed in great detail in Refs. [6,7,16] and we will use these values without further comment, so that we take $a=0.032\pm 0.003\ {\rm yr}^{-1}$ and $\tau=25$ yr, the mean generation time. Values of p can be based on the field observations of Ethiopian shifting agriculturist groups that have been used to estimate D previously [6,7,17,18]. For purposes of comparison we use the values of p for three groups identified in [18]. Denoting these as $S15$, $G15$, and $G20$, where S indicates Shiri and G indicates Gilishi and 15 and 20 denote the average age of each group, we have $p(S15)=0.81$, $p(G15)=0.46$, and $p(G20)=0.52$; note that the $p(G20)$ is aggregated from two subgroups which provide a better picture of generational mobility than either single group [17,18]. These

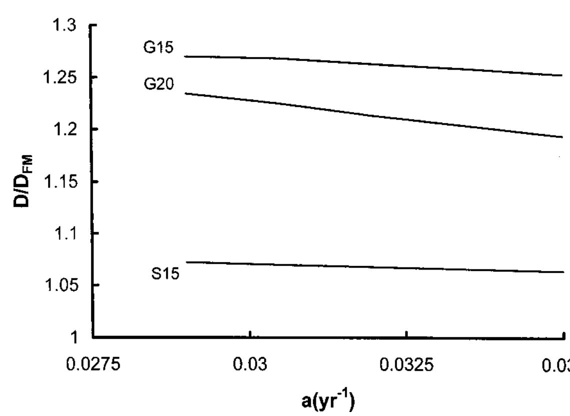

FIG. 3. D/D_{FM} as a function of a for the three groups studied for which $C=C_{FM}$. The values of p for each group and the value of τ are the same as used in Fig. 2.

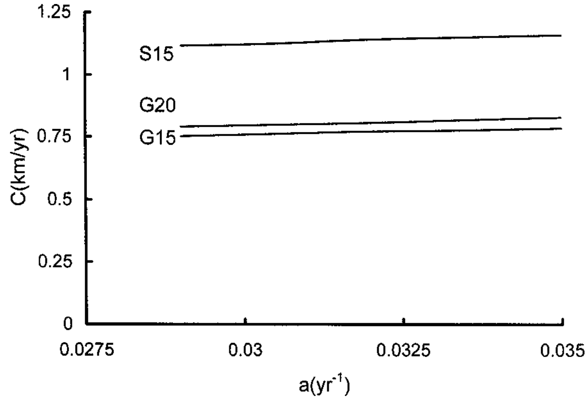

FIG. 4. C as a function of a for the three groups studied. The values of D were found from the data given in [18], see also [17]; $D(\mathrm{S15})=21.53\ \mathrm{km}^2/\mathrm{yr}$; $D(\mathrm{G15})=11.57\ \mathrm{km}^2/\mathrm{yr}$; and $D(\mathrm{G20})=12.24\ \mathrm{km}^2/\mathrm{yr}$ [19]. The values of p and τ for each group are the same as used in Figs. 2 and 3.

values of p indicate that the Cook model without time delay does not lead to values of C consistent with historical evidence, i.e., the value of p required is much too small.

To begin we will make direct comparison with the results of [6,7] using the same mean values of D ($=15.44\ \mathrm{km}^2/\mathrm{yr}$) and a ($=0.032/\mathrm{yr}$) used there. Comparing their result, $C_{\mathrm{FM}}=2(aD)^{1/2}/(1+a\tau/2)$ [Eq. (24) of [6]], with the value C found here we have

$$C/C_{\mathrm{FM}}=\Gamma(a,p,\tau)^{1/2}, \tag{11}$$

where $\Gamma=(1/2)+(R_2\tau/4)(1/2-1/a\tau)+(1/4a^{1/2})(4R_1+2\tau R_1R_2)^{1/2}$. Since Γ is independent of D, Eq. (11) implies that for given τ,D, the difference between C found here and in [6] can only depend on a and p. In Fig. 2, we show $I^{1/2}$ as a function of a and p for the groups $S15$, $G15$, and $G20$ for the range of $a=0.032\pm0.003\ \mathrm{yr}^{-1}$ considered in [6,7]. As might be expected, the wavespeeds found here are somewhat lower than C_{FM}, but except for those values of a and D for which $C_{\mathrm{FM}}<0.90$ km/yr they all remain within the accepted range of $0.80<C<1.2$ km/yr. Note also that using a slightly different value of D from that used to determine C_{FM} results in $C=C_{\mathrm{FM}}$. Since the range of D used in [6,7] is quite large, $D=15.44\pm3.68\ \mathrm{km}^2/\mathrm{yr}$, this comparison appears equally satisfactory. In Fig. 3, we show the ratio of D/D_{FM} as a function of a for which $C=C_{\mathrm{FM}}$.

A direct test of our results is also possible since values of D for the three groups considered can also be determined from the literature [17]. We use these values to directly calculate the wavespeed over the same range of a considered above. These results are shown in Fig. 4. The only values of C outside the accepted range are for the $G15$ group. But, as noted earlier, this group is not representative, and the values for the more representative $G20$ fall within the acceptable range [19] for $a>0.030\ \mathrm{yr}^{-1}$.

In summary, the incorporation of time-delay effects into the Cook model leads to results that compare well with the historical record and also allow us to make use of additional, surrogate data (values of p) in describing the wave of expansion during the Neolithic transition in Europe.

APPENDIX

As Murray [2] has pointed out, for values of p sufficiently large, $c_{\min}^{-2}$ can be used in the manner of Canosa [10] as a small parameter to find a perturbation solution to Eqs. (2). Some of these results, which are easily found, are presented below since they do not appear to be in the published literature and we have made use of them for comparative purposes (in Fig. 1). Changing the wave variable to $z'=z/c$, in lowest order we find that $n_0=(u_0+v_0)=1/(1+e^{z'})$, the corresponding Canosa FE solution (except that c here is different). Substituting this back into the equation for u_0 we find that, as might be intuitively expected, $u_0=pn_0$ so that $v_0=(1-p)n_0$. For p near 1 we would expect that this approximation, as for the FE, is very good. To verify this we consider n_1, which satisfies

$$n_{1z'}+n_1(1-2n_0)=-pn_{0z'z'}, \tag{A1}$$

which is identical to the corresponding FE equation with $p=1$. Here the solution is

$$n_1=\frac{pe^{z'}}{(1+e^{z'})^2}\ln\frac{4e^{z'}}{(1+e^{z'})^2}, \tag{A2}$$

so that the correction to the total density in this order is even smaller than that for the FE solution. The disperser and nondisperser densities can also be found; since we do not make use of these we only state the result for v_1 ($u_1=n_1-v_1$), which is

$$v_1=p(1-p)\left[\frac{e^{z'}}{(1+e^{z'})^2}\ln\frac{4e^{z'}}{(1+e^{z'})^2}+\frac{e^{z'}}{(1+e^{z'})^2}\right]. \tag{A3}$$

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class of plausible initial conditions [5]. The initial conditions that result in a wavespeed $c=5/\sqrt{6}$ are not known, and the quantitative differences between the waveform for this wavespeed and the numerically calculated waveform for $c=2$ limit the usefulness of this result [2], but not its mathematical interest.

[12] The Cook model is described in Ref. [2], pp. 471–478.

[13] See the Appendix for the Canosa solution results.

[14] See Eq. 13.119 in Ref. [2].

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[16] See Ref. [15], p. 155, note 16.

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[19] We use a value of D for this calculation weighted according to the number of dispersers in each of the two subgroups that make up the composite group.