THE ROLE OF THE DELAY TIME IN THE MODELING OF BIOLOGICAL RANGE EXPANSIONS

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Abstract. The time interval between successive migrations of biological species causes a delay time in the reaction–diffusion equations describing their space–time dynamics. This lowers the predicted speed of the waves of advance, as compared to classical models. It has been shown that this delay-time effect improves the modeling of human range expansions. Here, we demonstrate that it can also be important for other species. We present two new examples where the predictions of the time-delayed and the classical (Fisher) approaches are compared to experimental data. No free or adjustable parameters are used. We show that the importance of the delay effect depends on the dimensionless product of the initial growth rate and the delay time. We argue that the delay effect should be taken into account in the modeling of range expansions for biological species.

Key words: Carpodacus mexicanus; delay time; Eurasian Collared-Dove; House Finch; range expansions; Streptopelia decaocto; wavefront speed.

INTRODUCTION

The spread of biological species is a problem of utmost ecological importance. The classical mathematical formulation of these phenomena is due to Fisher (1937). Fisher’s model has been applied to human range expansions (Ammerman and Cavalli-Sforza 1984, Rendine et al. 1986) and other species (Hengeveld 1989, Shigesada and Kawasaki 1997). On the other hand, individuals reproduce themselves, but it takes some time for the subsequent generation to migrate and reproduce. Fort and Méndez (1999a, b) showed that this implies that Fisher’s model should be refined. The resulting time-delayed theory has up to now been compared to observations only for humans (Fort and Méndez 1999a, Fort 2003, Fort et al. 2003).

Time delays have been widely used in biology (e.g., in population dynamics) but seldom in the prediction of the speed of population expansions. Holmes (1993) modeled spatial spread using the telegrapher’s equation, which she derived under the assumption of a correlated random walk. She found negligible changes (<8%) to the classical predictions for five species (cabbage butterfly, Eurasian Collared-Dove, etc.). She did not analyze the delay due to the rest time between subsequent migrations (generations). Kot and co-workers (Kot 1992, Kot et al. 1996) have derived many interesting theoretical results (such as accelerating invasions and front shapes) using integrodifference equations, which, as discrete-time models, naturally incorporate a delay. Neubert and Caswell (2000) developed a method to determine the speed of the wave front for a model resting on integrodifference equations for structured populations. Van den Bosch et al. (1990, 1992) developed continuous-time age-structured models and applied them to the expansion of populations and plant diseases. Thus, progress has been made on delay times and biological invasions. But the effect of the rest time between successive migrations (generations) has so far been taken into account in telegraph-dispersal models, only for human expansions.

Here, we will consider two avian range expansions, of Eurasian Collared-Dove Streptopelia decaocto and House Finch Carpodacus mexicanus, and compare their observed range expansion rates to the predictions of both Fisher’s equation and the time-delayed telegraph dispersal model developed here. For these birds, reproduction does not occur throughout the year; instead it is episodic and relatively synchronous. Therefore, one way to model their spread would be the building of a discrete-time model. Clearly, this would be necessary if the time scale of measurements were of the order of (or lower than) the typical reproduction time (i.e., about a year). However, measurements of population invasion speeds usually span several decades. Under those conditions it is a reasonable approximation of the use of a continuous model for bird reproductive dynamics.

TIME-DELAYED EXTENSION OF FISHER’S THEORY

Traditionally Fick’s law has been used to establish the relation between population flux, J, and the population density gradient, ∂ρ. This “law” hypothesizes
a linear relationship between the two, via a factor known as the diffusion coefficient, $D$:

$$J(x, t) = -D \nabla p(x, t).$$

(1)

In addition to motion, reproduction and mortality also contribute to changes in the density of individuals at a given point in space. In differential form, this corresponds to the well-known equation

$$\frac{\partial p(x, t)}{\partial t} = -\nabla \cdot J(x, t) + F[p(x, t)]$$

(2)

where $F[p]$ is the source term and accounts for the births and deaths per unit area. From Eqs. 1 and 2 one finds

$$\frac{\partial p(x, t)}{\partial t} = D \nabla^2 p(x, t) + F[p(x, t)].$$

(3)

This is Fisher’s equation. It is also known as the parabolic reaction–diffusion equation (PRDE).

Fick’s law (Eq. 1) implies an instantaneous response to a suddenly established population gradient, thus neglecting the inertia and other possible additional sources of delay when dealing with biological individuals. On the other side, when the mean-free-path of the individuals (i.e. the average length of the path they may follow without change in direction) becomes indefinitely long (the so-called ballistic limit in physical literature), Fick’s law predicts a divergent flux, because the diffusion coefficient diverges in this case (as it is proportional to the square of the mean-free-path). In contrast, the actual maximum possible value for the flux of individuals is the maximum individual speed times their number density. Both features (instantaneous response and divergent flux) may be avoided if delay effects are included (Jou et al. 2001). This delay takes into account the time that the individuals need in order to adopt a definite mean speed and direction of motion after nonuniformity appears in their concentration. Then Fick’s law (Eq. 1) is replaced by

$$J(x, t + \tau) = -D \Delta p(x, t)$$

(4)

where $\tau$ is the delay time. Again we can make use of the balance equation (Eq. 2), which now leads to

$$\frac{\partial p(x, t + \tau)}{\partial t} = D \nabla^2 p(x, t) + F[p(x, t + \tau)]$$

(5)

and this equation generalizes Eq. 3.

We have introduced Eq. 5 in the simplest possible way (namely, by invoking the causality principle), but Eq. 5 can also be derived by analyzing the random motion of individuals with a characteristic mean rest time after birth (Fort and Méndez 1999a).

Assuming that the delay time $\tau$ is much smaller than the typical observation times, we expand Eq. 5 in powers of $\tau$. Discarding all terms in which $\tau$ appears to second or higher power gives the following:

$$\frac{\partial^2 p(x, t)}{\partial t^2} + \frac{\partial p(x, t)}{\partial t} = D \nabla^2 p(x, t) + F[p(x, t)] + \tau \frac{\partial F[p(x, t)]}{\partial t}.$$  

(6)

Eq. 6 is called the hyperbolic reaction–diffusion equation (HRDE), and it is the center of the present paper. Note that it relies on keeping terms of Taylor expansions up to a higher order than within the classical (Fisher or PRDE) framework. For the full Eq. 5, Fort and Méndez (1999a) give an implicit formula for the speed of fronts for arbitrarily large $\tau$. Here, however, we will use Eq. 6 instead of Eq. 5. This makes it possible to find an explicit formula for $v$ which is more easy to use, and quite accurate in practice (Fort and Méndez 1999b).

One cannot use the HRDE to make any quantitative prediction unless one can estimate the value of the delay time $\tau$. A microscopic derivation of the HRDE (Eq. 6) (Fort and Méndez 1999a) has shown that, if $T$ is the mean time elapsed between two successive migrations (i.e., the generation time), then

$$\tau = \frac{T}{2}.$$  

(7)

The microscopic theory then leads to a diffusion coefficient that is in agreement with previous work by many authors, namely,

$$D = \frac{1}{4T} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \Phi(\Delta x, \Delta y) \Delta^2 \Phi d\Delta x d\Delta y = \frac{\Delta^2}{4T}$$

(8)

where $\Delta^2 = \Delta x^2 + \Delta y^2$ and $\Delta^2$ is the mean square displacement per jump (or migration). The function $\Phi(\Delta x, \Delta y)$ is the normalized probability distribution for a jump of length $\Delta$.

We use Eq. 6 not only because of conceptual arguments, but because it has been derived from a microscopic theory (Fort and Méndez 1999a). We stress that such an approach is necessary because it is precisely the microscopic derivation that makes it possible to identify the factor appearing in the first and last terms in Eq. 6 as half the mean time interval between subsequent migrations, $T$.

According to Eqs. 6 and 7, the density of individuals per unit area, $p(x, t)$, evolves according to the HRDE:

$$\frac{T}{2} \frac{\partial^2 p(x, t)}{\partial t^2} + \frac{\partial p(x, t)}{\partial t} = D \nabla^2 p(x, t) + F[p(x, t)] + \frac{T}{2} \frac{\partial F[p(x, t)]}{\partial t}$$

(9)

with the diffusion coefficient given by Eq. 8. Eq. 9 has the same form as the reaction-telegraph equation in Holmes (1993). However, in the case considered by Holmes (1993), the following expressions for the parameters $T$ and $D$ were used:
Although the derivations in the present paper and in Holmes (1993) lead to the same equation (Eq. 9), they have been made in very different contexts because we do not assume a correlated random walk. Consequently, the meaning of the parameters $T$ and $D$ is rather different. Holmes’s model assumes that individuals perform steps in one dimension whose lengths are in space, $\gamma$, and in time, $\lambda$, are always the same ($\gamma$ is the organism velocity), and then, the macroscopic delay terms in Eq. 9 come from the characteristic time to reverse direction, i.e., $1/\lambda$. In contrast, in our model, which holds in two dimensions, the steps can have different lengths and the delay time is due to the assumption of a characteristic time interval $T$ during which newborn individuals do not disperse (Fort and Méndez 1999a).

In the limit in which the effect of the delay time is neglected ($T \rightarrow 0$), Eq. 9 becomes Fisher’s equation Eq. 3. It is well known that Fisher’s equation allows instantaneous response and divergent flux. Time-delayed equations such as Eq. 9 were long ago introduced in the physics literature (Jou et al. 2001) to get around this problem. We must mention that this problem is also solved in the context of methods that rest on integrodifference equations by making use of dispersal kernels with finite support (Neubert and Caswell 2000). That approach in terms of multiple life stages, each with their own life traits and dispersal, has more generality than the approach we take in this paper. However, Eq. 9 has advantages over integrodifference equations in some situations. First, dispersal kernels can be applied only if the dispersion histogram of the species considered is known. In contrast, the diffusion coefficient (Eq. 8) can be estimated even if the dispersion histogram is not known (Lubina and Levin 1988), although it is true that its uncertainty increases in turn. Second, it is easier to estimate invasion speeds from Eq. 9, because a simple, explicit analytic expression for the speed can be applied.

Méndez and Camacho (1997) and Méndez, Fort and Farjas (1999) show that the asymptotic ($t \rightarrow \infty$) speed of the wavefront solutions to Eq. 9 is given by

$$v = \frac{2 \sqrt{DF'(0)}}{1 + \frac{T}{2} F'(0)}$$  

where $F'(0) = dF/dp|_{p=0}$ is the intrinsic rate of population growth and conditions $\nu^2 < 2 D/\nu$ and $F'(0)/2T^2 < 1$ must be satisfied (Méndez et al. 1999). In the limit $T \rightarrow 0$, Eq. 10 becomes Fisher’s result, namely,

$$v_{T=0} = 2 \sqrt{F'(0)D}.$$  

In the next sections, we compare the predictions of Eqs. 10 and 11 to observation of range expansions of Eurasian Collared-Doves and House Finches.
data below. We stress that this applies only to the initial, exponential stage of population growth.

Eq. 15 can easily be integrated to yield the following temporal evolution of the total population size:

$$P(t) = P_0 e^{at}$$  \hspace{1cm} (16)

(if $P \rightarrow 0$ where $P_0 = P(0)$.

From the observed population numbers (Fig. 1), we can estimate in a simple way the value of $a$, making use of Eq. 16. We have done so by fitting a straight line to the logarithms of the observed data (USGS, 2001) for the total population vs. time. The slope of the fitted line gives the value of $a$ (Fig. 1), namely $a = 0.020 \pm 0.003$ yr$^{-1}$ (mean $\pm 1$ se).

**Estimation of the delay time.**—The parameter $T$ appearing in Eqs. 9 and 13 is the mean time interval elapsed between two successive migrations (Fort and Méndez 1999a). Thus $T$ may be estimated as the time needed for a newborn individual to grow into an adult and reproduce. When the adult age is reached, individuals leave the paternal territory and fly to new places. The value of this time has been estimated from observations to lie between 1.5 and 2 yr (Hochachka and Dhondt 2000), so we shall take as a typical value 1.75 yr. In fact, values of $T$ between 1.5 and 2 yr do not change the results we will derive below.

**Dispersal.**—The diffusion coefficient can be estimated from Eq. 8. To determine the value of $\bar{\Delta}^2$ we use the histogram in Fig. 2. From these data, we can estimate the mean-squared displacement as

$$\bar{\Delta}^2 = \sum_i \Delta_i^2 f_i$$ \hspace{1cm} (17)

where $\Delta_i$ are the observed distances and $f_i$ their respective observed frequencies ($\Sigma_i f_i = 1$). From Eq. 17 and Fig. 2, we get $\bar{\Delta}^2 = (71 \pm 13) \times 10^3$ km$^2$ and so

$$\sqrt{\bar{\Delta}^2} = (41 \pm 9) \times 10^3$$ km$^2$/yr, which leads us to the diffusion coefficient:

$$D = (10.1 \pm 2.4) \times 10^3$$ km$^2$/yr.  \hspace{1cm} (18)

**Prediction of the front speed and comparison to the observed value.**—Now that we have estimated the necessary parameter values, we can compute the front speed predicted by the time-delayed model, Eq. 9. This yields $v = 28 \pm 4$ km/yr. The observed speed, $v_{exp} = 28 \pm 1$ km/yr (Okubo 1986), agrees rather well with the value predicted above (Fig. 3). Fig. 4 shows the values of the parameters $a$ and $\bar{\Delta}^2/T$ that are compatible with the observed speed. Many combinations of these
parameters, obtained from the observations in Figs. 1 and 2 (shaded areas in Fig. 4), yield a range expansion speed consistent with that observed (Fig. 3).

Eurasian Collared-Dove

We now turn our attention to the range expansion of Eurasian Collared-Dove (Streptopelia decaocto Friv.) into Europe. Using the same method as for the House Finch, the graph of survey-wide data for the dove (USGS 2001) allows us compute $a = 0.29 \pm 0.02 \text{ yr}^{-1}$ (see Fig. 5). Van Den Bosch et al. (1992: Tables 3 and 4) report: $T = 1.81 \pm 0.73 \text{ yr}$ and $\Delta t = (36 \pm 10) \times 10^3 \text{ km}^2$. Thus, $D = 5026 \pm 2400 \text{ km}^2/\text{yr}$, and the speed (Eq. 13) predicted by HRDE is $v = 60 \pm 19 \text{ km}^2/\text{yr}$, whereas the classical speed (Eq. 14) is $v_{\text{class}} = 76 \pm 19 \text{ km}^2/\text{yr}$. Van Den Bosch et al. (1992) also report that the observed velocity of the Eurasian Collared-Dove population expansion is $v_{\text{exp}} = 44 \pm 3 \text{ km}^2/\text{yr}$. Note that the time-delayed model gives a range for the front speed compatible with observations, whereas Fisher’s model does not. Fig. 6 shows the values of the parameters $a$ and $\Delta t$ that are compatible with the observed speed for the Eurasian Collared-Dove expansion.

**DISCUSSION**

In this paper we have shown that the House Finch and Eurasian Collared-Dove invasion speeds can be explained (Figs. 4 and 6) by a simple time-delayed model. Our model provides an analytical result (Eq. 10), which reduces to Fisher’s classical value (Eq. 11) in the appropriate limit. It is interesting to point out that several other models have been put forward in connection with the House Finch invasion. Veit and Lewis (1996) made use of a discrete-time model with two stages (adults and juveniles) and, in contrast to Eq. 12, they did not consider a logistic growth term. Their focus was fundamentally different from ours: their purpose was to explain the initial acceleration of the invasion, so they do not derive a simple formula for the speed over long periods. Shigesada and Kawasaki (1997) took into account the habitat preference of the House Finch in some regions. Theirs is also a very interesting, more detailed approach, which uses the observed range expansion speed as an input parameter. In contrast, we have predicted its value from theory and seen that it is close to that observed.

We now turn to the relevance of the time-delayed model (Eqs. 9 and 10) as compared to Fisher’s model (Eqs. 3 and 11). First we notice that for the House Finch expansion analyzed in the previous section, the
speed predicted in the framework of the classical theory due to Fisher (Eq. 11) is different from the time-delayed prediction (Eq. 10, used above) by only ~2%. This is due to the small value of the product of the delay time $T$ and the initial growth rate $a$, which is much lower than unity in this specific example. In fact, if we compare Eq. 10 to Eq. 11, it is easy to show that $v_T \approx 0.08$ (197). Therefore, for this particular species, Fisher’s model provides a relatively adequate framework (provided that the parameter values are carefully evaluated, as done in the present paper). However, the validity of Fisher’s approximation breaks down for other species. In some cases, such as human populations, $T$ is much higher and the correction of the time-delayed model, as compared to Fisher’s, is ~40% (Table 1: column 1). In other cases, including the Eurasian Collared-Dove, $a$ can be much larger. As shown in the last column in Table 1, this happens for the dove: in contrast to Fisher’s model, our time-delayed theory then provides a range for the speed that is consistent with the experimental value. To the best of our knowledge, this is the first time that such an important correction has been derived for a nonhuman species. Therefore, in order to progress toward the unification of the theory of range expansions, it is in general necessary to take into account the role of the delay time. We stress that Holmes (1993) finds negligible corrections for all species she studied simply because the effect she analyzed (namely, correlations in direction of motion between subsequent steps) is completely different from ours (i.e., a rest time between subsequent migrations). This is why the value of $T$ for the House Finch in Holmes (1993) is different from ours. The value of $a$ is also different because Holmes (1993) used life table data instead of whole-surveys numbers (Fig. 1 in the present paper). Besides, the value of $D$ in Holmes (1993) is different, because it is based on an equation in Holmes (1993: Eq. 19), which in fact holds in diffusion, not in reaction-diffusion systems, and for a very specific initial condition (see its derivation in Shigesada and Kawasaki 1997, Section 3.2).

Here, we have presented an example of each of the three distinct possible situations (Table 1): (1) in some cases, $aT/2$ is much smaller than unity and Fisher’s model is a fair approximation (e.g., when dealing with the House Finch expansion). In other cases, this is not so, either because (2) $a$ is much larger (e.g., in the Eurasian Collared-Dove expansion), or (3) because $T$ is larger (e.g., in human population expansions). Thus, whenever the value of the product $a \times T$ is high enough (say, $a \times T > 0.2$), the delay effect should be taken into account since it will induce an important change to Fisher’s prediction. Therefore, it seems essential to take Eq. 9 into account in future studies of biological range expansions.

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**LITERATURE CITED**


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**Table 1.** Comparison between the time-delayed and Fisher’s models for range expansions of several biological species.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Preindustrial farmers (Fort and Méndez 1999a)</th>
<th>House Finch (Carpodacus mexicanus)</th>
<th>Eurasian Collared-Dove (Streptopelia decaocto)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T$ (yr)</td>
<td>25</td>
<td>1.75 ± 0.25</td>
<td>1.81 ± 0.73</td>
</tr>
<tr>
<td>$D$ (km/yr)</td>
<td>15.44</td>
<td>10 100 ± 2400</td>
<td>5026 ± 2400</td>
</tr>
<tr>
<td>$a$ (yr⁻¹)</td>
<td>0.032</td>
<td>0.020 ± 0.003</td>
<td>0.29 ± 0.02</td>
</tr>
<tr>
<td>$v_{T,0}$ (km/yr)</td>
<td>1.41</td>
<td>28 ± 4</td>
<td>76 ± 17</td>
</tr>
<tr>
<td>$v$ (km/yr)</td>
<td>1.00</td>
<td>28 ± 4</td>
<td>60 ± 19</td>
</tr>
<tr>
<td>$(v_{T,0} - v)/v$</td>
<td>41</td>
<td>1.8 ± 0.4</td>
<td>26 ± 11</td>
</tr>
<tr>
<td>$v_{ep}$ (km/yr)</td>
<td>1.0 ± 0.2</td>
<td>28 ± 1</td>
<td>44 ± 3</td>
</tr>
</tbody>
</table>

*Note:* All values stated with an error term are mean ± 1 SE.