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AN EXTENSION OF THE FORMULA FOR SPREADING SPEEDS

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Dedicated to Horst R. Thieme on the Occasion of his 60th Birthday

Abstract. A well-known formula for the spreading speed of a discrete-time recursion model is extended to a class of problems for which its validity was previously unknown. These include migration models with moderately fat tails or fat tails. Examples of such models are given.

1. Introduction.

We are concerned with the rightward asymptotic spreading speed c^* of a single-species discrete-time recursion

$$u_{n+1} = Q[u_n], \tag{1}$$

where Q is an order-preserving translation invariant operator which takes the family

$$\mathcal{C}_\beta := \{u(x) :\ u(x) \text{ is continuous and } 0 \le u(x) \le \beta \text{ for all } x \in \mathbb{R}\} \tag{2}$$

into itself. Here x is a coordinate on the one-dimensional habitat, $Q[0] = 0$, and $\beta > 0$ is an equilibrium, so that $Q[\beta] = \beta$. Such recursions include integro-difference and discrete time discrete space (stepping stone) models for ecological invasions, but can also be used to study reaction-diffusion models by letting Q be the time-τ solution operator of the initial value problem for some fixed value of τ.

We shall assume that the recursion (1) is monostable in the sense that if $u_0 \equiv \alpha$ for some constant α with $0 < \alpha \le \beta$, then the sequence of constants u_n defined by (1) converges to β. It is known that under mild restrictions on Q, such problems have a rightward spreading speed c^*. An explicit formula for c^* is only known under special circumstances. In particular, one needs to know that the operator Q has a linearization

$$M[u](x) := \int_{-\infty}^{\infty} u(x-y)m(y;dy),$$

where m is a finite nonnegative measure, with the properties that

$$Q[u] \le M[u], \quad \forall u \in \mathcal{C}_\beta,$$

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and that for every positive δ there is a positive number ϵ such that

$$Q[u] \geq (1-\delta)M[u], \quad \forall u \in \mathcal{C}_\epsilon. \tag{3}$$

The natural formula for c^* is then

$$c^* = \inf_{\mu>0}(1/\mu)\ln\left\{\int_{-\infty}^{\infty} e^{\mu y} m(y; dy)\right\}. \tag{4}$$

In the case of a reaction-diffusion model, this formula was given by Aronson and Weinberger [1]. Weinberger [7, 8] showed that it holds for general recursions, provided the integral on the right is finite for all $\mu > 0$.

A related formula for the spreading speed of the integro-differential model

$$u(t,x) = u_0(t,x) + \int_0^t \int_{-\infty}^{\infty} k(s,|y|)g(u(t-s,x+y))dsdy$$

was found independently by Horst Thieme [6] and Odo Diekmann [2, 3]. They showed that if one defines

$$A(c,\mu) := \int_0^\infty \int_{-\infty}^{\infty} e^{-\mu(cs+y)}k(s,|y|)dsdy,$$

then, under suitable assumptions on g and k,

$$c^* = \inf\{c \geq 0 : g'(0)A(c,\mu) < 1 \text{ for some } \mu > 0\}. \tag{5}$$

Thieme pointed out that in the limiting case when k has the form $k(s,|y|) = k(|y|)\delta(s-1)$, where δ is the Dirac measure, the integral equation reduces to an integro-difference equation, and the formula (5) becomes (4). Diekmann's proof in [3] permits the integral which defines $A(c,\mu)$ to diverge for some values of c and μ.

The purpose of the present work is to combine Thieme's observation with the idea behind Diekmann's proof to show that the formula (4) is valid even when the integral on the right has the value $+\infty$ for some or all positive values of μ. This permits one to handle population models with arbitrarily fat migration kernels. Because the formula (4) shows that the spreading speed depends only on the linearization M, the recursion (1) is, by definition, linearly determinate under these circumstances. This extends a result in a recent paper of Hsu and Zhao [4], where it is shown that the formula (4) is valid under the additional condition that the infimum in (4) is attained at an interior point of the set where the integral in (4) is finite (see also [5, 9]).

The extension of our results to multidimensional habitats will be discussed in Section 4.

2. A formula for the spreading speed.

Throughout this section, we impose the following hypotheses on the operator Q in the recursion (1).

Hypotheses 2.1. (i) The operator Q is defined for all functions $u(x)$ in the set $\mathcal{C}_\beta$ defined in (2), where β is a fixed positive number.

(ii) Q is order preserving in the sense that $u \leq v$ implies that $Q[u] \leq Q[v]$.

(iii) $Q[0] = 0$ and $Q[\beta] = \beta$. Together with (ii), this implies that if $u \in \mathcal{C}_\beta$, then $Q[u] \in \mathcal{C}_\beta$.

(iv) Q is translation invariant. That is, $Q[u(\cdot)](x-a) = Q[u(\cdot - a)](x)$ for any constant a. In particular, replacing a by $-x$ and x by zero shows that Q has the form

$$Q[u(\cdot)](x) = Q[u(x+\cdot)](0).$$

(v) If α is a constant with $0 < \alpha < \beta$, then $Q[\alpha] > \alpha$. This implies that the equilibrium 0 of the recursion (1) is unstable and the equilibrium β is stable, so that the recursion is monostable.

(vi) If $u_n(x)$ converges to $u(x)$ uniformly on each bounded interval, then $Q[u_n](x)$ converges to $Q[u](x)$ uniformly on each bounded interval. That is, Q is continuous in the topology of uniform convergence on bounded sets.

(vii) There is a bounded linear operator M on the set of bounded continuous functions with the following properties:

   (a) M is translation invariant and order-preserving, and hence can be written in the form
$$M[u](x) = \int_{-\infty}^{\infty} u(x-y)m(y;dy),$$
   where m is a finite nonnegative measure.

   (b) For every positive δ there is a positive number ϵ such that $Q[u] \geq (1-\delta)M[u]$ for all $u \in \mathcal{C}_\epsilon$.

   (c) $Q[u] \leq M[u]$ for all $u \in \mathcal{C}_\beta$.

It is shown in [8] that if Q satisfies the first six of these hypotheses, then there is a rightward spreading speed $c^* \in (-\infty, \infty]$, which can be characterized in the following manner.

Definition 2.1. c^* is called the rightward asymptotic spreading speed of the recursion (1) if the solutions of the recursion (1) have the following properties:

(i) If $u_0 \in \mathcal{C}_\beta$, $u_0(x) = 0$ for all sufficiently large x, and u_0 is bounded away from β, then for any $c > c^*$
$$\lim_{n\to\infty} \sup_{x \geq cn} u_n(x) = 0. \tag{6}$$

(ii) If $u_0 \in \mathcal{C}_\beta$ and $\liminf_{x\to-\infty} u_0(x) > 0$, then for any $c < c^*$
$$\lim_{n\to\infty} \sup_{x\leq cn} [\beta - u_n(x)] = 0. \tag{7}$$

The Corollary on page 371 of [8] shows that if $\int_{-\infty}^{\infty} e^{\mu y} m(y;dy)$ converges for all μ, then c^* can be found from the formula (4). We shall show that this formula is still valid when the integral diverges for some or all positive μ, provided we assign the value $+\infty$ to the integral when this happens. We first treat the case where there is at least one positive value of μ at which the integral is finite.

Theorem 2.1. *Suppose that $\int_{-\infty}^{\infty} e^{\mu y} m(y;dy)$ converges for at least one positive value of μ. Then the formula (4) is valid, with the infimum taken only over the μ for which the integral converges.*

The following result says that the formula (4) is still correct when $\int_{-\infty}^{\infty} e^{\mu y} m(y;dy) = +\infty$ for all positive μ, so that the infimum is $+\infty$. When $c^* = +\infty$, statement (i) of Definition 2.1 is vacuous, but statement (ii) holds for every real number c.

Theorem 2.2. *The spreading speed c^* of the recursion is $+\infty$ if and only if $\int_{-\infty}^{\infty} e^{\mu y} m(y;dy) = +\infty$ for all positive μ.*

We shall present the proofs of these theorems in the next section, but we first present some examples to illustrate their applications.

Example 2.1. Consider the integro-difference model

$$u_{n+1}(x) = \int_{-\infty}^{\infty} k(y)\{(1+\beta)u_n(x-y)/[1+u_n(x-y)]\}dy,$$

where $k(z)$ is the probability density

$$k(z) = \left[\int_{-\infty}^{\infty} \{e^{-|y|}/[1+(y-1)^4]\}dy\right]^{-1} e^{-|z|}/[1+(z-1)^4],$$

and $\beta > 0$ is the positive equilibrium. The linearization of the operator Q on the right of the recursion is

$$M[u](x) = (1+\beta)\int_{-\infty}^{\infty} k(y)u(x-y)dy,$$

so that $m(y; dy) = (1+\beta)k(y)dy$. Then

$$\int_{-\infty}^{\infty} e^{\mu y} m(y; dy) = (1+\beta)K(\mu),$$

where

$$K(\mu) = \left[\int_{-\infty}^{\infty} \{e^{-|y|}/[1+(y-1)^4]\}dy\right]^{-1} \int_{-\infty}^{\infty} \{e^{(-|y|+\mu y}/[1+(y-1)^4]\}dy,$$

which converges for $|\mu| \le 1$ but diverges for $|\mu| > 1$. To locate the point where the infimum in (4) is attained, we define

$$\Phi(\mu) := (1/\mu)\ln\left\{\int_{-\infty}^{\infty} e^{\mu y} m(y; dy)\right\},$$

and calculate

$$\Phi'(1) = -\ln(1+\beta) - \ln K(1) + [\ln K]'(1). \tag{8}$$

Because $\ln K(\mu)$ is strictly convex (see, e.g., equation(9.7) of [8]) and vanishes at $\mu = 0$, the mean value theorem shows that the sum of the last two terms on the right of (8) is strictly positive. Thus, $\Phi'(1)$ decreases from a positive number to $-\infty$ as β increases from 0 to ∞. When β is so small that $\Phi'(1) > 0$, the infimum of Φ is attained at an interior point of the interval (0,1], and the results of [4] give the formula (4). If, on the other hand, β is so large that $\Phi'(1) \le 0$ so that the infimum is attained at $\mu = 1$, then we must use Theorem 2.1 to show that $c^* = \ln\{(1+\beta)K(1)\}$.

Example 2.2. Consider the integro-difference model

$$u_{n+1}(x) = \left[\int_{-\infty}^{\infty} e^{-|y|^\gamma} dy\right]^{-1} \int_{-\infty}^{\infty} e^{-|y|^\gamma}\{(1+\beta)u_n(x-y)/[1+u_n(x-y)]\}dy$$

with $0 < \gamma < 1$. The linearization of the operator Q on the right is given by

$$M[u](x) = (1+\beta)\left[\int_{-\infty}^{\infty} e^{-|y|^\gamma} dy\right]^{-1} \int_{-\infty}^{\infty} e^{-|y|^\gamma} u(x-y)dy.$$

Because $\gamma < 1$, $\int_{-\infty}^{\infty} e^{\mu y} m(y; dy)$ diverges for all positive μ. Then Theorem 2.2 shows that $c^* = \infty$ because the tail of the migration kernel is too fat.

3. **Proofs of the theorems.** In this section, we give the proofs of our main results.

Proof of Theorem 2.1. In order to treat cases in which the integral in (4) diverges for some μ, we first approximate the operator Q from below by an operator where this does not happen. For this purpose, we introduce the continuous cutoff function

$$\eta(x) := \begin{cases} 1 \text{ for } |x| \le 1 \\ 2 - |x| \text{ for } 1 \le |x| \le 2 \\ 0 \text{ for } |x| \ge 2, \end{cases}$$

and define the sequence of operators

$$Q_j[u](x) := Q[\eta(\cdot/j)u(x+\cdot)](0).$$

Because the sequence $\eta(x/j)$ increases to 1 uniformly on every bounded interval, we see that for each $u \in \mathcal{C}_\beta$, $Q_j[u]$ increases to $Q[u]$ uniformly on every bounded interval. The linearization of Q_j is clearly the operator

$$M_j[u](x) := \int_{-\infty}^{\infty} u(x-y)\eta(y/j)m(y;dy).$$

Because the function $e^{\mu y}\eta(y/j)$ is bounded for every $\mu \in \mathbb{R}$, the function

$$\lambda_j(\mu) := \int_{-\infty}^{\infty} e^{\mu y}\eta(y/j)m(y;dy) \tag{9}$$

is well-defined and continuous, and nondecreasing in j. We define $\int_{-\infty}^{\infty} e^{\mu y} m(y;dy)$ to be the limit

$$\lambda(\mu) := \lim_{j\to\infty} \lambda_j(\mu), \tag{10}$$

which may be finite or $+\infty$. For convenience, we shall also use the notations

$$\Phi_j(\mu) := (1/\mu)\ln \lambda_j(\mu)$$

and

$$\Phi(\mu) := (1/\mu)\ln \lambda(\mu),$$

with the convention that $\Phi(\mu) = +\infty$ when $\lambda(\mu) = +\infty$.

A simple application of Schwarz's inequality shows that for any finite integer j, the function $\ln \lambda_j(\mu)$ is convex in μ (see, e.g., equation (9.7) of [8]). It is easily seen that this implies that the limit function $\ln \lambda(\mu)$ is again convex in the sense that

$$\ln \lambda((1/2)(\mu_1 + \mu_2)) \le (1/2)[\ln \lambda(\mu_1) + \lambda(\mu_2)].$$

for all μ_1 and μ_2, even when some of the values are infinite. Because the function 1 is bounded and continuous, we see that $\lambda(0) = M[1](0)$ is finite. It follows that if the set of positive μ where $\lambda(\mu)$ is finite is not empty, then it is an interval of the form $(0, \Delta)$ or $(0, \Delta]$, with $0 < \Delta \le \infty$. Because the Corollary in [8] gives (4) when $\Delta = \infty$, we shall assume here that Δ is finite.

The proof of Theorem 6.4 of [8] still shows that

$$c^* \le \inf_{\mu>0} \Phi(\mu). \tag{11}$$

Because $\Phi(\mu) < \infty$ for $0 < \mu < \Delta$, c^* is finite.

Hypotheses 2.1 (ii), (iv), and (v) show that Q takes positive constants into positive constants. Therefore, the same is true of its linearization M. Hypothesis 2.1 (vii) (c) and the linearity of M show that for any positive constant $\alpha < \beta$

$$Q[\alpha] \le \alpha M[1] = \alpha\lambda(0).$$

If $\lambda(0) \leq 1$, then $Q[\alpha] \leq \alpha$ for all α. Since this would contradict Hypothesis 2.1 (v), we conclude that

$$\lambda(0) > 1.$$

Because $\lambda_j(0)$ increases to $\lambda(0)$, there is an integer J such that

$$\lambda_j(0) > 1 \text{ for all } j \geq J. \tag{12}$$

It quickly follows that when $j \geq J$, the operator Q_j satisfies the Hypotheses 2.1 with β replaced by some $\beta_j \leq \beta$ and M replaced by M_j. Since the function $\lambda_j(\mu)$ is continuous for all μ, $\ln \lambda_j(\mu) > 0$ uniformly on some open interval which contains 0. Therefore, the function

$$\Phi_J(\mu) := (1/\mu) \ln \lambda_J(\mu)$$

has the limit $+\infty$ as μ decreases to 0. The same is then true of Φ_j for all $j \geq J$.

We wish to show that there is an integer $\tilde{J} \geq J$ such that $\Phi_{\tilde{J}}(\mu) > c^*$ when μ is sufficiently large. For this purpose, we observe that $\sum_{\ell=-\infty}^{\infty} \eta(y - 3\ell) \equiv 1$. Therefore,

$$\int_{-\infty}^{\infty} e^{(\Delta+1)y} m(y; dy) = \sum_{\ell=-\infty}^{\infty} \int_{3\ell-2}^{3\ell+2} \eta(y - 3\ell) e^{(\Delta+1)y} m(y; dy).$$

Since $\int_{-\infty}^{\infty} e^{(\Delta+1)y} m(y; dy) = \infty$, this series diverges. Therefore, there must be a sequence ℓ_i such that

$$\lim_{i\to\infty} \ell_i = \infty \text{ and } \int_{3\ell_i-2}^{3\ell_i+2} \eta(y - 3\ell_i) e^{(\Delta+1)y} m(y; dy) > 0.$$

Because $\eta \geq 0$, this inequality implies that

$$\int_{3\ell_i-2}^{3\ell_i+2} \eta(y - 3\ell_i) m(y; dy) > 0.$$

When $\ell_i \geq 1$, the inequality $|y - 3\ell_i| \leq 2$ implies that $0 \leq y \leq 3\ell_i + 2$. Thus, $\eta(y - 3\ell_i) \leq \eta(y/(3\ell_i + 2))$ when $\ell_i \geq 1$. Therefore,

$$\begin{aligned} \lambda_{3\ell_i+2}(\mu) &= \int_{-\infty}^{\infty} \eta(y/(3\ell_i + 2)) e^{\mu y} m(y; dy) \\ &\geq \int_{3\ell_i-2}^{3\ell_i+2} \eta(y - 3\ell_i) e^{\mu y} m(y; dy) \\ &\geq e^{\mu(3\ell_i-2)} \int_{3\ell_i-2}^{3\ell_i+2} \eta(y - 3\ell_i) m(y; dy). \end{aligned}$$

Thus, we find that

$$\liminf_{\mu\to\infty} \Phi_{3\ell_i+2}(\mu) \geq 3\ell_i - 2.$$

We choose an integer $\tilde{i}$ so large that

$$3\ell_{\tilde{i}} - 2 > c^* \text{ and } 3\ell_{\tilde{i}} + 2 \geq J,$$

and define

$$\tilde{J} := 3\ell_{\tilde{i}} + 2.$$

Then $\Phi_{\tilde{J}}(\mu) > c^*$ for μ both near 0 and near infinity. Thus, there is an interval $[a, b]$ with $0 < a < b$ such that $\Phi_{\tilde{J}}(\mu) > c^*$ outside this interval.

Because Φ_j is nondecreasing in j, we conclude that

$$\Phi_j(\mu) > c^* \text{ outside the interval } [a, b] \text{ when } j \geq \tilde{J}.$$

Let c_j^* be the spreading speed of the recursion (1) with Q replaced by Q_j. The definition of spreading speed and the fact that $Q_j \le Q$ show that $c_j^* \le c^*$. Moreover, the Corollary in [8] shows that $\Phi_j(\mu_j) = c_j^* \le c^*$ for some $\mu_j \in (0, \infty)$. Therefore, $\mu_j \in [a, b]$ for all $j \ge \tilde{J}$. By using the monotonicity of the Φ_j, we see that if $k \ge j \ge \tilde{J}$, then

$$\Phi_j(\mu_k) \le \Phi_k(\mu_k) = c_k^* \le c^*. \tag{13}$$

Because all the μ_k lie in the closed and bounded interval $[a, b]$, the Bolzano-Weierstrass theorem implies that they have at least one point of accumulation $\hat{\mu} \in [a, b]$. That is, there is a sequence μ_{k_i} which converges to $\hat{\mu}$ as i goes to infinity. We replace k by k_i in (13), let i approach infinity, and use the continuity of Φ_j to see that

$$\Phi_j(\hat{\mu}) \le c^* \text{ for all } j \ge \tilde{J}. \tag{14}$$

Now we let j approach infinity to obtain the inequality $\Phi(\hat{\mu}) \le c^*$. We combine this inequality with (11) to see that

$$c^* \le \inf_{\mu > 0} \Phi(\mu) \le \Phi(\hat{\mu}) \le c^*.$$

This clearly shows that $c^* = \inf_{\mu>0} \Phi(\mu)$, which is the statement of Theorem 2.1.

Proof of Theorem 2.2. Suppose that $\Phi(\mu) = \infty$ for all $\mu > 0$. Assume for the sake of contradiction that c^* is finite. Then the above proof of Theorem 2.1 still leads to the inequality (14) for all $j \ge \tilde{J}$. Since $\Phi(\hat{\mu}) = \infty$, the left-hand side can be made arbitrarily large, and, in particular, larger than the right-hand side, by taking j sufficiently large. Thus, the assumption that c^* is finite leads to a contradiction. This shows that if $\Phi(\mu) = \infty$ for all $\mu > 0$, then $c^* = \infty$.

To obtain the converse, we note that if $\Phi(\mu)$ is finite for some $\mu > 0$, then the inequality (11) shows that c^* is also finite. Therefore, $c^* = \infty$ only if $\Phi(\mu) = \infty$ for all μ, and Theorem 2.2 is proved.

4. **Discussion.** We have extended the validity of the formula (4) to a class of recursions with fat tails in a one-dimensional habitat. The Corollary of [8] shows how to apply such a result to a recursion in a multi-dimensional habitat. For each unit direction vector $\boldsymbol{\xi}$ in the habitat, one defines the spreading speed $c^*(\boldsymbol{\xi})$ as the rightward spreading speed of the recursion with the one-dimensional habitat operator

$$Q_{\boldsymbol{\xi}}[u(\cdot)](x) := Q[u(\boldsymbol{\xi}^T\{x\boldsymbol{\xi} + \cdot\})](\mathbf{0}).$$

The spreading behavior is then described in terms of the convex set

$$\mathcal{S} := \{\mathbf{x} : \boldsymbol{\xi} \cdot \mathbf{x} \le c^*(\boldsymbol{\xi}) \text{ for all } \boldsymbol{\xi}\}.$$

The formula (4) becomes

$$c^*(\boldsymbol{\xi}) = \inf_{\mu>0} (1/\mu) \ln\{M[e^{-\mu\boldsymbol{\xi}^T\mathbf{x}}](0)\}.$$

It is shown in the proof of Theorem 6.4 of [8] that $\mathcal{S}$ contains the drift velocity $\mathbf{V}$, whose ith coordinate is given by

$$V_i := \frac{\int x_i m(\mathbf{x}; d\mathbf{x})}{\int m(\mathbf{x}; d\mathbf{x})},$$

and that, with the exception of trivial cases, $\mathbf{V}$ is an interior point of $\mathcal{S}$.

When the habitat is one-dimensional, the unit vectors are 1 and -1. Then $c^*(1)$ is the rightward spreading speed, and $c^*(-1)$ is the leftward spreading speed.

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