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Appendix C from S. P. Ellner and M. Rees, “Integral Projection Models for Species with Complex Demography”

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Stable Population Theory for Integral Projection Models by Stephen P. Ellner and Michael R. Easterling

This appendix provides proofs for stable population properties of integral projection models (IPM) based on chapter 5 of Easterling (1998) but reorganized to emphasize models with a compact domain. Our main mathematical sources are Dunford and Schwartz (1988), Krasnosel’skij et al. (1989), and Zabreyko et al. (1975), which we refer to as DS, KLS, and Z, respectively. The proofs require some familiarity with basic functional analysis, but reading this appendix is not necessary for building and using IPMs—the conclusions are all stated and explained in the main text.

First, we need to restate the model, filling in some technical details omitted in the main text. The space of individual states **X** consists of a finite (possibly empty) set of discrete points $\mathbf{D} = \{x_1, \ldots, x_D\}$ and a finite number of continuous domains $\mathbf{C} = \{\Omega_{D+1}, \Omega_{D+2}, \ldots, \Omega_{D+C}\}$, which are compact sets in Euclidean space of finite dimension $d \geq 1$. These are called components and are denoted as Ω_j, $j = 1, 2, \ldots, N = D + C$. Each Ω_j is regarded as sitting in its own copy of Euclidean space. **X** is given the topology induced by the components (i.e., a set is open iff its intersection with each continuous component is open in the Euclidean metric topology). This topology is metrizible by the Urysohn metrization theorem (or concretely by embedding the components as widely separated subsets in a high-dimensional Euclidean space), so we can regard **X** as a compact metric space. The measure on **X** is the sum of counting measure on **D** and Lebesgue measure on each component in **C**. The integral of a function on **X** is therefore

$$\int_{\mathbf{X}} f(x)dx = \sum_{j=1}^{D} f(x_j) + \sum_{j=D+1}^{N} \int_{\Omega_j} f_j(x)dx. \tag{C1}$$

The state of the population is described by $n(x, t) \in L_1$, the distribution of individual states at time t (L_1 means $L_1(\mathbf{X})$, with the measure stated above and similarly for other spaces). To be more general, we could let **X** be any compact metric space equipped with a finite measure on the Borel σ-field, and only minor changes are needed below. The population dynamics are defined by a nonnegative projection kernel $K(y, x)$:

$$n(y, t + 1) = \int_{\mathbf{X}} K(y, x)n(x, t)dx, \tag{C2}$$

and we use **T** to denote the operator defined by the right-hand side of equation (C2). We always assume that K is a continuous function on $\mathbf{X} \times \mathbf{X}$, which is equivalent to our assumption in the main text that all kernel components are continuous.

Operator Properties

The natural domain for **T** is L_1, the space of state distributions for a population of finite total size, but it is helpful to work in L_2. The following properties make this possible: first, **X** is a finite measure space and compact; therefore, K is bounded and square integrable on $\mathbf{X} \times \mathbf{X}$. Consequently, **T** is a compact operator from L_2 into itself (DS, p. 518; KLS, p. 85). Second, because **X** is a finite measure space and is compact, $C \subset L_2 \subset L_1$; the second inclusion follows from $|n| < 1 + |n|^2$ and the fact that $1 \in L_2$ on a finite measure space. Finally, because K is bounded, $\mathbf{T}$ maps L_1 into C (by the dominated convergence theorem) and therefore also maps L_1 into L_2 and L_2 and C into C.

In short, $\mathbf{T}$ maps $L_1 \cup L_2 \cup C$ into $L_1 \cap L_2 \cap C$ and is compact as an operator from L_2 into itself. Mapping into L_1 is important because it implies that any eigenvector of $\mathbf{T}$ on L_2 represents a finite population distribution. Mapping into C is important in sensitivity analysis because it implies that any L_2 eigenvector is well defined pointwise. $\mathbf{T}$ also preserves the cone Λ of nonnegative functions in L_2, which is reproducing and normal in L_2 (KLS, pp. 9, 37).

As in the main text, we consider two different assumptions for stable population theory: first, uniform power positivity (UPP), where some iterate m of the kernel satisfies $K^{(m)}(y, x) \geq c > 0$, and second, u-boundedness of some kernel iterate, where there is a probability distribution $u(x)$ such that for any initial population distribution $n(x, 0) = n_0(x) \in L_1$, there are positive numbers α, β depending on n_0 such that $\alpha(n_0)u(x) \leq n(m, t) \leq \beta(n_0)u(x)$. With compact domains, UPP is the stronger assumption; for if $0 < a \leq K^{(m)}(x, y) \leq A < \infty$, then for any population state n, we have

$$a \int_{\mathbf{X}} n(x)dx \leq \int_{\mathbf{X}} K^{(m)}(x, y)n(x)dx \leq A \int_{\mathbf{X}} n(x)dx,$$

so $K^{(m)}$ is u_0-bounded with $u_0(x) \equiv 1$, $\alpha(n) = a\int_{\mathbf{X}} n(x)dx$, and $\beta(n) = A\int_{\mathbf{X}} n(x)dx$. Also, if $\mathbf{T}$ is u-bounded in L_1 (as above), then the same also holds in L_2; because $\mathbf{T}$ maps L_1 into L_2, the inequality $\alpha(n_0)u(x) \leq n(m, t)$ implies that u is in L_2, and if $n_0 \in L_2$, then $\mathbf{T}n_0 \in L_1$, so we have $\alpha(\mathbf{T}n_0)u(x) \leq n(m+1, t) \leq \beta(Tn_0)u(x)$.

So, we can think of $\mathbf{T}$ as an operator on L_2, with the following properties implied by our assumptions on $\mathbf{X}$ and the kernel:

P1. $\mathbf{T}$ and therefore its iterates are compact operators from L_2 into itself that preserve the cone Λ of nonnegative functions in L_2.

P2. Some iterate $\mathbf{T}^m$ is u_0-bounded with $u_0 \in \Lambda$.

P3. $\mathbf{T}$ maps L_2 into $L_1 \cap L_2 \cap C$.

Dominant Eigenvalue

We recall an important property of the spectral radius of an operator $\mathbf{A}$,

$$r(\mathbf{A}^m) = r(\mathbf{A})^m. \tag{C3}$$

This follows from the Gel’fand formula $r(\mathbf{A}) = \lim_{n\to\infty} \|\mathbf{A}^n\|^{1/n}$; then, $r(\mathbf{A}^m) = \lim_{n\to\infty} \|\mathbf{A}^{mn}\|^{1/n} = (\lim_{n\to\infty} \|\mathbf{A}^{mn}\|^{1/mn})^m = r(\mathbf{A})^m$. Let λ be the spectral radius of $\mathbf{T}$. Taking $n = u_0$ in P2, we have $\mathbf{T}^m u_0 \geq \alpha(u_0)u_0$, which implies that the spectral radius of $\mathbf{T}^m$ is at least $\alpha(u_0) > 0$ (KLS, p. 89); hence, $\lambda > 0$. Because $\mathbf{T}$ is compact and the cone Λ is reproducing, the fact that $\lambda > 0$ implies that it is an eigenvalue of $\mathbf{T}$ (KLS, p. 85).

P1 and P2 are exactly (but not coincidentally) the assumptions of theorem 11.5 in KLS for the u_0-bounded iterate T^m. The conclusions are that (*a*) T^m has an eigenvalue equal to its spectral radius λ^m, with corresponding eigenvector w in Λ; (*b*) λ^m is simple, and w is the unique (up to normalization) eigenvector of $\mathbf{T}^m$ in Λ; and (*c*) all points ρ in the spectrum of $\mathbf{T}^m$ other than λ^m satisfy $|\rho| \leq q\lambda^m$ for some $q < 1$.

Theorem 1: Conclusions (*a*)–(*c*) also hold for $\mathbf{T}$, with λ, w as the dominant eigenvalue and eigenvector.

Proof: The arguments are very similar to those for power-positive matrices (e.g., Pullman 1976).

Proof of (*a*): We have already seen that λ is an eigenvalue of $\mathbf{T}$. Let y be an eigenvector of $\mathbf{T}$ corresponding to λ. Then, y is an eigenvector of $\mathbf{T}^m$ corresponding to eigenvalue λ^m. Because λ^m is a simple eigenvalue of $\mathbf{T}^m$, y must be a multiple of w.

Proof of (*b*): Suppose λ is not a simple eigenvalue of $\mathbf{T}$. Then, $\mathbf{T}$ has linearly independent eigenvectors w_1, w_2, both corresponding to λ. Both of these therefore are eigenvectors of $\mathbf{T}^m$ corresponding to λ^m, which is impossible because λ^m is a simple eigenvector of $\mathbf{T}^m$. Similarly, if $\mathbf{T}$ has two linearly independent eigenvectors in Λ, these would also both be eigenvectors of $\mathbf{T}^m$ in Λ, contradicting (*b*).

Proof of (*c*): Let μ be any eigenvalue of $\mathbf{T}$ with magnitude greater than $q^{1/m}\lambda$. Then, μ^m is an eigenvalue of $\mathbf{T}^m$, and $|\mu^m| = |\mu|^m \geq q\lambda^m$, so by (*c*), we must have $\mu = \lambda$. Thus, all eigenvalues ρ of $\mathbf{T}$ other than λ satisfy $|\rho| \leq Q\lambda^m$ for some $Q < 1$.

Thus, $\mathbf{T}$ has strictly dominant eigenvalue $\lambda = r(\mathbf{T}) > 0$, which is simple and corresponds to a nonnegative eigenvector w, which is the unique nonnegative eigenvector of $\mathbf{T}$. Because $\mathbf{T}$ maps L_2 into $L_1 \cap C$, the eigenvector is necessarily a finite population distribution and is well defined pointwise.

Convergence to Stable Distribution

We now show that the long-term population behavior is described by the dominant eigenvalue λ and its associated eigenvector w. Let $\mathbf{P}$ denote projection onto the space spanned by w, and $\mathbf{Q} = \mathbf{I} - \mathbf{P}$. $\mathbf{Q}$ is also a projection operator because $\mathbf{Q}^2 = \mathbf{Q}$. Let E_0 and E_1 denote the ranges of $\mathbf{P}$ and $\mathbf{Q}$, respectively. Because λ is a nonzero point in the spectrum of the compact operator $\mathbf{T}$, the Riesz-Schauder theory for compact operators (e.g., theorem 3.2 of Z) implies that (*d*) E_0 and E_1 are mutually complementary, meaning that any f in L_2 can be uniquely represented as $f = f_0 + f_1$, with $f_i \in E_i$; (*e*) E_0 and E_1 are both invariant under $\mathbf{T}$; (*f*) the projection operators $\mathbf{P}$ and $\mathbf{Q}$ both commute with $\mathbf{T}$; and (*g*) $\mathbf{T}$ has the representation $\mathbf{T} = \mathbf{T}_0 + \mathbf{T}_1$, where $\mathbf{T}_0 = \mathbf{TP}$ and $\mathbf{T}_1 = \mathbf{TQ}$. The spectrum of $\mathbf{T}_0$ consists of the single point λ, and the spectrum of $\mathbf{T}_1$ is the spectrum of $\mathbf{T}$ with the point λ deleted.

We need to note some properties of w and u_0; w is the dominant eigenvalue of $\mathbf{T}$ considered as an operator on L_2, but by property P3, w is also in L_1 because $w = \lambda^{-1}\mathbf{T}w$. Because $\mathbf{T}^m$ is u_0-bounded and $w \neq 0$, we have $\lambda^m w = \mathbf{T}^m w \geq \alpha(w)u_0$, with $\alpha(w) > 0$ and, therefore,

$$w \geq cu_0 \tag{C4}$$

for some constant $c > 0$.

Lemma 1: If n_0 is a nonnegative initial population distribution, then $\langle \mathbf{T}^m n_0, w\rangle > 0$.

Proof: $\mathbf{T}^m n_0 \geq \alpha(n_0)u_0$ because $\mathbf{T}^m$ is u_0-bounded, so

$$\langle \mathbf{T}^m n_0, w\rangle \geq \langle \alpha(n_0)u_0, cu_0\rangle = c\alpha(n_0)\,\|u_0\|^2 > 0.$$

This is the analogue of the fact that repeated multiplication of any nonnegative initial vector by a power-positive matrix eventually results in a strictly positive vector, whose inner product with the (positive) dominant eigenvector must be positive.

Theorem 2: Let n_0 be any nonnegative initial population distribution, and let λ, w be the dominant eigenvalue/eigenvector. Then,

$$\lim_{t\to\infty} \frac{\mathbf{T}^t n_0}{\lambda^t} = Cw \tag{C5}$$

for some constant $C > 0$ depending on $n(x, 0)$.

Proof: This again is very similar to the matrix case. Note that $\mathbf{T}_0\mathbf{T}_1 = \mathbf{T}_1\mathbf{T}_0 = 0$ as a result of property (*f*) and the fact that $\mathbf{PQ} = \mathbf{QP} = 0$. Therefore, $\mathbf{T}^t = \mathbf{T}_0^t + \mathbf{T}_1^t = \mathbf{T}^t\mathbf{P} + \mathbf{T}^t\mathbf{Q}$. By the last lemma, $\mathbf{PT}^m n_0 = cw$ for some $c > 0$. So,

$$\frac{\mathbf{T}^t n_0}{\lambda^t} = \frac{\mathbf{T}^{t-m}\mathbf{T}^m n_0}{\lambda^t} = \frac{\mathbf{T}^{t-m}\mathbf{PT}^m n_0}{\lambda^t} + \frac{\mathbf{T}^{t-m}\mathbf{QT}^m n_0}{\lambda^t} = \left(\frac{c}{\lambda^m}\right)w + \frac{\mathbf{T}^k\mathbf{Q}x}{\lambda^k}, \tag{C6}$$

where $k = t - m$ and $x = \mathbf{T}^m n_0/\lambda^m$. Because $\mathbf{T}$ and $\mathbf{Q}$ commute, the last term in equation (C6) equals $\mathbf{T}_1^k x/\lambda^k$. We know that $r(\mathbf{T}_1) < r(\mathbf{T}) = \lambda$, so by the Gel’fand formula, there exist $\varepsilon, N > 0$ such that $\|\mathbf{T}_1^k\|^{1/k} < \lambda - \varepsilon$ for all $k > N$. The last term in equation (C6) therefore has a norm less than $[(\lambda - \varepsilon)/\lambda]^k\,\|x\|$ for k large and therefore converges to 0.

Theorem 2 proves convergence in L_2, but this implies convergence in L_1. Both sides of equation (C5) are in $L_1 \cap L_2$ for $t > 0$. Suppose $x_k \to x$ in L_2; then, because $1 \in L_2$ on a finite measure space, by Hölder’s inequality, $\|x_k - x\|_1 \leq \|x_k - x\|_2\,\|1\|_2 \to 0$.

Reproductive Value

Existence of a dominant left eigenvector v (meaning an eigenvector of the adjoint operator $\mathbf{T}^*$) follows from the fact that any nonzero element in the spectrum of a compact operator has corresponding left and right eigenvectors (DS, p. 578). A direct calculation shows that the adjoint operator corresponds to the transposed kernel $K^*(y, x) = K(x, y)$, which is also continuous, so $\mathbf{T}^*$ also maps L_2 into $L_1 \cap C$, implying that v has finite integral and is well defined pointwise.

As in the matrix model, the dominant left eigenvector can be interpreted as the state-dependent relative reproductive value of individuals, that is, their long-term relative contributions to population growth. The derivation of this property follows the matrix case. It is easy to see that the total reproductive value $V(t) = \langle v, n(x, t)\rangle$ grows geometrically at rate λ, $V(t+1) = \lambda V(t)$; hence, $V(t) = \lambda^t V(0)$. Let $V(x, t)$ denote the reproductive value that results if the initial population n_0 is a smooth approximate δ function centered at x so that $V(x, t)/\lambda^t = V(x, 0) = \langle v, n_0\rangle$. On the other hand, by theorem 2, we have that $V(x, t)/\lambda^t \to \langle v, C(x)w\rangle = C(x)\langle v, w\rangle$, where $C(x)$ is the constant in equation (C5). Equating these two expressions gives

$$C(x) = \frac{\langle v, n_0\rangle}{\langle v, w\rangle}. \tag{C7}$$

Then, letting n_0 converge to a δ function at x, we get $C(x) = v(x)/\langle v, w\rangle$; hence, the population at (large) time t resulting from a type x founder is proportional to $v(x)$. More generally, equation (C7) says that the population at time t from a mixed initial population is asymptotically proportional to the total reproductive value of the initial population.

Sensitivity and Elasticity

We now show that the main results about sensitivity and elasticity for matrix models extend to the integral model. In the physics literature, the sensitivity formula (C10) is well enough known to be used without a literature citation, but for the sake of completeness, we give a derivation here based on the familiar one for matrix models. Consider a smooth perturbation of the kernel, in particular to $K(y, x) + \varepsilon f_r(y, x|y_0, x_0)$, where $0 \leq \varepsilon \ll 1$ and f_r is a smooth approximate δ function with support limited to a ball of radius r centered at (y_0, x_0). Then, exactly as in section 9.1 of Caswell (2001), differentiating $\mathbf{T}w = \lambda w$ with respect to ε and taking the inner product with v gives

$$\langle v, \mathbf{T}dw\rangle + \langle v, (d\mathbf{T})w\rangle = \langle v, \lambda dw\rangle + \langle v, d\lambda w\rangle. \tag{C8}$$

Then, because $\langle v, \mathbf{T}dw\rangle = \langle \mathbf{T}^* v, dw\rangle = \lambda\langle v, dw\rangle = \langle v, \lambda dw\rangle$, we can cancel terms and rearrange to obtain $d\lambda = \langle v, (d\mathbf{T})w\rangle / \langle v, w\rangle = d\varepsilon\langle v, \mathbf{F}_r w\rangle / \langle v, w\rangle$, where $\mathbf{F}_r$ is the operator corresponding to the approximate δ function kernel f_r, so

$$\frac{d\lambda}{d\varepsilon} = \frac{\langle v, \mathbf{F}_r w\rangle}{\langle v, w\rangle}. \tag{C9}$$

When we let $r \to 0$, the left-hand side of equation (C9) is (by definition) the sensitivity of λ to a change in the kernel at (y_0, x_0), and the right-hand side converges to $v(y_0)w(x_0)/\langle v, w\rangle$, so we have

$$s(y, x) = \frac{v(y)w(x)}{\langle v, w\rangle}. \tag{C10}$$

In a matrix model, the approximate δ function is a unit perturbation of a single matrix entry, and the expressions above collapse to the usual definition of sensitivity. In the integral model, the size of a kernel perturbation is measured by its integral, and the sensitivity at a point is defined by shrinking the support of the perturbation to that point.

The elasticity function is

$$e(y,x) = \frac{K(y,x)s(y,x)}{\lambda}. \tag{C11}$$

In a matrix model, the elasticities sum to 1; in an integral model, the elasticity function integrates to 1: combining equations (C10) and (C11), we have

$$\int\int e(y,x)dydx = \frac{1}{\lambda\langle v,w\rangle}\int v(y)\int K(y,x)w(x)dxdy$$

$$= \frac{1}{\lambda\langle v,w\rangle}\langle v,Kw\rangle = \frac{1}{\lambda\langle v,w\rangle}\langle v,\lambda w\rangle = 1. \tag{C12}$$

Similarly,

$$\int e(y,z)dy = \int e(z,x)dx = \frac{v(z)w(z)}{\langle v,w\rangle}, \tag{C13}$$

which is the analogue of the result for matrix models that corresponding row and column sums of the elasticity matrix are equal.

The intuitive meaning of equation (C12) is that if the entire kernel is increased by 5%, then λ is increased by 5%. This property is also implied by the definition of elasticity as the proportional change in λ for a proportional change in the kernel. Consequently, the fact that equation (C12) can be derived from equation (C10) validates our definition of sensitivity for the integral model—it leads to an elasticity function that corresponds to the intuitive definition of elasticity.

Noncompact Domains

Bounded noncompact domains are no problem: replace each component by its closure and extend the kernel by continuity. For any realistic model, this should give a continuous kernel and compact domains. But unbounded components are more problematic for two reasons.

The first reason is that on an unbounded domain, a kernel mapping L_1 into itself cannot be uniformly power positive because $K^{(m)} \geq c > 0$ would imply that $n(y,m) \geq c\,\|n_0\|_1$ for all y and, hence, an infinite total population at time m. Therefore, stable population theory has to depend on directly showing u-boundedness. In the main text and appendix B, we gave some conditions implying P2 based on mixing at birth. Another condition, suggested by Easterling (1998), is as follows: suppose that some kernel iterate satisfies

$$a(x)u_0(y) \leq K^{(m)}(y,x) \leq b(x)u_0(y), \tag{C14}$$

with a, b in L_2 and everywhere positive on $\mathbf{X}$; then, that iterate is u_0-bounded.

Proof: For any $n \in L_2$, equation (C14) implies that

$$u_0(y)\int_{\mathbf{X}} a(x)n(x)dx \leq \int_{\mathbf{X}} K^{(m)}(x,y)n(x)dx \leq u_0(y)\int_{\mathbf{X}} b(x)n(x)dx.$$

The outer integrals are L_2 inner products and therefore finite, so the mth iterate is u_0-bounded with $\alpha(n) = \langle a,n\rangle$, $\beta(n) = \langle b,n\rangle$.

The second problem is that the operator properties P1 and P3 no longer follow from continuity of the kernel. If, in addition,

$$\int_{\mathbf{X}}\int_{\mathbf{X}} K(y,x)^2 dxdy \leq M, \tag{C15}$$

then $\mathbf{T}$ is a compact operator from L_2 into itself (DS, p. 518) and $\mathbf{T}$ clearly preserves the cone of nonnegative functions. Then, if P2 holds, we have stable population growth in L_2 (existence of λ and w and theorem 2 above). However, for sensitivity analysis, the eigenfunctions must be in C and must be well defined pointwise, and the stable distribution w needs to be in L_1. Unfortunately, “there exists no simply formulated necessary and sufficient conditions on the kernel … which ensure that the operator … maps from L_p into L_q” (Z, p. 92).

Why not work directly in L_1? If the kernel satisfies the mild assumptions

$$\begin{array}{ll} K(y,x) \le M & x, y \in \mathbf{X} \\ \int_{\mathbf{X}} K(y,x)dy \le M & x \in \mathbf{X} \end{array},$$

then $\mathbf{T}$ maps L_1 into $L_1 \cap C$. The problem is compactness; our approach and the basic results in KLS require that some iterate of $\mathbf{T}$ is compact. Combining theorem 3.1.10 in Dunford and Pettis (1940) and theorem 8.21 in DS, a necessary condition for compactness in L_1 of an integral operator with kernel k on Euclidean space is that for any $\varepsilon > 0$, there is finite cube $\mathbf{C}(\varepsilon)$ such that

$$\int_{\mathbf{C}(\varepsilon)} k(y,x)dy \ge 1 - \varepsilon \tag{C16}$$

for all x in $\mathbf{X}$. That is, extreme individuals of a type x outside $\mathbf{C}(\varepsilon)$ must either die or immediately shrink back into $\mathbf{C}(\varepsilon)$ with a probability of at least $1 - \varepsilon$—it’s acceptable to create them in the model so long as most of them go away before too long. In terms of biological generality, this is not really better than bounding the model by “killing off” individuals outside some large cube before they come into being—which implies compactness in L_2 for a continuous kernel but not necessarily in L_1 (see Eveson 1995, corollary 5.1).

As noted in the main text, these problems disappear if a change of variables transforms the model onto a compact domain and leaves the kernel continuous. Whether this holds depends largely on how the model is defined outside the range of the data. For example, consider a size-structured model where individual size at time $t + 1$ follows a Gaussian distribution with mean $\mu(x)$ and variance $\sigma^2(x)$, where x is the size variable at time t. Several empirical applications have used this model with linear growth and constant variance: $\mu(x) = a_0 + a_1 x$, $\sigma^2(x) \equiv \sigma^2$, where x is the log of some linear size measurement. Suppose, in addition, that survival is an increasing function of size, reaching some asymptote as $x \to \infty$. Then, if the linear growth model is extended to all $-\infty \le x \le \infty$, then no bounded transformation exists that can give a bounded kernel (suppose the transform is $u = g(x)$, monotonically taking $(-\infty, \infty) \to (a, b)$ and producing a transformed kernel $\tilde{K}(v, u)$ on $[a, b] \times [a, b]$; then, as $u \to b$, the transformed kernel assigns 99% probability to smaller and smaller intervals of the form $b - \varepsilon \le v \le b$, so the transformed kernel is unbounded). On the other hand, if the linear model is extended as a sigmoid curve outside the range of the data, so that $\mu(x)$ has finite limits as $x \to \pm\infty$, then logistic transformation $u = e^x/(1 + e^x)$ results in a bounded continuous kernel via the change-of-variables formula for probability densities.

Finally, we reiterate our advice that integral models be constructed on bounded domains. On an unbounded domain, a biologically reasonable model has to be constrained so that it cannot produce individuals vastly different from those actually observed, so you might as well impose a bounded domain from the outset.

Additional References for Appendix C

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