

Chaotic attractors and physical measures for some density dependent Leslie population models

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Abstract

Following ecologists' discoveries, mathematicians have begun studying extensions of the ubiquitous age structured Leslie population model that allow some survival probabilities and/or fertility rates to depend on population densities. These nonlinear extensions commonly exhibit very complicated dynamics: through computer studies, some authors have discovered robust Hénon-like strange attractors in several families.

Population biologists and demographers frequently wish to average a function over many generations and conclude that the average is independent of the initial population distribution. This type of 'ergodicity' seems to be a fundamental tenet in population biology. In this paper we develop the first rigorous ergodic theoretic framework for density dependent Leslie population models. We study two generation models with Ricker and Hassell (recruitment type) fertility terms. We prove that for some parameter regions these models admit a chaotic (ergodic) attractor which supports a unique physical probability measure. This physical measure, having full Lebesgue measure basin, satisfies in the strongest possible sense the population biologist's requirement for ergodicity in their population models.

We use the celebrated work of Wang and Young 2001 *Commun. Math. Phys.* **218** 1–97, and our results are the first applications of their method to biology, ecology or demography.

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1. Introduction

The Leslie model is the principal age structured discrete population model, and is commonly used in demography and conservation ecology [4]. In this linear model, the population is divided into age classes, and each age class has an associated survival probability and a per capita fertility rate, which are all assumed to be constant. For example, the standard two-age class Leslie model can be described by a mapping of the form

$$T(x, y) = (a_1x + a_2y, bx),$$

where a_1 and a_2 are the group's fertility rates and b is the survival probability from the first age group to the second age group.

However, ecologists have discovered many examples of populations where some survival probabilities and/or fertility rates depend on the population density or population size. There is now a large literature on this subject; see [5] for an early list of eight insect species with density dependent feedbacks. The second author is currently studying a population of brown trout in a Central Pennsylvania stream where some vital rates have been shown to be density dependent [3]. To help ecologists model such populations, mathematicians have begun studying extensions of the Leslie model that allow some survival probabilities and/or fertility rates to depend on population densities. These nonlinear extensions commonly exhibit very complicated dynamics: some authors have discovered robust Hénon-like strange attractors in families of such models [13, 16].

Population biologists and demographers frequently wish to average a function over many generations and conclude that the average is independent of the initial population distributions. To them, ergodicity is useful because then population patterns reveal something about the underlying process (rather than initial conditions). Many population biologists seem to strongly believe that what is important is the underlying population process, with the initial conditions being historical accidents [4]. For instance, demographers refer to the fact that the asymptotic behaviour for primitive Leslie matrices is independent of the initial age distribution, as the fundamental theorem of demography. Thus 'ergodicity' is an important tenet to population biologists.

In this paper we develop the first rigorous ergodic theoretic framework for density dependent Leslie population models. We study the two generation models with Ricker [11] and Hassell [6] (recruitment type) fertility terms. In both cases, all fertility rates monotonically decrease as a function of the total population size. For the Ricker model the decay is exponential, and for the Hassell model the decay is polynomial.

Ricker-type recruitment population model [10]. This model is described by the two-dimensional map $R_{a,b} : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$

$$R_{a,b}(x, y) = ((ax + \gamma ay) \cdot e^{-\lambda(x+y)}, bx), \quad (\mathcal{R})$$

where a and γa are the group's initial fertility rates ($a, \gamma \geq 0$), b is the survival probability from the first age group to the second age group and $\lambda > 0$. (See [13, 16] for a detailed description of this model.)

Hassell-type recruitment population model [10]. This model is described by the two-dimensional map $H_{a,b} : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$

$$H_{a,b}(x, y) = ((ax + \gamma ay) \cdot (1 + x + y)^{-\beta}, bx), \quad (\mathcal{H})$$

where a and γa are the group's initial fertility rates, b is the survival probability from the first age group to the second age group and $\beta > 1$.

Remark. The case when $\beta = 1$ is a well known and important recruitment model, called the Beverton–Holt model [1]. The dynamics for this model is much simpler than for Ricker and Hassell models; the only attractors are fixed points.

Definition 1.1. Let $T : M \rightarrow M$ be an arbitrary continuous map on a compact metric space M and μ a T -invariant Borel probability measure. The measure μ is called a *physical measure* (or *empirical measure*) if there exists a positive Lebesgue measure set $B(\mu) \subset M$ such that

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{j=0}^{n-1} \phi(T^j(x)) = \int_M \phi d\mu$$

for all $x \in B(\mu)$ and every continuous function $\phi : M \rightarrow \mathbb{R}$.

The crucial property of a physical measure μ is that the phase space average of a continuous function ϕ with respect to μ can be computed using the orbital average of T for a set of initial conditions having positive measure. In this sense a physical measure is observable and can be studied on a computer. A physical measure (which by definition is ergodic), especially one having full Lebesgue measure basin, satisfies in the strongest possible sense the population biologist’s requirement for ergodicity in their population models.

There exist several definitions in the literature for chaotic (strange) attractors. In this paper, by a chaotic attractor we mean a compact invariant set with the property that it attracts all orbits starting in a neighbourhood set (called the basin of attraction) and such that Lebesgue almost every orbit has a positive Lyapunov exponent.

Our main results are the following two theorems on the existence of a chaotic attractor and physical measure with strong stochastic properties.

Theorem 1.2. Consider the two-dimensional Ricker map (\mathcal{R}). For any $\lambda > 0$, and $\gamma \in (0, 0.2) \cup (6.3, \infty)$ there exists a positive Lebesgue measure set $\Delta(\lambda, \gamma) \subset \mathbb{R}_+^2$ such that for all $(a, b) \in \Delta$, the map $R_{a,b}$ admits a chaotic attractor which supports a unique physical probability measure. The basin of the attractor (and the measure) is \mathbb{R}_+^2 .

Theorem 1.3. Consider the two-dimensional Hassell map (\mathcal{H}). For any $\beta > 0$ sufficiently close to $\beta_0 \approx 20.194$, and $\gamma > 8.2$ there exists a positive Lebesgue measure set $\Delta(\beta, \gamma) \subset \mathbb{R}_+^2$ such that for all $(a, b) \in \Delta$, the map $H_{a,b}$ admits a chaotic attractor which supports a unique physical probability measure. The basin of the attractor (and the measure) is \mathbb{R}_+^2 .

Remark 1.4. The unique natural measure in both theorems is hyperbolic, in the sense that one Lyapunov exponent is positive and the other is negative on a set of full Lebesgue measure. This measure has strong stochastic properties: it is mixing (after taking a power of the map) and satisfies the central limit theorem.

Remark 1.5. The remarks at the end of section 3 will explain the choices of parameters in these theorems.

Remark 1.6. We believe that there is an abundance of other parameter values such that both maps admit a chaotic attractor with natural measure. This would follow from an abundance of Misiurewicz maps satisfying all the necessary conditions stated in step 1) of the Wang–Young set-up.

Furthermore, even for larger values of the survival probability, computer studies show that a ‘Hénon-like’ [13] chaotic attractor with a physical probability measure frequently exists (see figure 1).

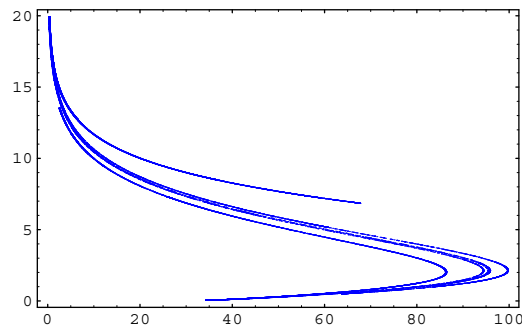


Figure 1. ‘Hénon-like’ attractor for Ricker map with $a = 61$, $\gamma = 0.2$, $b = 0.2$, $\lambda = 0.1$.
(This figure is in colour only in the electronic version)

We use the celebrated work of Wang and Young [14], and our results are the first applications of their method to biology, ecology or demography. In greater than two dimensions, more complicated techniques allow the construction of chaotic attractors with SRB measures (see [15]), but they do not show that the SRB measures are also physical measures. We have verified that one can apply their method to construct chaotic attractors which support SRB measures for the n -dimensional versions of the Ricker and Hassell models. The calculations are similar, but since the conclusion is much weaker, we chose not to include the details in this paper.

2. The Wang–Young theorem

We begin by defining a Sinai–Ruelle–Bowen (SRB) measure.

Definition 2.1. Let $T : M \rightarrow M$ be a diffeomorphism on a compact Riemannian manifold M and μ a T -invariant Borel probability measure. The measure μ is a *SRB measure* if

- (i) T has a positive Lyapunov exponent μ -a.e.
- (ii) the conditional measures of μ on unstable manifolds are absolutely continuous with respect to the induced Riemannian measure on these manifolds.

While attractors for dissipative diffeomorphisms cannot possess smooth or absolutely continuous invariant probability measures, SRB measures share some of the desirable properties of smooth invariant measures. The usual way to construct a physical measure in higher dimensions is to construct an SRB measure having certain additional properties, which force the SRB measure to be a physical measure. Most of the effort of Yang and Young goes into constructing an SRB measure.

Bowen [2] showed that a transitive uniform hyperbolic (axiom A) attractor $\Lambda \subset M$ admits a unique physical SRB measure with $\text{supp}(\mu) = \Lambda$. From the work of Pesin [9] it also follows that every ergodic SRB measure with nonzero Lyapunov exponents is a physical measure. However, the existence of SRB measures or physical measures for general dynamical systems is a very difficult problem.

The state-of-the-art results for strongly dissipative diffeomorphisms with one direction of instability are due to Wang and Young [14, 15], who proved the existence of chaotic attractors supporting SRB measures. We refer to the above papers for a comprehensive review of the the most important results in this area preceding their work. We now briefly describe their requirements, in the form of axioms.

Wang–Young axioms for existence of SRB/physical measures. Consider a two-parameter family of maps in \mathbb{R}^2 constructed as follows:

- (1) Start with a one-dimensional C^4 Misiurewicz map defined on a closed interval I , $f : I \rightarrow I$ such that $f(I) \subset I$. Recall that a map f is called a Misiurewicz map (see also [7, 8, 12]) if it has no periodic attractors and if critical orbits do not accumulate on the critical set, that is, $C \cap \omega_f(C) \neq \emptyset$, where $C = \{c \in I : f'(c) = 0\}$. We also assume that all critical points are nondegenerate, and that f has negative Schwarzian derivative on $I \setminus C$.
There are uncountably many Misiurewicz maps in a unimodal family of maps. If the orbit of the critical point intersects an unstable periodic orbit, then the map is a Misiurewicz map. Countably many Misiurewicz maps can be constructed this way.
- (2) Let $\{f_a\}$, $a \in [a_0, a_1]$, be a one-parameter family of maps from I to I with $f_{a^*} = f$ for some $a^* \in [a_0, a_1]$. The family $\{f_a\}$ is required to satisfy a certain transversality condition in a neighbourhood of a^* (see the discussion about unimodal maps);
- (3) Extend $\{f_a\}$ to a 2-parameter family of maps $\{f_{a,b}\}$, $a \in [a_0, a_1]$, $b \in [0, b_1]$, where $f_{a,b} : I \rightarrow A$, with $A = I \times [c, d]$ ($0 \in [c, d]$) and such that $f_{a,0} = f_a$ and $f_{a,b}$ is an embedding for $b > 0$.
- (4) Extend $f_{a,b}$ to $T_{a,b} : A \rightarrow A$ in such a way that $T_{a,0}(A) \subset I \times \{0\}$ and $T_{a,b}$ maps A diffeomorphically onto its image $T(A) \subset A$ for $b > 0$. We assume that the map $(a, b, x, y) \mapsto T_{a,b}(x, y)$ is C^4 , and also require a nondegeneracy condition of the map $T_{a^*,0}$:

$$\frac{\partial}{\partial y} T_{a^*,0}(x, 0) \neq (0, 0) \quad \text{whenever } f'_{a^*}(x) = 0. \tag{*}$$

Wang and Young proved the following theorem.

Theorem 2.2 ([14]). *Given $T_{a,b}$ as above, there exists a chaotic attractor which supports a SRB measure. Furthermore, if $T_{a,b}$ satisfies the Jacobian estimate*

$$K_1 b \leq |\det(DT_{a,b}(x, y))| \leq K_2 b \tag{**}$$

for some $K_1, K_2 > 0$ and all $(x, y) \in A$, there is a positive measure set $\Delta \subset [a_0, a_1] \times (0, b_1]$ such that for all $(a, b) \in \Delta$:

1. The map $T_{a,b}$ admits at most r chaotic attractors each supporting an ergodic SRB measure μ_i , where r is the cardinality of the critical set C of the one-dimensional map f ;
2. Each μ_i is a physical measure, and the union of their basins has full Lebesgue measure in A ;
3. Each μ_i is mixing (after taking a power of T) and satisfies the central limit theorem.

Remark 2.3. The set Δ contains $(a^*, 0)$ and has the additional property that for all sufficiently small b , the projection set $\Delta_b = \{a : (a, b) \in \Delta\}$ has positive one-dimensional Lebesgue measure.

3. Unimodal maps and absolutely continuous invariant measures

We recall here one of the main results from the theory of one-dimensional dynamics concerning the existence of SRB measures for unimodal maps. (See [12] for an excellent survey of this topic or [7] for a detailed presentation of the theory.) Following the set-up from [12], we

assume that:

- (U1) $\{f_a\}$ is a one-parameter family of C^2 unimodal maps of an interval I with negative Schwarzian derivative.
- (U2) Each f_a has a nondegenerate critical point c (one can assume that c is independent of λ).
- (U3) Each f_a has a repelling fixed point on the boundary of I .
- (U4) The map $(x, a) \mapsto (f(x), f'_a(x), f''_a(x))$ is C^1 .
- (U5) There exists a parameter value a^* such that f_{a^*} is a Misiurewicz map. For simplicity we assume that the critical orbit is mapped onto an unstable periodic point p^* in a finite number of steps.

Since an unstable periodic orbit persists and changes smoothly under small perturbations of the map, for a sufficiently close to a^* we can find a point $x(a) \in I$ and an unstable periodic orbit $p(a)$ such that: $a \mapsto x(a)$ is differentiable; $x(a^*) = f_{a^*}(c)$; $p(a)$ moves continuously with a and $p(a^*) = p^*$; $x(a)$ is mapped onto $p(a)$ in the same number of steps as $x(a^*)$ onto the corresponding point p^* . An additional condition is required: the map must change nontrivially with the parameter at $a = a^*$ in the sense that

- (U6) $(d/da)(x(a) - f_a(c))|_{a=a^*} \neq 0$.

Then one has

Theorem 3.1 ([7, 12]). *If $\{f_a\}$ satisfies (U1)–(U6), there exists a positive measure set E of parameters with a^* as a Lebesgue density point such that if $a \in E$, then*

- (i) f_a admits an absolutely continuous invariant probability measure μ ;
- (ii) μ is a physical measure describing the asymptotic distribution of almost all orbits;
- (iii) f_a has positive Lyapunov exponent almost everywhere.

In [12], the author shows that the above theorem can be applied to a Ricker-type family of one-dimensional maps, $R_{a,\lambda} = ae^{-\lambda x}$ (with $a > 1$ and $\lambda > 0$), and to a Hassell-type family of one-dimensional maps $H_{a,\beta} = ax(1+x)^{-\beta}$ (with $a > 1$ and $\beta > 1$). More precisely,

- (a) For each $\lambda > 0$, the family $R_a = R_{a,\lambda}$ is S -unimodal and satisfies (U1)–(U4); there exists a Misiurewicz parameter $a^* \approx 16.999$ (independent of λ) such that (U5)–(U6) are also satisfied. This gives the existence of a positive measure set $E_R(\lambda)$ such that any $R_{a,\lambda}$ with $a \in E_R$ satisfies (i)–(iii) of theorem 3.1.
- (b) If $\beta > 2$ is arbitrarily fixed, then the one-parameter family $H_a = H_{a,\beta}$ is S -unimodal and satisfies (U1)–(U4); there exists $\beta_0 \approx 20.914$ such that for each fixed β sufficiently close to β_0 , there exists a Misiurewicz parameter $a^*(\beta)$ (with $a^*(\beta_0) = 21.5$) such that conditions (U5)–(U6) are fulfilled, too. This shows that there exists a nonempty, parameter open set B such that for each $\beta \in B$, there exists a positive measure set $E_H(\beta)$ with $H_{a,\beta}$ satisfying (i)–(iii) of theorem 3.1, whenever $\beta \in B$.

4. Proofs

Proof of theorem 1.2. Let $\lambda > 0$ and $\gamma \in (0, 0.2) \cup (6.3, \infty)$ arbitrarily fixed. We show that the two-parameter Ricker family $R_{a,b}$ given by (R) can be constructed following the Wang–Young procedure.

Step 1. Start with R_{a^*} , the Misiurewicz map defined as above. Since the critical point $c = 1/\lambda$ satisfies the inequality $R_{a^*}^2(c) < c < R_{a^*}(c)$ for $a^* \approx 16.999$, we can always consider R_{a^*} to

be defined on $I = [R_{a^*}^2(c), R_{a^*}(c)]$. Such an interval I absorbs all initial conditions $x \neq 0$. Note that $R_{a^*}(c) = a^*/(\lambda e)$ and $R_{a^*}^2(c) = (a^*)^2/(\lambda e^{1+a^*/e})$.

Step 2. Consider the one-parameter family R_a for a in some interval $[a_0, a_1]$ containing a^* . For a_0, a_1 close enough to a^* , we can consider R_a to be defined on the same interval I as in step 1. We still have $R_a(I) \subset I$, because R_a is strictly increasing on $[R_{a^*}^2(c), c]$ and strictly decreasing on $[c, R_{a^*}(c)]$.

Step 3. Extend R_a to a 2-parameter family

$$R_{a,b} : I \rightarrow I \times [0, b_1 a / (\lambda e)], \quad R_{a,b}(x) = (R_a, bx) = (ax e^{-\lambda x}, bx),$$

with $a \in [a_0, a_1], b \in [0, b_1]$. Clearly $R_{a,0} = (R_a, 0)$ and $R_{a,b}$ is an embedding if $b > 0$.

Step 4. Now let $A = I \times [0, b_1 a / (\lambda e)]$ and $R_{a,b} : A \rightarrow A$ given by (R). One can easily check that $R_{a,b}$ takes A strictly into A and $R_{a,0}(x, y) \subset I \times \{0\}$.

We prove that $R_{a,b}$ is an injective local diffeomorphism. Assume that $R_{a,b}(x_1, y_1) = R_{a,b}(x_2, y_2)$. This implies immediately that $x_1 = x_2 (= x)$ and

$$(ax + \gamma a y_1) e^{-\lambda(x+y_1)} = (ax + \gamma a y_2) e^{-\lambda(x+y_2)}.$$

Hence

$$(ax + \gamma a y_1) e^{-\lambda y_1} = (ax + \gamma a y_2) e^{-\lambda y_2}.$$

Consider the function $g(y) = (x + \gamma y) e^{-\lambda y}$ and note that

$$g'(y) = e^{-\lambda y} (\gamma - \lambda(x + \gamma y)).$$

One can choose the intervals $[a_0, a_1], [0, b_1]$ so small that

$$0 < |\lambda(x + \gamma y) - \gamma|$$

for all $(x, y) \in A$. Indeed, if $\gamma < 0.2$, then

$$\lambda(x + \gamma y) - \gamma > \lambda x - \gamma \geq \lambda \frac{a^2}{\lambda e^{1+a/e}} - \gamma = \frac{a^2}{e^{1+a/e}} - \gamma.$$

By choosing a_0, a_1 close enough to $a^* \approx 16.999$, we have $\frac{a^2}{e^{1+a/e}} > 0.2 > \gamma$, for all $a \in [a_0, a_1]$. If $\gamma > 6.3$, then

$$\gamma - \lambda(x + \gamma y) > \gamma - \lambda(x + \gamma y) \geq \gamma - \lambda \left(\frac{a}{\lambda e} + \gamma \frac{ab_1}{\lambda e} \right) = \gamma - \frac{a}{e} - \gamma \frac{ab_1}{e} > 0,$$

if one chooses b_1 small enough and a_0, a_1 close enough to a^* such that

$$\gamma \left(1 - \frac{ab_1}{e} \right) > \frac{a}{e},$$

for all $a \in [a_0, a_1]$. Therefore, $g'(y)$ does not vanish for all $y \in [0, ab_1/(\lambda e)]$, and $x \in I$ arbitrarily fixed. This shows that $y \mapsto g(y)$ is injective, hence $y_1 = y_2$, and $R_{a,b}$ is injective.

Let us analyse the Jacobian $DR_{a,b}(x, y)$ of $R_{a,b}$:

$$DR_{a,b}(x, y) = \begin{pmatrix} ae^{-\lambda(x+y)}(1 - \lambda(x + \gamma y)) & ae^{-\lambda(x+y)}(\gamma - \lambda(x + \gamma y)) \\ b & 0 \end{pmatrix}.$$

The determinant of the Jacobian is

$$\det(DR_{a,b}(x, y)) = abe^{-\lambda(x+y)}(\lambda(x + \gamma y) - \gamma).$$

We have already proved that one can choose the intervals $[a_0, a_1], [0, b_1]$ so small that

$$0 < |\lambda(x + \gamma y) - \gamma|$$

for all $(x, y) \in A$. Since A is compact, there exists $K_1, K_2 > 0$ such that

$$K_1 \leq a e^{-\lambda(x+y)} |\lambda(x + \gamma y) - \gamma| \leq K_2 \quad \text{for all } (x, y) \in A.$$

Hence

$$K_1 b \leq |\det(DR_{a,b}(x, y))| \leq K_2 b.$$

In particular, $\det(DR_{a,b}(x, y)) \neq 0$, for all $(x, y) \in A$. Using the fact that $R_{a,b}$ is also one-to-one we obtain that $R_{a,b}$ is a diffeomorphism from A to $R_{a,b}(A)$.

We are left to check the nondegeneracy condition (*). For that, we have

$$\frac{\partial}{\partial y} R_{a^*,0}(x, y) = (a^* e^{-\lambda(x+y)} (\gamma - \lambda(x + \gamma y)), 0).$$

Note that $R'_{a^*}(x) = 0$ if and only if $x = c = (1/\lambda)$, hence

$$\frac{\partial}{\partial y} R_{a^*,0}(c, 0) = (a^* e^{-1} (\gamma - 1), 0) \neq (0, 0) \quad \text{if } \gamma \neq 1.$$

We showed that $R_{a,b}$ can be constructed following steps 1–4, for some parameter intervals $a \in [a_0, a_1], b \in [0, b_1]$. Moreover $R_{a,b}$ satisfies condition (**), so by using theorem 2.2, there exists a positive Lebesgue measure set $\Delta(\lambda, \gamma) \subset \mathbb{R}_+^2$ such that any map $R_{a,b}$ with $(a, b) \in \Delta$ has a unique natural invariant probability measure $\mu_{a,b}$ with the following properties:

- (a) $\mu_{a,b}$ describes the asymptotic distribution of orbits of Lebesgue almost all points $(x, y) \in A$;
- (b) $\mu_{a,b}$ has a positive Lyapunov exponent $\mu_{a,b}$ -a.e.

Note also that for any initial point $(x, y) \in \mathbb{R}_+^2$, a certain iterate of the map $R_{a,b}$ maps the point (x, y) into A . Hence the measure $\mu_{a,b}$ describes the asymptotic distribution of Lebesgue almost all orbits in \mathbb{R}_+^2 . □

Proof of theorem 1.3. Let β be sufficiently close to $\beta_0 \approx 20.194$ and $\gamma > 8.2$ arbitrarily fixed. We show that the two-parameter Hassell family $H_{a,b}$ given by (H) can be constructed following the Wang–Young procedure.

Step 1. Start with $H_{a^*}(x) = a^* x(1+x)^{-\beta}$, the one-dimensional Misiurewicz map described in section 3 (a^* depends on β , β is sufficiently close to $\beta_0 \approx 20.914$ and $a^*(\beta_0) = 21.5$). Since the critical point $c = 1/(\beta - 1)$ satisfies the inequality $H_{a^*}^2(c) < c < H_{a^*}(c)$ for β sufficiently close to β_0 , we can always consider H_{a^*} to be defined on $I = [H_{a^*}^2(c), H_{a^*}(c)]$. Such an interval I absorbs all initial conditions $x \neq 0$. Note that $H_{a^*}(c) = a/(\beta - 1)((\beta - 1)/\beta)^\beta$.

Step 2. Consider the one-parameter family H_a for a in some interval $[a_0, a_1]$ containing a^* . For a_0, a_1 close enough to a^* , we can consider H_a to be defined on the same interval I as in Step 1. We still have $H_a(I) \subset I$, because H_a is strictly increasing on $[H_{a^*}^2(c), c]$ and strictly decreasing on $[c, H_{a^*}(c)]$.

Step 3. Extend H_a to a 2-parameter family

$$H_{a,b} : I \rightarrow I \times \left[0, b_1 \frac{a}{\beta - 1} \left(\frac{\beta - 1}{\beta} \right)^\beta \right], \quad H_{a,b}(x) = (H_a, bx) = (ax(1+x)^{-\beta}, bx),$$

where $b \in [0, b_1]$. Clearly $H_{a,0} = (H_a, 0)$ and $H_{a,b}$ is an embedding for $b > 0$.

Step 4. Now let $A = I \times [0, b_1(a/(\beta - 1))((\beta - 1)/\beta)^\beta]$ and $H_{a,b} : A \rightarrow A$ given by (H). One can easily check that $H_{a,b}$ takes A strictly into A and $H_{a,0}(x, y) \subset I \times \{0\}$. We now

prove that $H_{a,b}$ maps A diffeomorphically onto $H(A)$ by showing that $H_{a,b}$ is an injective local diffeomorphism. Assume that $H_{a,b}(x_1, y_1) = H_{a,b}(x_2, y_2)$. This implies immediately that $x_1 = x_2 (= x)$ and

$$(ax + \gamma ay_1)(1 + x + y_1)^{-\beta} = (ax + \gamma ay_2)(1 + x + y_2)^{-\beta}.$$

Consider the function $g(y) = (x + \gamma y)(1 + x + y)^{-\beta}$ and note that

$$g'(y) = \gamma(1 + x + y)^{-\beta} - \beta(x + \gamma y)(1 + x + y)^{-\beta-1}.$$

One can choose the intervals $[a_0, a_1], [0, b_1]$ so small that

$$0 < |\gamma(1 + x + y) - \beta(x + \gamma y)|$$

for all $(x, y) \in A$. Indeed,

$$\gamma(1 + x + y) - \beta(x + \gamma y) > \gamma - \beta(x + \gamma y) > \gamma - \beta \frac{a}{\beta - 1} \left(\frac{\beta - 1}{\beta} \right)^\beta (1 + \gamma b_1).$$

For b_1 sufficiently small and a_0, a_1 close enough to a^* we get:

$$\beta \frac{a}{\beta - 1} \left(\frac{\beta - 1}{\beta} \right)^\beta < 8.2 < \frac{\gamma}{1 + \gamma b_1} < \gamma,$$

for all $a \in [a_0, a_1]$. This implies that $g'(y) \neq 0$ for all $y \in [0, b_1(a/(\beta - 1))((\beta - 1)/\beta)^\beta]$, so the map $y \mapsto g(y)$ is injective. Therefore $y_1 = y_2$ and $H_{a,b}$ is injective.

We now analyse the determinant of the Jacobian $DH_{a,b}(x, y)$ of $H_{a,b}$:

$$\det(DH_{a,b}(x, y)) = -ab(1 + x + y)^{-\beta-1}(\gamma(1 + x + y) - \beta(x + \gamma y)).$$

We have already proved that one can choose the intervals $[a_0, a_1], [0, b_1]$ so small that

$$0 < |\gamma(1 + x + y) - \beta(x + \gamma y)|$$

for all $(x, y) \in A$. Since A is compact, there exists $K_1, K_2 > 0$ such that

$$K_1 \leq |a(1 + x + y)^{-\beta-1}(\gamma(1 + x + y) - \beta(x + \gamma y))| \leq K_2 \quad \text{for all } (x, y) \in A.$$

Hence

$$K_1 b \leq |\det(DH_{a,b}(x, y))| \leq K_2 b.$$

In particular, $\det(DH_{a,b}(x, y)) \neq 0$, for all $(x, y) \in A$. From the fact that $H_{a,b}$ is also an injective map we conclude that $H_{a,b}$ is a diffeomorphism from A to $H_{a,b}(A)$.

We are left to check the nondegeneracy condition (*). For that, we have

$$\frac{\partial}{\partial y} H_{a^*,0}(x, y) = (a^*(1 + x)^{-\beta-1}(\gamma(1 + x) - \beta x), 0)$$

and

$$\frac{\partial}{\partial y} H_{a^*,0}(c, 0) = \left(a^* \left(\frac{\beta - 1}{\beta} \right)^\beta (\gamma - 1), 0 \right) \neq (0, 0).$$

We showed that $H_{a,b}$ can be constructed following steps 1–4, for some parameter intervals $a \in [a_0, a_1], b \in [0, b_1]$. Moreover, $H_{a,b}$ satisfies condition (**); thus by using theorem 2.2, there exists a positive Lebesgue measure set $\Delta(\lambda, \gamma) \subset \mathbb{R}_+^2$ such that any map $H_{a,b}$ with

$(a, b) \in \Delta$ has a unique natural invariant probability measure $\mu_{a,b}$ with the following properties:

- (a) $\mu_{a,b}$ describes the asymptotic distribution of orbits of Lebesgue almost all points $(x, y) \in A$;
- (b) $\mu_{a,b}$ has a positive Lyapunov exponent $\mu_{a,b}$ -a.e.

Note also that for any initial point $(x, y) \in \mathbb{R}_+^2$, a certain iterate of the map $H_{a,b}$ takes the point (x, y) into A . Hence the measure $\mu_{a,b}$ describes the asymptotic distribution of Lebesgue almost all orbits in \mathbb{R}_+^2 .

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References

- [1] Beaverton R and Holt S 1957 *On the dynamics of exploited fish populations MAFF Fish. Invest. (Ser. II)* **19** 533
- [2] Bowen R 1975 *Equilibrium States and the Ergodic Theory of Anosov Diffeomorphisms (Lecture Notes in Mathematics vol 470)* (Berlin: Springer)
- [3] Carline R 2006 Regulation of an unexploited brown trout population in Spruce Creek, Pennsylvania *Trans. Am. Fish. Soc.* **135** 943–54
- [4] Caswell H 2001 *Matrix Population Models* (Sunderland: Sinauer)
- [5] Clark L, Geier P, Hughes R and Morris R 1967 *The Ecology of Insect Populations in Theory and Practice* (London: Methuen)
- [6] Hassell M 1974 Density-dependence in single species populations *J. Animal Ecol.* **44** 283–96
- [7] de Melo W and van Strien S 1993 *One-Dimensional Dynamics* (Berlin: Springer)
- [8] Misiurewicz M 1981 Absolutely continuous measures for certain maps of an interval *Inst. Hautes Études Sci. Publ. Math.* **53** 17–51
- [9] Pesin Y 1977 Characteristic Lyapunov exponents and smooth ergodic theory *Russ. Math. Surv.* **32** 55–114
- [10] Quinn T and Deriso R 1999 *Quantitative Fish Dynamics* (Oxford: Oxford University Press)
- [11] Ricker W 1954 Stock and recruitment *J. Fish. Res. Board. Can.* **11** 559–623
- [12] Thunberg H 2001 Periodicity versus chaos in one-dimensional dynamics *SIAM Rev.* **43** 3–30
- [13] Ugarcovici I and Weiss H 2004 Chaotic dynamics of a nonlinear density dependent population model *Nonlinearity* **17** 1689–712
- [14] Wang Q and Young L-S 2001 Strange attractors with one direction of instability *Commun. Math. Phys.* **218** 1–97
- [15] Wang Q and Young L-S Toward a theory of rank one attractors *Ann. Math.* to appear
- [16] Wikan A and Mjølhus E 1996 Overcompensatory recruitment and generation delay in discrete age-structured population models *J. Math. Biol.* **35** 195–239