

INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

October 31, 2016

Exercise 6.1

(a) The condition for a period doubling bifurcation is $F'(\hat{N}) = -1$, hence the condition cannot be fulfilled in an undercompensating model, for which $F'(N) > 0$ for all N .

(b) Let $N_{t+1} = F(N_t)$ and consider the three discrete-time models considered in the lectures:

- Ricker:

$$F(N) = bNe^{-aN}, \quad F'(N) = be^{-aN}(1 - aN)$$

- Beverton–Holt:

$$F(N) = \frac{\lambda N}{1 + \alpha N}, \quad F'(N) = \frac{\lambda}{(1 + \alpha N)^2}$$

- Skellam:

$$F(N) = 1 - e^{-BN}, \quad F'(N) = Be^{-BN}$$

Therefore the undercompensating models are the Beverton–Holt and the Skellam model.

(c) Consider the Skellam model. The function $F(N)$ is increasing, such that $F(0) = 0$, $F'(0) = B$, $\lim_{N \rightarrow \infty} F'(N) = 0$, and $F''(N) = -B^2e^{-BN}$ is negative, so F' is decreasing monotonically. Hence, if $B > 1$ there exists a unique positive intersection between the curve $F(N)$ and the line $g(N) = N$. If $B \leq 1$, there is no positive intersection (but there is a unique intersection with $N < 0$, because $\lim_{N \rightarrow -\infty} F'(N) = \infty$). When $B > 1$, the stability of the positive equilibrium \hat{N} is easy to verify graphically with the cobweb method. In fact, at the intersection of the two curves we have

$$0 < F'(\hat{N}) < 1.$$

A similar reasoning applies to the Beverton–Holt model.

The properties of uniqueness and stability of the nontrivial equilibrium do not hold for any undercompensating model. For instance, consider a sigmoid function such that, for certain parameter values, there exist two nontrivial equilibria, one unstable and one stable (see Figure 1).

Exercise 6.2

Consider the Ricker model

$$N_{t+1} = bN_t e^{-aN_t}. \tag{1}$$

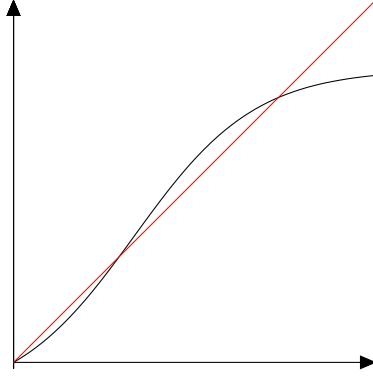


Figure 1: Sigmoid function with two positive equilibria (one unstable and one stable).

The trivial state $\hat{N}_0 = 0$ is always an equilibrium of the equation. The nontrivial equilibrium \hat{N} satisfies

$$1 = be^{-a\hat{N}} \Leftrightarrow \hat{N} = \frac{1}{a} \log b$$

and hence it exists positive if and only if $b > 1$.

For stability, we have

$$F'(N) = be^{-aN}(1 - aN). \quad (2)$$

By plugging the value of the equilibria into (2), we obtain

$$F'(0) = b, \quad F'(\hat{N}) = 1 - \log b.$$

Hence the trivial equilibrium is asymptotically stable if $b < 1$ and a transcritical bifurcation happens at $b = 1$. The positive equilibrium \hat{N} is asymptotically stable if

$$|1 - \log b| < 1 \Leftrightarrow 1 < b < e^2.$$

At $b = e^2$, $F'(\hat{N}) = -1$ and the nontrivial equilibrium loses stability in favor of a 2-cycle. The bifurcation diagram of the Ricker map is represented in Figure 2.

Exercise 6.3

Consider the within-year dynamics for adults $n(\tau)$ and juveniles $x(\tau)$

$$\begin{aligned} \frac{dn(\tau)}{d\tau} &= -\delta(\tau)n(\tau) & n(0) &= N_t \\ \frac{dx(\tau)}{d\tau} &= -[\mu(\tau) + cn(\tau)]x(\tau) & x(0) &= BN_t \end{aligned}$$

for $0 \leq \tau \leq 1$. The solution of the within-year dynamics is

$$n(\tau) = N_t e^{-\int_0^\tau \delta(s) ds} \quad (3)$$

$$x(\tau) = BN_t e^{-\int_0^\tau (\mu(s) + cn(s)) ds} \quad (4)$$

(a) Define the yearly averages

$$\bar{\delta} := \int_0^1 \delta(s) ds, \quad \bar{\mu} := \int_0^1 \mu(s) ds.$$

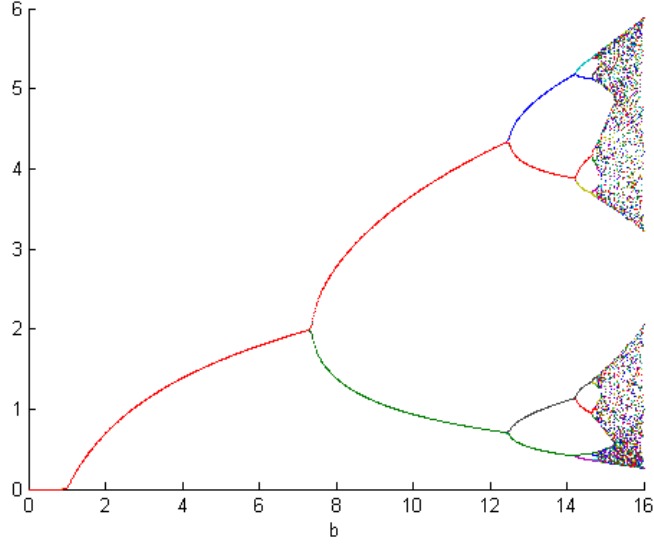


Figure 2: Bifurcation diagram of the Ricker map (1), for $a = 1$.

The map F reads

$$N_{t+1} = F(N_t) = n(1) + x(1) = N_t \left[e^{-\bar{\delta}} + B e^{-\bar{\mu}-c \int_0^1 n(\tau) d\tau} \right]$$

where $n(\tau)$ is given by (3).

(b) The model reduces to the Ricker map if $\bar{\delta} = \infty$ and

$$\int_0^1 e^{-\int_0^s \delta(\sigma) d\sigma} ds > 0.$$

For instance, we can take $\delta(s) < \infty$ for $s \in [0, \bar{\tau}]$, $\delta(s) = \infty$ for $s > \bar{\tau}$, for a fixed value $0 < \bar{\tau} < 1$.

(c) If δ and μ are constant,

$$N_{t+1} = N_t \left[e^{-\delta} + B e^{-\mu} e^{-\frac{c}{\delta}(1-e^{-\delta})N_t} \right].$$

The equilibrium $\hat{N} > 0$ satisfies

$$e^{-\delta} + B e^{-\mu} e^{-\frac{c}{\delta}(1-e^{-\delta})\hat{N}} = 1$$

$$\hat{N} = \frac{\delta}{c(1-e^{-\delta})} \log \frac{B e^{-\mu}}{1-e^{-\delta}}$$

and $\hat{N} > 0$ if and only if $B e^{-\mu} + e^{-\delta} > 1$ (in particular, the left-hand side $B e^{-\mu} + e^{-\delta}$ is the annual growth rate at low density, i.e., the number of offspring surviving one year with no cannibalism plus number of parent surviving, per initial parent).

For the stability, we look at

$$F'(\hat{N}) = 1 + \hat{N} \left[-\frac{c}{\delta}(1-e^{-\delta}) B e^{-\mu} e^{-\frac{c}{\delta}(1-e^{-\delta})\hat{N}} \right]$$

$$= 1 - (1-e^{-\delta}) \log \frac{B e^{-\mu}}{1-e^{-\delta}}$$

Notice that $F'(\hat{N}) < 1$ always, and hence \hat{N} is stable if and only if $F'(\hat{N}) > -1$, if and only if

$$g(\delta) := (1 - e^{-\delta}) \log \frac{Be^{-\mu}}{1 - e^{-\delta}} < 2.$$

Depending on the values of B and μ , increasing δ may destabilize the equilibrium (for instance, you can see this by studying the relative position of the curves $f(\delta) = \log(Be^{-\mu}/(1 - e^{-\delta}))$ and $g(\delta) = 2/(1 - e^{-\delta})$).

Exercise 6.4

Consider the discrete-time population model with k strains

$$N_{t+1}^{(i)} = \tilde{\lambda}_i f(N_t) N_t^{(i)}, \quad i = 1, \dots, k,$$

Assume the population exhibits cycles of length $T \in \mathbb{N}$, $T \geq 1$ (where $T = 1$ corresponds to an equilibrium state). Then, for all strains i which are not extinct, it holds $N_{t+T}^{(i)} = N_t^{(i)}$ and

$$N_{t+T}^{(i)} = \left(\prod_{j=0}^{T-1} \tilde{\lambda}_i f(N_{t+j}) \right) N_t^{(i)} = \tilde{\lambda}_i^T N_t^{(i)} \prod_{j=0}^{T-1} f(N_{t+j}),$$

from which we conclude that

$$\tilde{\lambda}_i = \left(\prod_{j=0}^{T-1} f(N_{t+j}) \right)^{-T}.$$

Hence, all the strains that are present in the cyclic/equilibrium population have the same value of $\tilde{\lambda}_i$. In a generic case, the factors $\tilde{\lambda}_i$ are different for any strain, hence generically there is only one strain present in the system.

Exercise 6.5

Consider the discrete-time model

$$N_{t+1} = \lambda(n, N_t) N_t$$

with

$$\lambda(n, N) = [ns + p(n)]f(N),$$

where p is a decreasing function of $n \in \mathbb{R}$, $0 \leq n \leq n_m$. The optimal strategy n^* is such that $(n^*, \hat{N}(n^*))$ is a maximum of λ :

$$\frac{\partial \lambda}{\partial n} \Big|_{(n^*, \hat{N}(n^*))} = [s + p'(n^*)]f(N) = 0 \Leftrightarrow p'(n^*) = -s \quad (5)$$

and

$$\frac{\partial^2 \lambda}{\partial n^2} \Big|_{(n^*, \hat{N}(n^*))} = p''(n^*) < 0 \quad (6)$$

If there exists $n^* < n_m$ such that (5) and (6) are satisfied, then the optimal population is an iteroparous population such that $p(n^*) > 0$.

Otherwise, assume (5) is satisfied but $p''(n^*) \geq 0$. In this case the stationary point n^* is a local minimum and the maximal value of λ is attained at $n = 0$ or $n = n_m$, depending on the shape of p .

Finally, if (5) is not satisfied then we distinguish two cases:

- $p'(n) < -s$ for all n : then the optimal value of λ is attained at $n^* = 0$ (no reproduction: extinction of the population);
- $-s \leq p'(n) < 0$ for all n : then the optimal value of λ is attained at $n^* = n_m$ (i.e., you should invest everything in reproduction and then die, semelparity);

In conclusion: with convex p , we cannot get iteroparity; hence a simple qualitative property of the trade-off (concavity) is necessary for iteroparity. Semelparity ($n^* = n_m$) results if p is convex or s is very high; the latter means the offspring are “valuable” (they have a high survival probability, so it is good to invest into them). When $n = 0$ is the optimum, then the population will obviously go extinct with any n , but $n = 0$ is the slowest way to extinction, and in this sense is “optimal”.