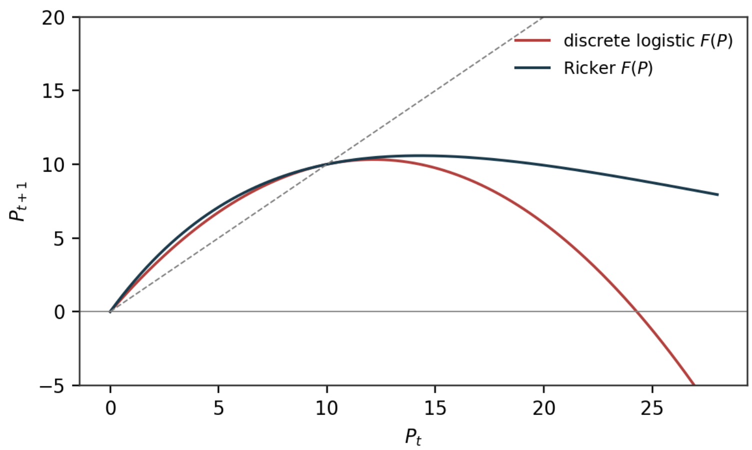
MATH 448 — Lecture 4

§1.4: the Ricker model; introduction to continuous-time models

Today: repair a flaw in the logistic model, then introduce continuous-time models.

Why the logistic model needs repair

The discrete logistic model $F(P) = P\big(1 + r(1 - P/K)\big)$ is a downward parabola: for P_t large enough, $F(P_t) < 0$, which has no biological meaning. A repair should keep the same small-P behavior and the same equilibria $0, K$, but stay positive for every $P \geq 0$.



The discrete logistic F dips below zero for large P; the Ricker F, defined below, does not.

The Ricker model

Assume instead that the per-capita growth rate decays *exponentially* in P rather than linearly, but can never go below -1 (a population cannot lose more than 100% of itself in a step):

$$\frac{\Delta P}{P} = ae^{-bP} - 1, \qquad a, b > 0.$$

Setting $a = e^r$ and $b = r/K$ gives the *Ricker model*:

$$P_{t+1} = P_t\, e^{r(1-P_t/K)} =: F(P_t).$$

Its equilibria are still $P^* = 0$ and $P^* = K$ (check: $F(0) = 0$, $F(K) = Ke^0 = K$), and $F(P) > 0$ for every $P \geq 0$.

Problem 4.1. Verify that the substitution $a = e^r$, $b = r/K$ turns $\Delta P/P = ae^{-bP} - 1$ into the Ricker model above.

Solution. Substituting,

$$\frac{\Delta P}{P} = e^r e^{-rP/K} - 1 = e^{r(1-P/K)} - 1.$$

Then $P_{t+1} = P_t + \Delta P = P_t\big(1 + \frac{\Delta P}{P_t}\big) = P_t\, e^{r(1-P_t/K)}$, which is the Ricker model.

Problem 4.2. Find $F'(P)$ for the Ricker model, and use it to determine for which values of $r > 0$ the equilibrium $P^* = K$ is stable.

Solution. By the product rule,

$$F'(P) = e^{r(1-P/K)} + P \cdot e^{r(1-P/K)} \cdot \Big(-\frac{r}{K}\Big) = e^{r(1-P/K)}\Big(1 - \frac{rP}{K}\Big).$$

At $P = K$: $F'(K) = e^0(1-r) = 1-r$. So $P^* = K$ is stable exactly when $|1-r| < 1$, i.e. $0 < r < 2$: the same threshold as the discrete logistic model, although the two models are different functions.

Now do Exercise 4.1 from Homework 3.

From discrete to continuous. Every model so far has assumed population change happens in discrete jumps. This description fits organisms with rigid, non-overlapping generations (annual plants, many insects), but many organisms reproduce continuously, with overlapping generations (bacteria, humans), for which no discrete time step is natural. Writing Δt for the step size,

$$\frac{\Delta P}{\Delta t} \longrightarrow \frac{dP}{dt} \qquad \text{as } \Delta t \to 0.$$

Applying this to the discrete logistic model: write the model with an explicit step size Δt (so $\Delta t = 1$ recovers Lecture 2's model exactly), subtract P_t, and divide by Δt:

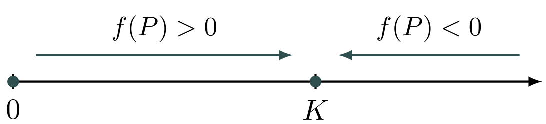
$$P_{t+1} = P_t\Big(1 + r\Delta t\Big(1 - \frac{P_t}{K}\Big)\Big) \implies \frac{P_{t+1} - P_t}{\Delta t} = rP_t\Big(1 - \frac{P_t}{K}\Big) \xrightarrow[\Delta t \to 0]{} \frac{dP}{dt} = rP\Big(1 - \frac{P}{K}\Big) =: f(P).$$

The logistic differential equation

$$\frac{dP}{dt} = rP\Big(1 - \frac{P}{K}\Big) =: f(P), \qquad r, K > 0.$$

Equilibria satisfy $f(P^*) = 0$: $P^* = 0$ and $P^* = K$.

- **Phase line.** Mark the equilibria on a number line and determine the sign of $f(P)$ in each region; that sign gives the direction of motion. For $0 < P < K$: $f(P) > 0$ and P increases. For $P > K$: $f(P) < 0$ and P decreases.
- **Stability test.** P^* is stable if $f'(P^*) < 0$, unstable if $f'(P^*) > 0$.



Phase line for the logistic ODE: every trajectory with $P_0 > 0$ converges to K.

Problem 4.3. Show that $f'(K) = -r$ for *every* $r > 0$, and conclude that $P^* = K$ is stable regardless of r.

Solution. Differentiating $f(P) = rP - \dfrac{r}{K}P^2$,

$$f'(P) = r - \frac{2r}{K}P.$$

At $P = K$: $f'(K) = r - 2r = -r$, which is negative for every $r > 0$. So $P^* = K$ is stable for all r, unlike the discrete logistic model, where K loses stability once $r > 2$.

This equation has a closed-form solution, $P(t) = \dfrac{K}{1 + Ce^{-rt}}$, with C determined by P_0; most differential equations do not. The phase-line and stability results above are sufficient for what follows.

Now do Exercise 4.2 from Homework 3.

Dimension and chaos

- A single continuous variable moves monotonically: the sign of dP/dt cannot change without P passing through an equilibrium, and P cannot reach an equilibrium in finite time. A one-dimensional continuous model therefore cannot oscillate or become chaotic.
- Two coupled continuous variables (e.g. predator–prey) can oscillate, but the Poincaré–Bendixson theorem* rules out chaos in two dimensions.
- Chaos in continuous time requires *at least three* coupled variables. The Lorenz system* (three coupled ODEs, modeling atmospheric convection) is the classic example.

Discrete-time chaos requires only one variable; continuous-time chaos requires at least three.

*Potential project topic!

Now do Exercise 4.3 from Homework 3.

So how common is chaos in real populations? There is evidence. In 1996, Cushing et al. found the first unambiguous case of chaos in a real population: laboratory colonies of the flour beetle *Tribolium*, a discrete-generation organism, matching the setting the discrete logistic model describes. An earlier study of measles epidemics in New York City suggested chaos might be present, but mumps and chickenpox data from the same period showed no such pattern, and there is still not enough high-quality, long-duration data to settle the measles case either way. The honest answer: confirmed chaos in nature is hard to demonstrate, not because the mathematics is exotic, but because it takes exceptionally clean, long-running data to distinguish real chaos from noise.

Next time.

- Euler's method: approximating continuous differential equations with discrete difference equations.
- Applying equilibrium/stability methods to evolution questions.