(1) $n_t = n_0 e^{rt}$

$$\frac{n_t}{n_0} = e^{rt}$$

$$\ln\left(\frac{n_t}{n_0}\right) = rt$$

$$\frac{\ln\left(\frac{n_t}{n_0}\right)}{t} = r \quad [2 \text{ marks}]$$

Further reading

Kramer, A.M., B. Dennis, A. Liebhold, J.M. Drake. 2009. The evidence for Allee effects. *Population Ecology* 51:341-354.

Homework

1. Derive the estimator in equation 5 from equation 2.
2. The standard deviation of our estimate for the intrinsic rate of increase of the Nunivak Island muskox population is shown in parentheses in the last line of Table 1. Using this and other information in the table estimate the 95% confidence interval of r. Use this information to put lower and upper bounds on the population size extrapolated to 2010.
3. Our record of the population of muskox on Nunivak Island is remarkably good. Suppose instead of annual censuses the only follow up censuses had been conducted at year 10 (1946) and year 20 (1956). What would you predict the population size to be in 2010. What are the lower and upper bounds of your estimate?
4. Derive an estimator for λ from equation 4.
5. Derive the canonical form of the logistic model in equation 9 from the form in equation 8.
6. Solve equation 9 to obtain the solution in equation 10
7. In the equation for exponential growth, the per capita population growth rate at all population sizes is given by the parameter r and was called the intrinsic rate of increase. In the logistic equation the percapita population growth rate declines with population size, but is at its maximum, which also is equal to r, in the limiting case where $n = 0$ (*i.e.*, as population size becomes small the behavior of the exponential growth model is recovered). Thus, in this case, also, r may be called the intrinsic rate of increase because it is the maximum per capita growth rate. However, this interpretation of r no longer holds in the model for the Allee effect given in equation 11. Here the maximum per capita population growth rate occurs at an intermediate population size $\hat{n}$, $0 < \hat{n} < k$. Find an expression for $\hat{n}$ and the intrinsic rate of increase (maximum per capita population growth rate) for a population with an Allee effect as in equation 11.

EQN 11 FROM CHAPTER 2 →

(5) $\frac{dn}{dt} = (b_0 - b_1 n)n - (d_0 + d_1 n)n$

$$\frac{dn}{dt} = (b_0 - d_0)n - (b_1 + d_1)n^2$$

$$= (b_0 - d_0)n\left\{1 - \frac{(b_1 + d_1)n}{b_0 - d_0}\right\}$$

$$= rn\left\{1 - \frac{n}{k}\right\} \quad [2 \text{ marks}]$$

(2) s.d. $= \sigma = 0.0495$

$\hat{r}_{upper} = 0.1306 + 2\sigma = 0.235$

$\hat{r}_{lower} = 0.1306 - 2\sigma = 0.0316$

$N_{t,upper} = 640e^{(0.235)(2010-1966)} =$ 19,805,459

$N_{t,lower} = 640e^{(0.0316)(2010-1966)} =$ 2,571

(3) $r_1 = \ln(40/31)/10 = 0.02549$

$r_2 = \ln(148/40)/10 = 0.13083$

$\bar{r} = 0.7816 \quad \sigma_r = 0.7449$

$\hat{r}_{upper} = 0.7816 + 2\sigma_r = 2.27$

$\hat{r}_{lower} = 0.7816 - 2\sigma_r = -0.7082$

$N_{t\,upper} = 640e^{(2.27)(2010-1966)} \approx 1.5 \times 10^6$

$N_{t\,lower} = 640e^{(-0.7082)(2010-1956)} \approx 1.9 \times 10^{-11}$

(6) $\frac{dn}{dt} = rn\left(1-\frac{n}{k}\right)$ 'solve' means integrate so first we rearrange:

$$\frac{1}{n\left(1-\frac{n}{k}\right)}\,dn = r\,dt, \text{ then integrate } \int \frac{1}{n\left(1-\frac{n}{k}\right)}\,dn = \int r\,dt$$

We need to convert the "$\frac{1}{n\left(1-\frac{n}{k}\right)}$" to something we know how to integrate : use partial fractions: $\frac{1}{n\left(1-\frac{n}{k}\right)} = \frac{A}{n} + \frac{B}{1-\frac{n}{k}}$

$1 = A\left(1-\frac{n}{k}\right) + Bn$, when $n = \emptyset$ then $1 = A(1)$ ie $A = 1$

when $n = k$, $1 = A\left(1-\frac{k}{k}\right) + Bk$, $1 = Bk$, ie $B = \frac{1}{k}$. So we can write $\int \frac{1}{n\left(1-\frac{n}{k}\right)}\,dn = \int \frac{1}{n} + \frac{1}{k\left(1-\frac{n}{k}\right)}\,dn = \int r\,dt$

Which we tidy up to: $\int \frac{1}{n} + \frac{1}{(k-n)}\,dn = \int r\,dt$

This we can integrate $\ln(n) - \ln(k-n) = rt + C$ constant of integration

Define n_0 as pop. size when $t = 0$

$$\ln(n_0) - \ln(k-n_0) = C$$

$$\therefore \ln(n) - \ln(k-n) = rt + \ln(n_0) - \ln(k-n_0)$$

Remember rule for logs: $\log(x) - \log(y) = \log\left(\frac{x}{y}\right)$

$$\ln\left(\frac{n}{k-n}\right) = rt + \ln\left(\frac{n_0}{k-n_0}\right), \quad \ln\left(\frac{n}{k-n}\right) - \ln\left(\frac{n_0}{k-n_0}\right) = rt$$

$\ln\left\{\frac{n(k-n_0)}{n_0(k-n)}\right\} = rt$. Take "anti logs": $\frac{n(k-n_0)}{n_0(k-n)} = e^{rt}$

Rearrange to $n = \ldots$: $n(k-n_0) = n_0(k-n)e^{rt}$, $n(k-n_0) = n_0ke^{rt} - n_0ne^{rt}$

$nk - nn_0 = n_0ke^{rt} - n_0ne^{rt}$, $nk - nn_0 + nn_0e^{rt} = n_0ke^{rt}$, $n(k - n_0 + n_0e^{rt}) = n_0ke^{rt}$

$n = n_0ke^{rt}/(k - n_0 + n_0e^{rt})$, $n = k/\left(1 + \left(\frac{k}{n_0} - 1\right)e^{-rt}\right)$

Q7. $\frac{dn}{dt} = rn\left(\frac{n}{a}-1\right)\left(1-\frac{n}{k}\right)$

per capita growth rate (p.c.g.r) $\frac{1}{n}\frac{dn}{dt} = r\left(\frac{n}{a}-1\right)\left(1-\frac{n}{k}\right)$

for max (p.c.g.r.) calc. $\frac{d}{dn}$(p.c.g.r) and set to $\emptyset$

$$\frac{d}{dn}(\text{p.c.g.r}) = r\left\{\left(\frac{n}{a}-1\right)\left(\frac{-1}{k}\right)+\left(1-\frac{n}{k}\right)\left(\frac{1}{a}\right)\right\} = \emptyset$$

ie, $\frac{d}{dn}(\text{p.c.g.r}) = \emptyset$ when $\frac{1}{a} - \frac{n}{ka} - \frac{n}{ka} + \frac{1}{k} = \emptyset$

ie, when $\frac{1}{a} + \frac{1}{k} = \frac{2n}{ka}$

ie, when $n = \frac{a+k}{2}$

$\underbrace{\frac{1}{n}\frac{dn}{dt}}_{\text{p.c.g.r}}$ when $n = \frac{a+k}{2}$ is $r\left(\frac{a+k}{2a}-1\right)\left(1-\frac{a+k}{2k}\right)$

Complex Dynamics Homework Solutions

1. Find the equilibrium of Beverton-Holt model.

   The Beverton-Holt model is a discrete-time model (shown here with annual generations):

   $$S_{t+1} = S_t \frac{e^r}{1 + aS_t}. \quad (1)$$

   A discrete time model is at equilibrium then the left and right sides of the equation are identical, i.e.,

   $$S^* = S^* \frac{e^r}{1 + aS^*}. \quad (2)$$

   Dividing both sides by S^* we have

   $$1 = \frac{e^r}{1 + aS^*}, \quad (3)$$

   which can be rearranged to give the equilibrium value:

   $$S^* = \frac{e^r - 1}{a}. \quad (4)$$

2. Consider a population with density dependent growth given by the Beverton-Holt model with parameters $r = 0.96$ and $a = 0.0044$, and initial population size $S = 147$. What will be the population size after five generations?

   This problem is solved by evaluating the equation 1 successively five times. In the first time step we have $S_{t+1} = 147\frac{e^{0.96}}{1+0.0044(147)} = 233.1305$. In the second generation we have $S_{t+1} = 233.1305\frac{e^{0.96}}{1+0.0044(233.1305)} = 300.5597$. Similarly, for the third, fourth, and fifth generations, we calculate 337.9907, 354.9146 and 361.8521.

3. What is the carrying capacity of the population in the previous question? Is it stable?

   From the solution to question 1, we calculate that the carrying capacity is $S^* = \frac{e^{0.96}-1}{0.0044} = 366.2947$. By evaluating equation 1 at values slightly smaller and slightly larger than this (say, 365 and 367) and observing that they both move in the direction of the equilibrium we conclude that the equilibrium is stable. Specifically, $365\frac{e^{0.96}}{1+0.0044(365)} = 365.7979$ and $367\frac{e^{0.96}}{1+0.0044(367)} = 366.5644$.

4. The version of the Beverton-Holt model introduced in this chapter does not consider harvesting. Modify equation 8 to represent the dynamics of a harvested fish population.

   We will assume that fish harvest occurs after recruitment and prior to reproduction. This means that of stock size S in a given year, only a portion $U < S$ is available for reproduction. The difference between U and S is the number of individuals harvested, H. That is

$$S - U = H. \tag{5}$$

   We will assume a harvest proportional to the stock size with catch rate h. Thus, $H = hS$. Substituting this last equation into 5 and rearranging, we have

$$U = S - hS. \tag{6}$$

   Now, we insert this into out basic Beverton-Holt model, yielding:

$$S_{t+1} = (S_t - hS_t)\frac{e^r}{1 + a(S_t - hS_t)}. \tag{7}$$

5. Another discrete time density-dependent model is the *logistic map*, $x_{t+1} = rx_t(1-x_t/k)$, which is named for its similarity to the continuous time logistic equation. Find the equilibria of this model. Iterate the model for a range of values of r. Plot the bifurcation diagram. How is the logistic map like the Ricker model? How is it different?

   To find the equilibria of the logistic map we set $x_{t+1} = x_t = x^*$ and solve for x^*, i.e.,

$$\begin{aligned}
x^* &= rx^*(1 - x^*/k) && \text{Divide by } x_t \\
1 &= r(1 - x^*/k) && \text{Multiply through on the right hand side} \\
1 &= r - rx^*/k && \text{Subtract } r \text{ and divide by } -1 \\
r - 1 &= rx^*/k && \text{Multiply by } k/r \\
k(r-1)/r &= x^*.
\end{aligned}$$

6. Sometimes, for instance to prepare data for time series analysis, it is useful to think about the dynamics of the logarithm of population size. Consider the change of variable $x = \ln(S)$. What is the difference equation for the logarithm of population size according to the Ricker model, *i.e.*, find the expression for f in the difference equation $x_{t+1} = f(x_t)$. Recall that on the ordinary scale and with annual generations rather than biannual generations, Ricker model dynamics are give by $S_{t+1} = S_t e^{r-bS_t}$.

   First we rearrange the identity $x = \ln(S)$ to five $S = e^x$. Then we substitute e^x in the Ricker model yielding

$$e^{x_{t+1}} = e^{x_t}e^{r-be^{x_t}} = e^{x_t+r-be^{x_t}}. \tag{8}$$

Since we are looking for a description of the dynamics of x we log-transform both sides to get

$$x_{t+1} = x_t + r - be^{x_t}. \tag{9}$$