

$$\textcircled{1} \quad n_t = n_0 e^{rt}$$

### Further reading

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

### Homework

- Derive the estimator in equation 5 from equation 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.

- 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?

- Derive an estimator for  $\lambda$  from equation 4.
- Derive the canonical form of the logistic model in equation 9 from the form in equation 8.
- Solve equation 9 to obtain the solution in equation 10

- 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 per capita 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  $n$ ,  $0 < n < k$ . Find an expression for  $n$  and the intrinsic rate of increase (maximum per capita population growth rate) for a population with an Allee effect as in equation 11.

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

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

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

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

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

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

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

$$\textcircled{2} \quad \text{s.d.} = \sigma = 0.0495$$

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

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

$$N_{t,\text{upper}} = 640e^{(0.235)(2010-1946)} =$$

$$19,805,459$$

$$N_{t,\text{lower}} = 640e^{(0.0316)(2010-1946)} =$$

$$2,571$$

$$N_{t,\text{upper}} = 640e^{(2.27)(2010-1946)} \approx 1.5 \times 10^6$$

$$(0.0316)(2010-1946) \approx 1.9 \times 10^{-11}$$

$$\textcircled{3} \quad r_1 = \ln(40/31)/10 = 0.02549$$

$$r_2 = \ln(140/40)/10 = 0.13083$$

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

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

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

$$N_{t,\text{upper}} = 640e^{(2.27)(2010-1946)} \approx 1.5 \times 10^6$$

$$(0.0316)(2010-1946) \approx 1.9 \times 10^{-11}$$

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  $n=0$  then  $1=A(1)$   $\Rightarrow A=1$

when  $n=k$ ,  $1 = A\left(1 - \frac{k}{k}\right) + Bk$ ,  $1=Bk$ ,  $\Rightarrow B=\frac{1}{k}$ . 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:  $\log(x) - \log(y) = \log\left(\frac{x}{y}\right)$

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

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

Rearrange to  $n = \dots$ :  $n(k-n_0) = n_0(k-n)e^{rt}$ ,  $n(k-n_0) = n_0k e^{rt} - n_0 n e^{rt}$

$$nk - nn_0 = n_0 k e^{rt} - n_0 n e^{rt}, \quad nk - nn_0 + n_0 n e^{rt} = n_0 k e^{rt}, \quad n(k-n_0 + n_0 e^{rt}) = n_0 k e^{rt}$$

$$n = n_0 k e^{rt} / (k - n_0 + n_0 e^{rt}), \quad n = k / (1 + (\frac{k}{n_0} - 1) e^{-rt})$$

$$\textcircled{1} \text{7. } \frac{dn}{dt} = rn \left( \frac{n}{a} - 1 \right) \left( 1 - \frac{n}{K} \right)$$

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

for max (p.c.g.r) calc.  $\frac{d}{dn} (\text{p.c.g.r})$  and set to 0

$$\frac{d}{dn} (\text{p.c.g.r}) = r \left\{ \left( \frac{n}{a} - 1 \right) \left( -\frac{1}{K} \right) + \left( 1 - \frac{n}{K} \right) \left( \frac{1}{a} \right) \right\} = 0$$

i.e.,  $\frac{d}{dn} (\text{p.c.g.r}) = 0 \text{ when } \frac{1}{a} - \frac{n}{Ka} - \frac{n}{Ka} + \frac{1}{K} = 0$

i.e., when  $\frac{1}{a} + \frac{1}{K} = \frac{2n}{Ka}$

i.e., when  $n = \frac{a+K}{2}$

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