Density-Dependent Population Growth

Logistic Population Growth

• Density-independent models assume unlimited resources such that $b$ and $d$ are constant

• Consider:

\[
\begin{align*}
\frac{dN}{dt} &= bN - dN^2 \\
b &\propto N \quad \text{decrease}
\end{align*}
\]
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Consider:

\[
dN/dt = (b' - d')N
\]

where \( b' = b - aN \)

\( b= \) birth rate under ideal uncrowded conditions
\( a= \) strength of density limitation

and where \( d' = d + cN \)

and parameters as in \( b \), thus per capita death rate increases with \( N \) (when \( c \) is positive)

Note: these are the most simple functional forms (linear) of resource limitation
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Reality check…. density dependence is probably not linear, for example Allee Effect

\[ r = (b' - d') \]

Allee Effect

Generally attributed to problems in the social system at low density
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Back to the logistic model:

\[
\frac{dN}{dt} = (b' - d')N
\]
\[
\frac{dN}{dt} = [(b-aN) - (d+cN)]N \quad \text{(substituting)}
\]
\[
\frac{dN}{dt} = [(b-d) - (a+c)N]N
\]

Multiply through:
\[
= [(b-d)/(b-d)] [(b-d)-(a+c)N]N
\]
\[
= [(b-d)][(b-d)/(b-d) - (a+c)N/(b-d)]N
\]

Set \( (b-d) = r \)
\[
\frac{dN}{dt} = rN[1-(a+c)N/(b-d)]
\]

Note \( a, b, c, d \) are all constants, so
\[
K = (b-d)/(a+c) \quad \text{which is called Carrying Capacity}
\]

* \( b \) & \( d \) rates w/o resource limitation; \( a \) & \( c \) measure strength of density dependence
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Growth is most rapid at $N = K/2$

- Steepest slope at $N_t = K/2$

- $N_t > K$ decreases to $K$ faster than $N_t < K$ increases to $K$

Note: time to reach $K \propto r$
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Assumptions

- K is constant
- Density dependence is a linear function of N

(N dN/dt)

(1/N) dN/dt

N

N

Logistic

Exponential
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K = max sustainable pop size… where b=d, b>d below b<d above (fig. 2.1 Gotelli)

Substitute into logistic: \( \frac{dN}{dt} = rN[1-(N/K)] \)

This is the classic eqn from Verhulst (1838) where \((1-(N/K))\) is the unused portion of K.

If K=100 but N=7, \(1-(7/100) = 0.93\) or 93% of resource is unused.

… this is a damping function on exponential growth. If N>K, then \(1-(N/K)\) is negative and population declines

… \(\frac{dN}{dt} = 0\) when N = K, a stable equilibrium; no matter how far N is perturbed, it returns to K
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• … by integration \( N_t = \frac{K}{1+[(K-N_0)/N_0]e^{-rt}} \)

• Which is S-shaped

• per capita growth rate declines one unit for each individual added… \( (1/N)(dN/dt) \approx (b-d) = r \)
  when \( N \) is small (max growth rate)
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Variations:

1) Time Lags ($\tau$) . . . control at time $= t$ from $N$ in past

\[ N_{t-\tau} = N \text{ at } t - \tau \]

Thus: \[ \frac{dN}{dt} = rN(1 - (N_{t-\tau}/K)) \]

So solution depends on $r$ and $\tau$

and response time is inversely \( \propto \) $r$; response $= 1/r$

Note units: \[ r = \text{ind}/(\text{ind}\times\text{time}) = \text{per capita change} \]
\[ 1/r = (\text{ind}\times\text{time})/\text{ind} = \text{time} \]

where ind = individuals
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Ratio of time lag to response controls growth:

$ r \tau \quad 0 < r \tau < 0.368 $ gradual increase toward $ K $

$ r \tau \quad 0.368 < r \tau < 1.57 $ damped oscillation

$ r \tau \quad r \tau > 1.57 $ stable limit cycles

Figure 2.5 Logistic growth curves with a time lag. The behavior of the model depends on $ r \tau $, the product of the intrinsic rate of increase and the time lag. (a) “Small” $ r \tau $ behaves like the model with no time lag. (b) “Medium” $ r \tau $ generates dampened oscillations and convergence on carrying capacity. (c) “Large” $ r \tau $ generates a stable limit cycle and does not converge on the carrying capacity.
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Stable limit cycle has \( K \) as midpoint; will return if perturbed

Cyclic population characterized by amplitude and period between high and low oscillation

\[
\text{Period} = \text{time between peaks} \\
\text{Amplitude} = \text{range between high and low} \\
\text{Amplitude increases } \propto \tau \\
\text{Period} \approx 4 \tau \text{ for all } r
\]
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2. Discrete time model

\[ N_{t+1} = N_t + \lambda N_t (1 - (N_t/K)) \]

Recall \( N_{t+1}/N_t = \lambda \quad \therefore \quad N_{t+1} = \lambda N_t \)

set \( N_{eq} = K \) when \( \lambda = 1 \)

Now let \( \lambda = 1.0 - B(N-K) \)

where \(-B\) is slope

\[ N \]

\[ K \]

\[ \lambda \]

\[ N_{eq} \]

\[ B \]

\[ \lambda = 1 \]
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Discrete Time Model

So, \( N - K \) is the deviation from equilibrium density... set = \( z_t \)

\[ \therefore \lambda = 1 - B(N_t - K) \]

\[ = 1 - Bz_t \]

Return to \( N_{t+1} = \lambda N_t \) and substitute

\[ N_{t+1} = (1 - Bz_t)N_t = N_t + \lambda N_t\left(1-(N_t/K)\right) \]
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Note: discrete model has built-in time lag of 1 generation. Dynamics depend on $BK = L$

$L < 2.0$ approach $K$ with damped oscillations

$2 < L < 2.449$ stable 2-point limit cycles

$L > 2.57$ chaos*, complex non-repeating

*seemingly random complexity from simple deterministic equation; Not random, susceptible to initial conditions

Figure 2.6 The behavior of the discrete logistic growth curve is determined by the size of $r_d$. (a) “Small” $r_d$ generates damped oscillations ($r_d = 1.9$). (b) “Less small” $r_d$ generates a stable two-point limit cycle ($r_d = 2.4$). (c) “Medium” $r_d$ generates a more complex four-point limit cycle ($r_d = 2.5$). (d) “Large” $r_d$ generates a chaotic pattern of fluctuations that appears random ($r_d = 2.8$).
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Sensitivity to initial conditions

Figure 2.7 Divergence of population tracks with chaos. Both populations followed the same logistic equation, but the starting $N$ for one of the populations was 50 and the other was 51. Note that, as more time passes, the two populations begin to diverge from one another.
3. Random variation in K

Note: the approach to K is asymmetrical (decline faster N>K than increase N<K)

\[ \bar{N} \approx \bar{K} - \frac{\sigma_K^2}{2} \text{ so } \bar{N} \text{ always } < K \]

\[ \therefore \text{ more variable environment leads to smaller } \bar{N} \]

Also, size of \( r \propto \) to tracking of variation

… bigger \( r \), closer tracking of variable \( K \)

… \( N \) is smaller for same \( \sigma_K^2 \) with small \( r \)
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Logistic growth with random variation in K

Figure 2.8  Logistic population growth with random variation in carrying capacity. Note that the population with the larger growth rate ($r = 0.50$) tracks the fluctuations in carrying capacity, whereas the population with the small growth rate ($r = 0.10$) is less variable and does not respond as quickly to fluctuations in resources.
4. Periodic variation in K (seasonality)

- Acts like time lag, depends on r and period of cycle (c), thus \( \bar{N} \propto rc \)
- \( rc \) large, pop tracks K cycles at \( \bar{N} < K \) (insects?)
- \( rc \) small, converge on \( \bar{N} << K \) (small mammals?)

Figure 2.9 Logistic growth with periodic variation in the carrying capacity. The carrying capacity of the environment varies according to a cosine function. As with random variation, the population with the large growth rate (\( r = 10 \)) tends to track the variation (a), and the population with the small growth rate (\( r = 0.2 \)) tends to average it (b). The dashed line indicates K. (From May 1976.)