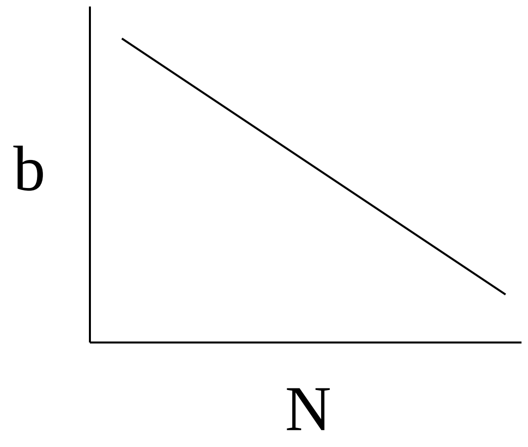
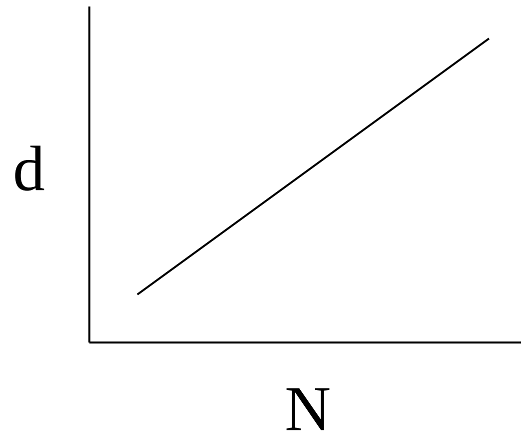
Density-Dependent Population Growth

Logistic Population Growth

- Density-independent models assume unlimited resources such that b and d are constant
- Consider:

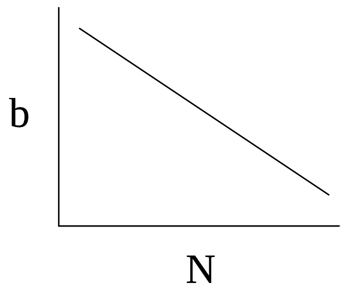




Density-Dependent Population Growth

Consider:

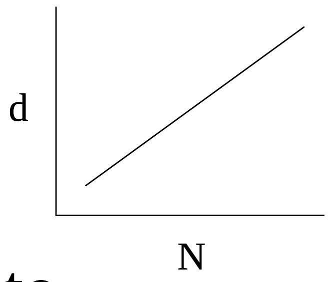
$$dN/dt = (b' - d')N$$



where $b' = b - aN$

b= birth rate under ideal uncrowded conditions

a=strength of density limitation



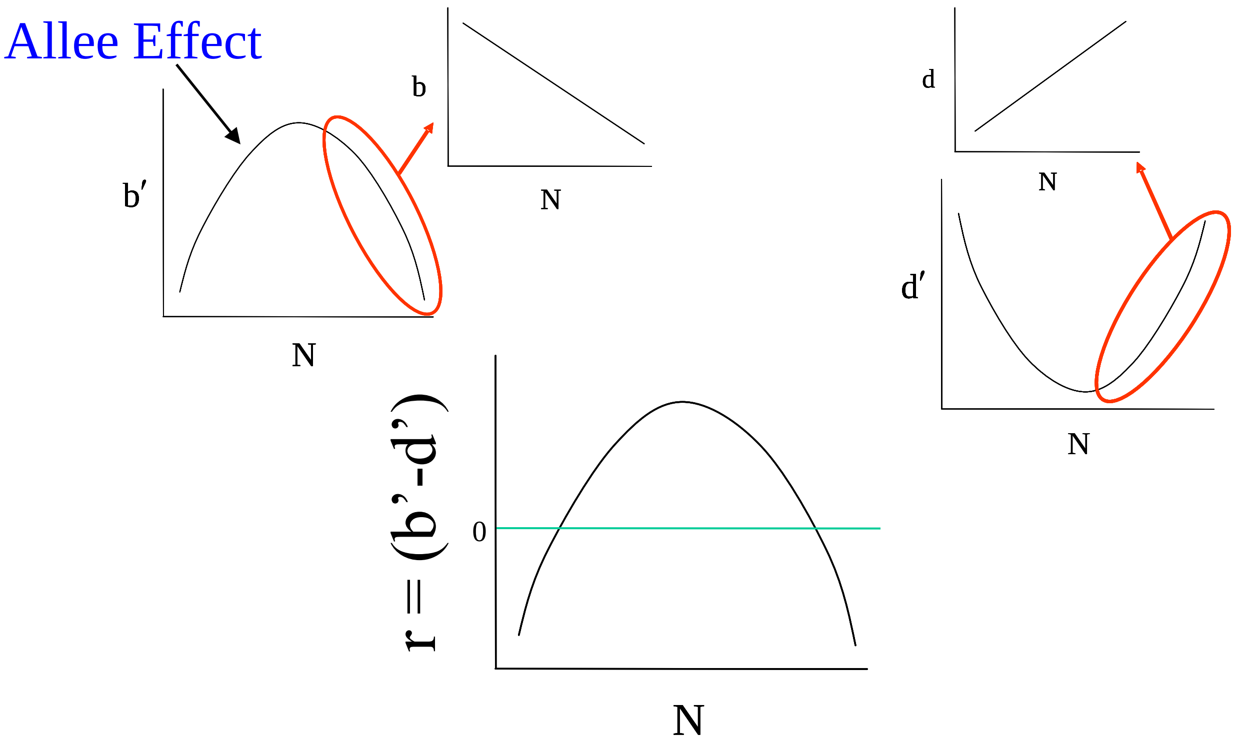
and where $d' = d + cN$

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

Density-Dependent Population Growth

Reality check…. density dependence is probably not linear, for example Allee Effect



Generally attributed to problems in the social system at low density

Density-Dependent Population Growth

Back to the logistic model:

$dN/dt = (b' - d')N$

$dN/dt = [(b\text{-}aN) – (d+cN)]N$ (substituting)

$dN/dt = [(b\text{-}d) – (a+c)N]N$

Multiply through:

$= [(b\text{-}d)/(b\text{-}d)]\ [(b\text{-}d)\text{-}(a+c)N]N$

$= [(b\text{-}d)][(b\text{-}d)/(b\text{-}d) – (a+c)N/(b\text{-}d)]N$

Set $(b\text{-}d)=r$

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

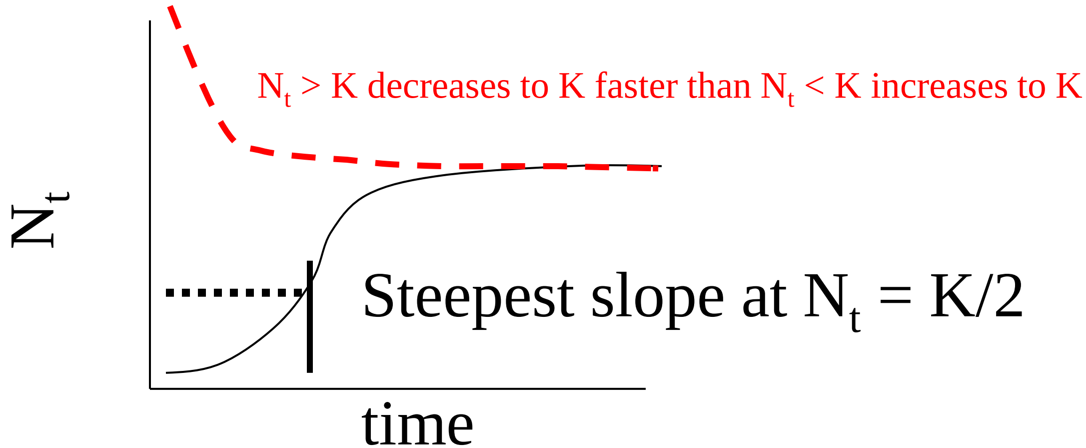
Note a, b, c, d are all constants, so

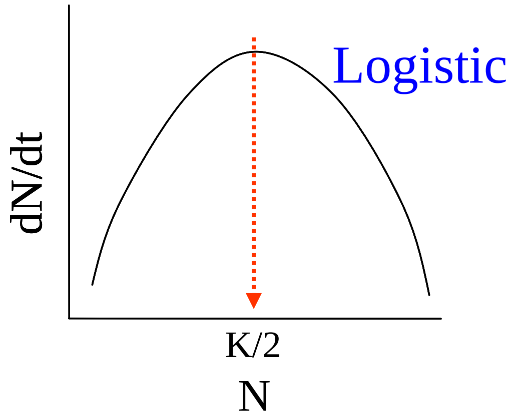
$K=(b\text{-}d)/(a+c)$ which is called Carrying Capacity

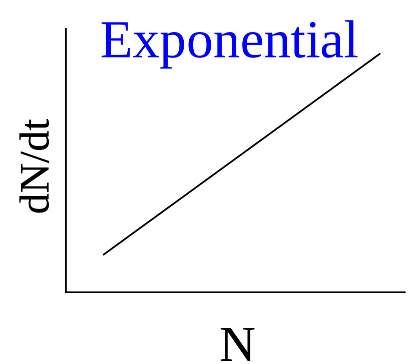
* b & d rates w/o resouce limitation; a & c measure strength of density dependence

Density-Dependent Population Growth

Growth is most rapid at N = K/2





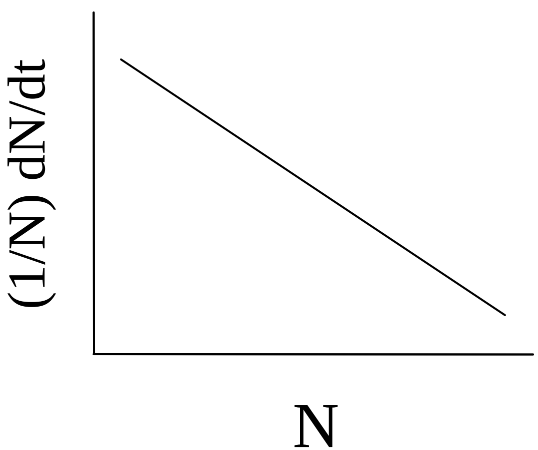


Note: time to reach K $\propto$ r

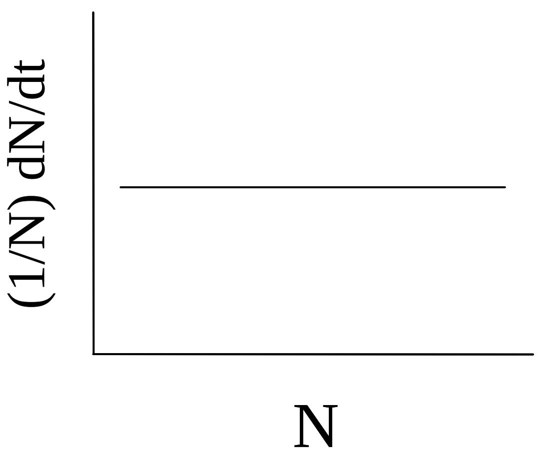
Density-Dependent Population Growth

Assumptions

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



Logistic



Exponential

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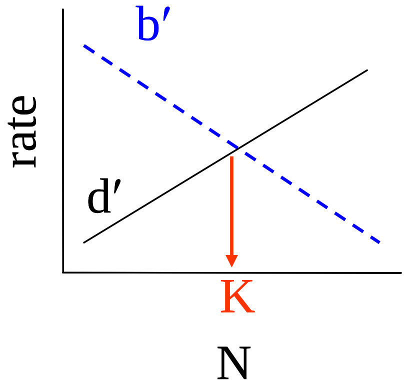


K = max sustainable pop size… where b=d, b>d below b<d above (fig. 2.1 Gotelli)

Substitute into logistic: 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.

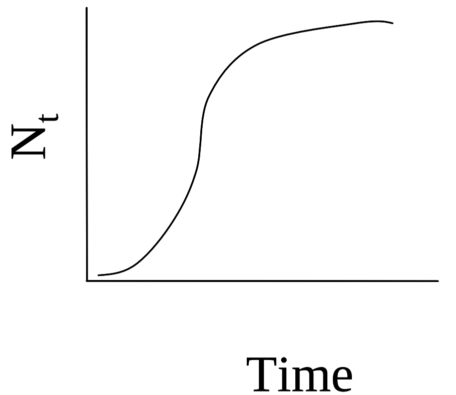
… this is a damping function on exponential growth. If N>K, then 1-(N/K) is negative and population declines

… dN/dt = 0 when N = K, a stable equilibrium; no matter how far N is perturbed, it returns to K

Density-Dependent Population Growth

- … by integration $N_t = \dfrac{K}{1+[(K-N_o)/N_o]e^{-rt}}$

- Which is S-shaped



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

Density-Dependent Population Growth

Variations:

1) Time Lags (τ)… control at time = t from N in past

$N_{t-\tau}$ = N at t - τ

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

So solution depends on r *and* τ

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

Note units: r = ind/(ind*time) = *per capita change*

1/r = (ind*time)/ind = time

where ind = individuals

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Ratio of time lag to response controls growth:

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

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

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

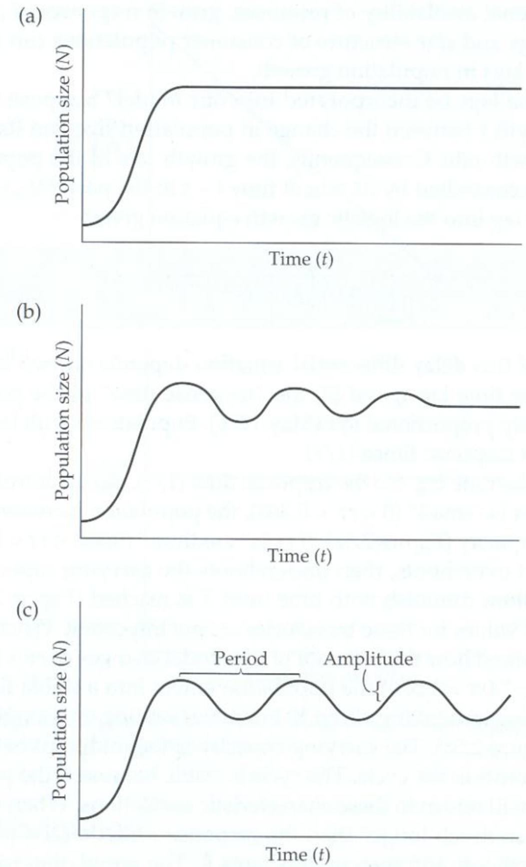

Figure 2.5 Logistic growth curves with a time lag. The behavior of the model depends on $r\tau$, the product of the intrinsic rate of increase and the time lag. (a) "Small" $r\tau$ behaves like the model with no time lag. (b) "Medium" $r\tau$ generates dampened oscillations and convergence on carrying 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

Period = time between peaks

Amplitude = range between high and low

Amplitude increases $\propto \tau$

Period $\cong 4\ \tau$ for all r

Density-Dependent Population Growth

2. Discrete time model

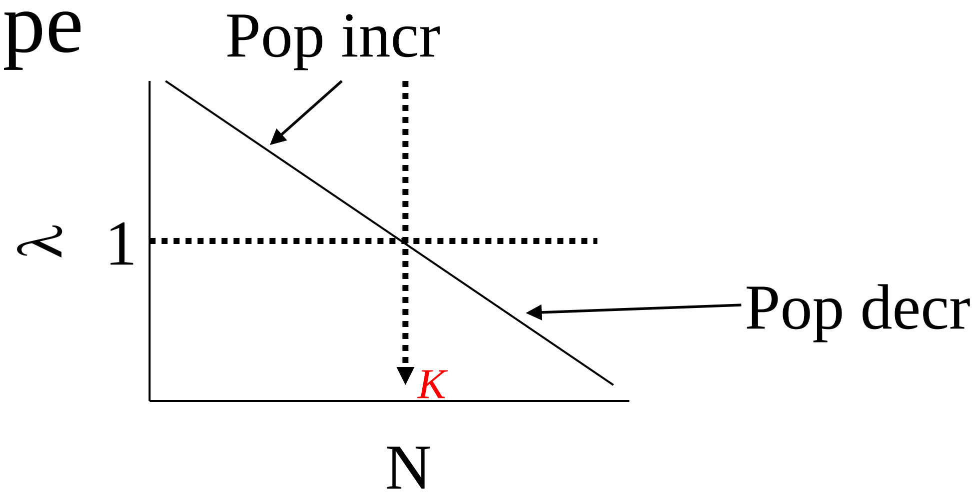
$N_{t+1} = N_t + \lambda N_t(1-(N_t/K))$

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

set $N_{eq}=K$ when $\lambda=1$

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

where $-B$ is slope



Density-Dependent Population Growth

Discrete Time Model

So, N-K is the deviation from equilibrium density… set = z_t

$\therefore \lambda = 1\text{-}B(N_t\text{-}K)$

$= 1 - Bz_t$

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

$N_{t+1} = (1\text{-}Bz_t)N_t = N_t + \lambda N_t(1\text{-}(N_t/K))$

Density-Dependent Population Growth

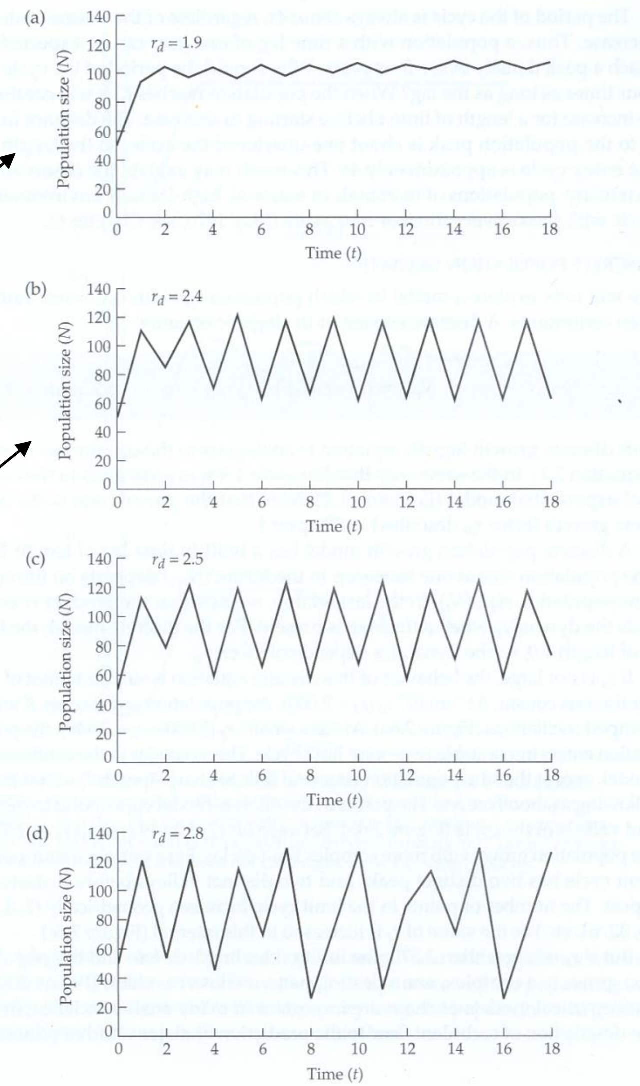
Note: discrete model has built-in time lag of 1 generation. Dynamics depend on BK = L

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 ($r_d = 2.8$).

Density-Dependent Population Growth

Sensitivity to initial conditions

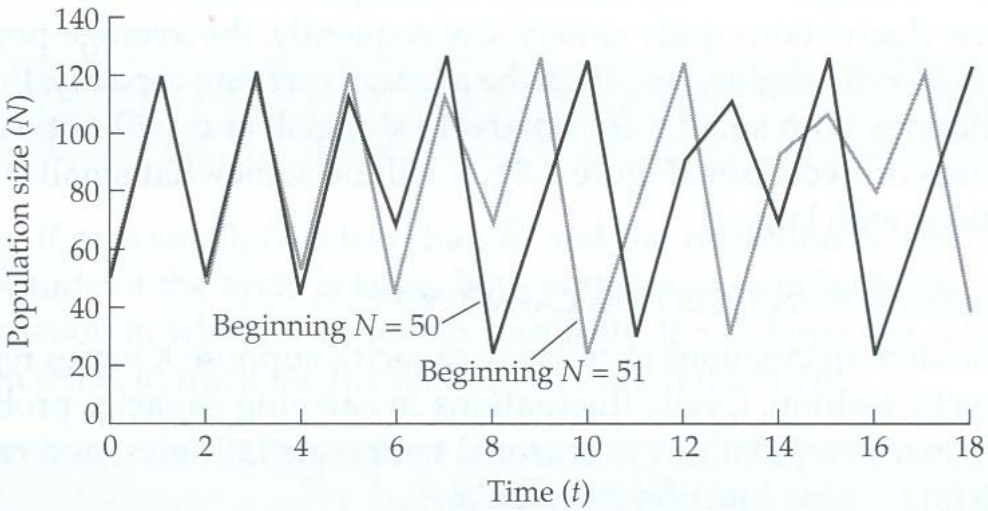


Figure 2.7 Divergence of population tracks with chaos. Both populations followed the same logistic equation, but the starting N for one of the populations was 50 and the other was 51. Note that, as more time passes, the two populations begin to diverge from one another.

Density-Dependent Population Growth

3. Random variation in K

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

$$\overline{N} \cong \overline{K} - \frac{\sigma_K^2}{2} \quad \text{so } \overline{N} \text{ always} < K$$

$\therefore$ more variable environment leads to smaller $\overline{N}$

Also, size of r $\propto$ to tracking of variation

… bigger r, closer tracking of variable K

… N is smaller for same σ_K^2 with small r

Density-Dependent Population Growth

Logistic growth with random variation in K

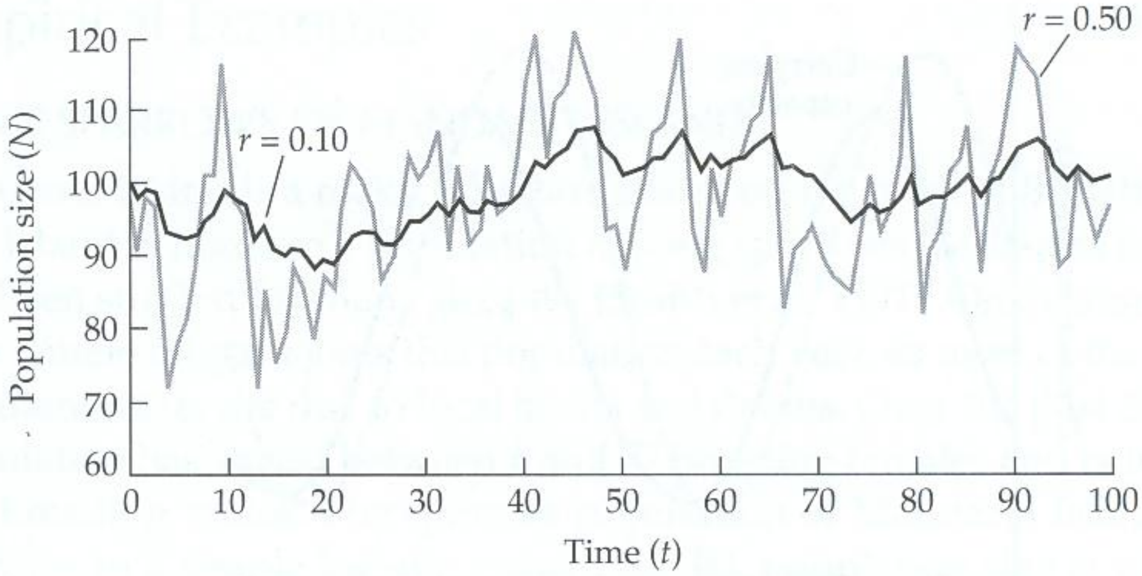


Figure 2.8 Logistic population growth with random variation in carrying capacity. Note that the population with the larger growth rate ($r = 0.50$) tracks the fluctuations in carrying capacity, whereas the population with the small growth rate ($r = 0.10$) is less variable and does not respond as quickly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

Density-Dependent Population Growth

4. Periodic variation in K (seasonality)

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

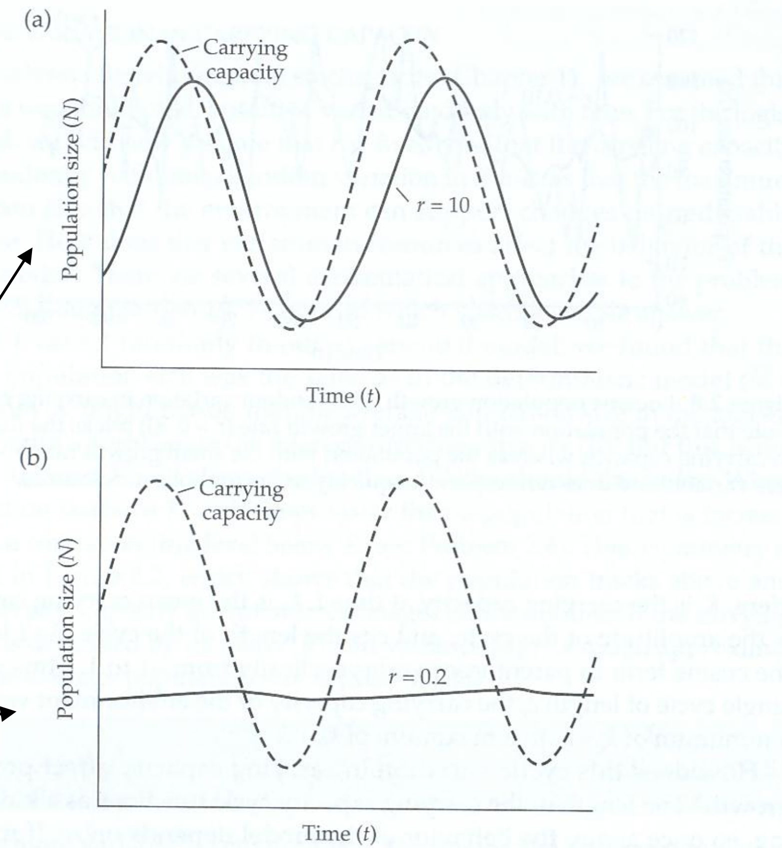


Figure 2.9 Logistic growth with periodic variation in the carrying capacity. The carrying capacity of the environment varies according to a cosine function. As with random variation, the population with the large growth rate ($r = 10$) tends to track the variation (a), and the population with the small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