

# Chapter 5 – Mills (2007)

Exponential or Geometric Population  
Change

# POPULATION GROWTH--EXPONENTIAL MODEL

- 
- MODEL DESCRIBING THE "RATE OF INCREASE" OF ANIMAL POPULATIONS FACING UNLIMITED RESOURCES
- 
- REASONS FOR STUDYING POPULATION GROWTH
- 
- 1. COMPARE RATES OF GROWTH AMONG POPULATIONS TO:
- 
- INDEX DEMOGRAPHIC VIGOR-demography?
- INDEX HABITAT POTENTIAL TO SUPPORT A SPECIES
- 
- 2. THEORETICAL MODELS OF POPULATION GROWTH ALLOW US TO PREDICT ANIMAL RESPONSES TO CONTROL EFFORTS OR HARVEST

# EXPONENTIAL

- SEVERAL THEORETICAL MODELS FOR THE FORM OF POPULATION INCREASE
- 
- EXPONENTIAL GROWTH--APPLIES TO ANIMAL POPULATIONS FACING UNLIMITED RESOURCES
- 
- UNDER SUCH CONDITIONS POPULATIONS INCREASE AT AN EVER INCREASING RATE
- 
- So, why use this model??

# DISCRETE MODEL

- $dN/dt = B(\text{TOTAL NUMBER OF BIRTHS}) - D(\text{TOTAL NUMBER OF DEATHS})$
- 
- $R_B = \text{"PER HEAD" BIRTH RATE}$
- 
- 
- $= \frac{\text{\# BORN SURVIVING TO AGE 1}}{\text{\# ADULTS}}$
- 
- 
- $R_D = \text{"PER HEAD" DEATH RATE}$
- 
- 
- $= \frac{\text{\# ADULTS (AGE 1+) DYING}}{\text{\# ADULTS}}$
- 
- 
- $dN/dt = R_B N - R_D N$

# DISCRETE MODEL

- SUPPOSE THAT  $dt = 1$  UNIT
- 
- $dN = R_B N - R_D N$
- 
- $dN = N_1 - N_0$
- 
- $N_1 - N_0 = R_B N_0 - R_D N_0$
- 
- $N_1 = N_0 + R_B N_0 - R_D N_0$
- 
- $N_1 = N_0 (1 + R_B - R_D)$

# DISCRETE MODEL

- FINITE RATE OF INCREASE =  $R = \text{LAMBDA}$
- 
- $N_1 = N_0 R$
- 
- $N_2 = N_1 R = (N_0 R) R = N_0 R^2$
- 
- $N_t = N_0 R^t$

# DERIVING R

- 
- A. FROM BIRTH AND DEATH SCHEDULES
- 
- B. FROM CENSUS DATA
- 
- $R = \frac{N_{t+1}}{N_t}$
- 
- $R = 1 + R_B - R_D$

# MEANING OF R

- 
- "PER CAPITA" RATE OF INCREASE
- 
- IF  $R = 1.8$
- 
- THEN FOR EVERY INDIVIDUAL IN POPULATION AT  $t_i$  THERE WILL BE 1.8
- 
- AT TIME  $t_{i+1}$
-

# CONTINUOUS MODEL

- IMAGINE SHRINKING OUR TIME INTERVALS SO SMALL THAT BIRTHS AND DEATHS ARE NOW OCCURRING AT AN INSTANTANEOUS SCALE, YIELDING A CONTINUOUS PATTERN OF GROWTH
- 
- WE CAN EXPRESS RATE OF CHANGE IN THE POPULATION AS A DIFFERENTIAL EQUATION

# CONTINUOUS MODEL

- $dN/dt = N(B) - N(D)$
- 
- WHERE N = NUMBER OF ANIMALS IN POPULATION
- 
- B = INSTANTANEOUS "PER HEAD" BIRTH RATE
- 
- D = INSTANTANEOUS "PER HEAD" DEATH RATE
-

# CONTINUOUS MODEL

- $dN/dt = N(B - D)$
- 
- $dN/dt = N(r)$
- 
- $dN/dt = rN$ ; hence,  $r = dN/dt/N$
- 
- WHERE  $r$  IS THE "PER HEAD" INSTANTANEOUS RATE OF INCREASE
- 
- NOTE: POPULATION RATE OF INCREASE ( $dN/dt$ ) VS. "PER HEAD RATE OF INCREASE

# CONTINUOUS MODEL

- INTEGRATION:
- 
- $N_t = N_0 e^{rT}$
- 
- WHERE:  $e = 2.7183$  (APPROX) = EULER'S CONSTANT AND HAS THE PROPERTY THAT ITS NATURAL LOGARITHM IS EQUAL TO 1.0.
-

# FINITE VS. INSTANTANEOUS

- $N = N_0 R^t$      $N = N_0 e^{rt}$
- 
- $R = e^r$
- 
- $\ln(R) = r$

# SAMPLE CALCULATIONS

- 
- 1. ASSUMING AN INSTANTANEOUS RATE OF INCREASE OF 0.69 WHAT IS POPULATION AT DIFFERENT TIME INTERVALS GIVEN 100 INTRODUCED ANIMALS?

- 
- $N_t = 100e^{0.69t}$

- 
- t     $N_t$

- 
- 0    100

- 
- 1    200

- 
- 2    400

- 
- 3    800

# SAMPLE CALCULATIONS

- ASSUMING 20 SHARP-TAILED GROUSE INTRODUCED IN 1990, 80 IN 1993,
- 
- WHAT IS  $r$ ?
- 
- $80 = 20e^{r^3}$
- 
- $\ln(80) = \ln(20) + 3r$
- 
- $4.38 = 2.99 + 3r$
- 
- $3r = 4.38 - 2.99$
- 
- $3r = 1.39$
- 
- $r = 1.39/3 = 0.46$
-

# FINITE VS. INSTANTANEOUS

- DEER POPULATION IS INCREASING AT A FINITE RATE OF INCREASE OF 1.6, WHAT IS THE INSTANTANEOUS RATE OF INCREASE?
- 
- $R = 1.6$
- 
- $\ln(1.6) = 0.47$
- 
- $0.47 = r$
- 
- RATE OF INCREASE MAY BE EXPRESSED AS FINE RATE =  $e^r$  OR  $R$
- 
- OR INSTANTANEOUS RATE =  $r$
-

# ADVANTAGES OF INSTANTANEOUS RATE

- 
- 1. CENTERED ON ZERO (WHEREAS  $e^r$  CENTERED ON 1)
- 
- RATES OF INCREASE AND DECREASE ARE DIRECTLY COMPARABLE FROM CHANGES IN SIGN
- 
- $r = 0.5$      $e^r = 1.649$
- 
- $r = -0.5$      $e^r = 0.607$
- 
- 2.  $r$  EASILY CONVERTS FROM ONE UNIT OF TIME TO ANOTHER
- 
- IF  $r$  IS MEASURED FOR AN ANNUAL PERIOD, THEN THE DAILY RATE OF INCREASE =  $r/365$
- 
- WEEKLY RATE OF INCREASE =  $r/52$
-

# COMPUTING R VS r

- 
- A.  $R = N_{t+1}/N_t$     $R = e^r$     $r = \text{Ln}(R)$
- 
- 
- B.  $N = N_0 e^{rt}$
- 
- $\text{Ln}(N) = \text{Ln}(N_0) + rt$
- 
- WHICH IS EQUIVALENT TO FORMULA FOR A STRAIGHT LINE:
- 
- $(Y = a + bX)$
-

# MEASURES OF RATE OF INCREASE

- $r_m = r_{max}$  = INTRINSIC RATE OF INCREASE  
WHEN NO RESOURCES ARE LIMITING
- 
- DETERMINED BY THE SPECIES GENETIC  
POTENTIAL
-

# MEASURES OF RATE OF INCREASE

- $r$  = OBSERVED RATE OF INCREASE IS THE EXPONENTIAL RATE OVER WHICH A POPULATION INCREASES OVER ANY OBSERVED PERIOD OF TIME
- 
- $r$  INCORPORATES ALL LIMITING FACTORS THAT MAY BE EXPERIENCED DURING THAT TIME
- 
- DOES NOT IMPLY CONSTANCY

# MEASURES OF RATE OF INCREASE

- $r_s$  = SURVIVAL-FECUNDITY RATE OF INCREASE
- 
- $r_s$  IS THE EXPONENTIAL RATE AT WHICH A POPULATION WOULD INCREASE IF IT HAD A STABLE AGE DISTRIBUTION APPROPRIATE TO ITS CURRENT SCHEDULES OF AGE-SPECIFIC SURVIVAL AND FECUNDITY—FROM LIFE TABLE.
- 
- $r_s$  USUALLY DIFFERS FROM THE ACTUAL RATE OF INCREASE BECAUSE AN AGE DISTRIBUTION IS SELDOM STABLE. HOWEVER, THE  $r_s$  RATE OF INCREASE REVEALS A POPULATION'S CURRENT CAPACITY TO INCREASE (BECAUSE IT IS BASED ON THE AGE STRUCTURE OF THE POPULATION).
-

# MEASURES OF RATE OF INCREASE

- $r_m$ ,  $r$ , AND  $r_s$  ALL MAY BE USED AS INDICES OF DEMOGRAPHIC VIGOR TO
- 
- COMPARE A POPULATION'S WELL BEING BASED ON, FOR EXAMPLE:
- 
- – FAT RESERVES, BODY SIZE, SEX RATIO
- 
- INDICES ARE USEFUL TO THE EXTENT THAT THEY INDEX  $r$

# MEASURES OF RATE OF INCREASE

- $r_p$  POTENTIAL RATE OF INCREASE
- 
- DEMOGRAPHIC VIGOR CAN BE MODIFIED FOR HARVESTED POPULATIONS.
- 
- IF HARVESTING IS ACCOMPLISHED “QUANTITATIVELY”, SO THAT  $r_s$  IS STABLE AT 0, THEN THE VALUE OF INTEREST BECOMES RATE OF INCREASE IF HARVESTING IS TERMINATED.
- 
- $r_p$  OF HARVESTED POPULATION CAN BE MEASURED DIRECTLY BY HALTING HARVESTING OR CAN BE ESTIMATED FROM A LIFE TABLE PARTITIONED INTO RATES OF HARVESTING MORTALITY AND NATURAL MORTALITY SO THAT YOU CAN REMOVE HARVEST MORTALITY AND ESTIMATE POTENTIAL RATE OF INCREASE.
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# ASSUMPTIONS FOR EXPONENTIAL GROWTH MODEL

- 1. NO AGE STRUCTURE (ALL INDIVIDUALS ALIKE).
- 
- 2.  $r$  IS CONSTANT (RESOURCES UNLIMITED DURING PERIOD MEASURED).

# EXAMPLES OF EXPONENTIAL GROWTH

- 
- A. PHEASANTS ON PROTECTION ISLAND, WASHINGTON
- 
- 400 ACRES OF IDEAL PHEASANT HABITAT
- 
- NO PREDATORS
- 
- MOSAIC OF WHEAT, BARLEY, OATS, GRASSLAND, PASTURE
- 
- 8 PHEASANTS RELEASED IN 1938
- 
- 1,500 PHEASANTS BY 1947

# EXAMPLES OF EXPONENTIAL GROWTH

- INSTANTANEOUS RATE OF INCREASE --pheasants
- 
- $1,500 = 8e^{r4}$
- 
- $\ln(1,500) = \ln(8) + 4r$
- 
- $7.31 = 2.07 + 4r$
- 
- $4r = 7.31 - 2.07$
- 
- $4r = 5.24$
- 
- $r = 1.31$
- 
- $R = 3.7$
-

# EXAMPLES OF EXPONENTIAL GROWTH

- INTRODUCED REINDEER ON ST. MATHHEWS ISLAND
- 
- 29 REINDEER INTRODUCED BY US COAST GUARD
- 
- 6,000 REINDEER BY 1963

# EXAMPLES OF EXPONENTIAL GROWTH

- $6,000 = 29e^{r19}$
- 
- $\ln(6,000) = \ln(29) + 19r$
- 
- $8.69 = 3.36 + 19r$
- 
- $19r = 8.69 - 3.36$
- 
- $19r = 5.33$
- 
- $r = 0.28$
- 
- $R = 1.32$

# EXAMPLES OF EXPONENTIAL GROWTH

- DEER OF GEORGE RESERVE
- 
- 6 DEER (4 DOES, 2 BUCKS) INTRODUCED IN 1928)--6 YEARS LATER 180 DEER
- 
- 1967-- DRASTIC REDUCTION TO 10 ANIMALS AND 6 YEARS LATER AFTER NO HUNTING-212 DEER
- 
- $r = \ln(N^6) - \ln(N_0)/t = \ln(180) - \ln(6)/6 = 5.19 - 1.79/6$
- 
- $r = 0.57$
- 
- $R = 1.76$
-

# Variation in Population Growth

- Demographic stochasticity—deviation in birth and death rates—more important at low population size
- Environmental stochasticity—arises from extrinsic factors (weather)
- Catastrophes and bonanzas—rare—outside the range of normal environmental stochasticity

# Implications for Variation in Population Growth

- Increasing variation in growth rate causes geometric mean of population growth to be less than arithmetic mean
- Variation in growth rate can lead to population decline despite  $r$  values greater than zero
- $R_g = (R_1 * R_2 * R_3)^{1/2}$

# Density-Independent Diffusion Approximation Method

- Used when missing estimates of growth rate
- Regress  $x_i$  (transformed time interval) with  $y_i$  (population change corrected for time interval)
- Slope = mean of  $r$  or  $\bar{r}$  and standard error from regression analysis provides estimate of variance to generate CI for  $\bar{r}$