

**Calculation of the intrinsic rate of increase (r) from life table data**

Information needed:

1. Age specific fecundity  $b(x)$
2. Age specific survival  $l(x)$

The rate of increase of a population is a function of the net reproductive rate and the generation time.

**Net reproductive rate ( $R_0$ )**- mean number of female offspring produced per female over her lifetime or:

$$R_0 = \sum_{x=0}^k l(x)b(x)$$

where  $k$  is the oldest age for which  $l(x)$  or  $b(x) > 0$ .

If  $R_0 > 1$  the population will increase,  $R_0 < 1$  the population will decline,  $R_0 = 1$  the population will remain the same.

**Generation time (G)**- is often calculated as the average age of the parents of a single cohort.

$$G = \frac{\sum_{x=0}^k l(x)b(x)x}{\sum_{x=0}^k l(x)b(x)}$$

Using  $R_0$  and  $G$  an approximation of  $r$  can be calculated:

$$r \approx \frac{\ln(R_0)}{G}$$

See Gotelli (p. 64) for a derivation of this equation.

The instantaneous rate of increase of a population,  $r$ , can be calculated exactly using Lotka's (or Euler's, pronounced Oiler's) equation which relates  $r$  to  $l(x)$  and  $b(x)$  values:

$$1 = \sum_{x=0}^k l(x)b(x)e^{-rx}$$

**Example of calculating r using Euler’s Equation.**

<b>Age (x)</b>	<b>0</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>
<b>l(x)</b>	1	0.98	0.95	0.5	0.3	0
<b>b(x)</b>	0	0	0	3	4	0

First, estimate r using  $R_0$  and G.

$$R_0 = \sum l(x)b(x) = (1*0) + (0.98*0) + (0.95*0) + (0.5*3) + (0.3*4) + (0*0) = 2.7$$

$$G = \frac{\sum l(x)b(x)x}{R_0} = \frac{(1*0*0) + (0.98*0*1) + (0.95*0*2) + (0.5*3*3) + (0.3*4*4) + (0*0*5)}{2.7} = \frac{9.3}{2.7} = 3.44$$

$$r \approx \ln(2.7)/3.44 = 0.288$$

Age(x)	l(x)	b(x)	-rx	$e^{-rx}$	$l(x)b(x)e^{-rx}$	Use r=0.28 and compute value of Euler’s Equation.
0	1.00	0	0.00	1.00	0.00	
1	0.98	0	-0.28	0.76	0.00	
2	0.95	0	-0.56	0.57	0.00	
3	0.50	3	-0.84	0.43	0.65	
4	0.30	4	-1.12	0.33	0.39	
5	0.00	0	-1.40	0.25	0.00	
sum=					1.039	

The sum is greater than 1.0 so try a **larger** value of r.

Iterative calculations of  $r$  using Euler's Equation  
 Assuming a pulse breeding species.

Age(x)	l(x)	b(x)	l(x)b(x)	xl(x)b(x)	l(x)b(x)e <sup>-rx</sup> r values					
					0.28	0.29	0.3			
0	1.00	0	0	0.00	0	0	0			
1	0.98	0	0	0.00	0	0	0			
2	0.95	0	0.00	0.00	0.00	0.00	0.00			
3	0.50	3	1.50	4.50	0.65	0.63	0.61			
4	0.30	4	1.20	4.80	0.39	0.38	0.36			
5	0.00	0	0.00	0.00	0.00	0.00	0.00			
R <sub>0</sub> =					2.700	9.300	sum=	1.039	1.005	0.971
G=					3.444					
estimate of r =					0.288					

So far we have assumed that the species are pulse breeders. For **continuously breeding species**, use the average  $x$  and  $l(x)$  values in the equation. For our previous example:

Iterative calculations of  $r$  using Euler's Equation  
 Assuming a continuously breeding species.

Age(x)	l(x)	b(x)	l(x)b(x)	xl(x)b(x)	l(x)b(x)e <sup>-rx</sup> r values					
					0.15	0.154	0.16			
0.5	0.99	0	0.00	0.00	0.00	0.00	0.00			
1.5	0.97	0	0.00	0.00	0.00	0.00	0.00			
2.5	0.73	0	0.00	0.00	0.00	0.00	0.00			
3.5	0.40	3	1.20	4.20	0.71	0.70	0.69			
4.5	0.15	4	0.60	2.70	0.31	0.30	0.29			
R <sub>0</sub> =					1.800	6.900	sum=	1.015	1.000	0.978
G=					3.833					
estimate of r =					0.153					

Life tables have been compiled for a number of species. The survival data in the table below are from the classic study of Dall sheep in Denali National Park conducted by Olhaus Murie. The fecundity data are hypothetical. Calculate  $l(x)$  from the data, estimate  $r$ , then calculate an exact value of  $r$  using Euler's equation.

Hypothetical life table for Dall Sheep from Murie 1944.

Age(x)	No. at start	b(x)
0	608	0
1	487	0
2	480	0.25
3	472	0.25
4	465	0.25
5	447	0.5
6	419	0.5
7	390	0.25
8	348	0.25
9	268	0.25
10	154	0
11	59	0
12	4	0
13	2	0
14	0	0

**Age distribution-** the number of individuals of each age class.

**Stable Age Distribution (SAD)-** the relative numbers of individuals in each age class remains constant. If  $B_x(t)=n_x(t)/n(t)$  then the SAD has been reached when  $B_x(t)=B_x(t+1)$ . The SAD can be calculated using the following formula:

$$c(x) = \frac{e^{-rx}l(x)}{\sum e^{-rx}l(x)}$$

**Stationary Age Distribution-** A special case of the stable age distribution when the population size does not change over time ( $r=0$ ).

**Reproductive value-** the relative number of offspring that remain to be born to individuals of a given age.

$$v(x) = \frac{e^{rx}}{l(x)} \sum_{y=x+1}^k l(y)b(y)e^{-ry}$$

Calculation of stable age distribution and reproductive value assuming  $r= 0.29$

<u>Stable Age Distribution</u>					<u>Reproductive Value Distribution</u>				
Age(x)	l(x)	b(x)	$l(x)e^{-rx}$	c(x)	$e^{rx}l(x)$	$e^{-ry}l(x)$ b(x)	sum( $e^{-ry}$ $l(x)b(x)$ )	v(x)	
0	1.00	0	1.00	0.39	1.00	0.00	1.00	1.00	
1	0.98	0	0.73	0.29	1.36	0.00	1.00	1.37	
2	0.95	0	0.53	0.21	1.88	0.00	1.00	1.89	
3	0.50	3	0.21	0.08	4.77	0.63	1.00	1.80	
4	0.30	4	0.09	0.04	10.63	0.38	0.38	0.00	
sum=			2.57						

**Derivation of Euler's Equation** (from Ricklefs, R. 1990. Ecology pp. 312-313)

The following follows Lotka's original derivation.

The number of newborns  $n_0$  at time  $t$  is the sum of offspring born to individuals of each age ( $x$ ) in the population:

$$n(0,t) = \sum_{x=0}^{x=k} n(x,t)b(x)$$

The number of individuals of age  $x$  alive at time  $t$  is equal to the number of newborns  $x$  years ago times their survival to the present ( $l_x$ ) thus:

$$n(0,t-x)l_x = n(x,t)$$

Substituting we get:

$$n(0,t) = \sum_{x=0}^{x=k} n(0,t-x)l_x b_x$$

In a stable age distribution each age class grows exponentially according to the equation  $n_x(t) = n_x(0)e^{rt}$ . The size of an age class some time in the past can also be calculated by simply reversing the sign of  $r$  hence:

$$n(0,t-x) = n(0,t)e^{-rx}$$

Substituting we get:

$$n(0,t) = \sum_{x=0}^{x=k} n(0,t)e^{-rx}l_x b_x$$

and dividing both sides by  $n(0,t)$  gives:

$$1 = \sum_{x=0}^{x=k} e^{-rx}l_x b_x$$

which is Euler's equation.

### Population projection matrices

The age distribution can be described with a vector (note: we are using age classes, hence the subscript):

$$\mathbf{n}(t) = \begin{bmatrix} n_1(t) \\ n_2(t) \\ \dots \\ n_k(t) \end{bmatrix}$$

Survival and fecundity are related to  $l(x)$  and  $b(x)$  but the conversion depends on the timing of the population census. Assume a birth pulse and postbreeding census.

To calculate survival (denote age class by  $i$ ):

$$P_i = \frac{l(i)}{l(i-1)}$$

Calculate the number of individuals in each age class from one time step to the next. The number of individuals in age class 2 at the next time step is:

$$n_2(t+1) = P_1 n_1(t)$$

or more generally

$$n_{i+1}(t+1) = P_i n_i(t)$$

Now calculate the number of newborns at time  $t+1$ :

Let

$$F_i = b(i)P_i$$

then,

$$n_1(t+1) = n_1(t)F_1 + n_2(t)F_2 + \dots + n_k(t)F_k = \sum_{i=0}^{i=k} F_i n_i(t)$$

and the total size of the population is the sum of its age classes so:

$$N(t+1) = \sum_{i=1}^k n_i(t)P_i + \sum_{i=0}^k F_i n_i(t)$$

These equations can be used to calculate the number of individuals in each age class over time, sometimes called a population projection. Below is a simple example:

Age	Age Class	Survival	Fecundity	Number in age class
0			$b(0)=0$	
1	1	$P_1=0.2$	$b(1)=2$	$n_1(0)=20$
2	2	$P_2=0.7$	$b(2)=3$	$n_2(0)=20$
3	3	$P_3=0.5$	$b(3)=3$	$n_3(0)=20$
4	4	$P_4=0$	$b(4)=0$	$n_4(0)=20$

Time	Number in each age class						Proportion in each age class			
	1	2	3	4	N	lambda	1	2	3	4
0	20	20	20	20	80	1.35	0.25	0.25	0.25	0.25
1	80	4	14	10	108	0.81	0.74	0.04	0.13	0.09
2	61	16	3	7	87	1.00	0.70	0.18	0.03	0.08
3	62	12	11	1	87	1.08	0.71	0.14	0.13	0.02
4	68	12	9	6	94	0.98	0.72	0.13	0.09	0.06
5	66	14	9	4	93	1.02	0.71	0.15	0.09	0.05
6	68	13	9	4	95	1.02	0.72	0.14	0.10	0.05
7	69	14	9	5	97	1.01	0.71	0.14	0.10	0.05
8	70	14	10	5	98	1.02	0.71	0.14	0.10	0.05
9	71	14	10	5	100	1.02	0.71	0.14	0.10	0.05
10	72	14	10	5	101	1.02	0.71	0.14	0.10	0.05

**Age-structured models: Leslie Matrix.****Reading:**

Gotelli pp. 59-62

For a thorough review (using different notation!) read:

Noon, B. R. and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 In D. R. McCullough and R. H. Barrett, eds. Wildlife 2001: Populations. Elsevier Applied Science, New York.

The bible on Matrix Population models is Caswell's book:

Caswell, H. 2001. Matrix population Models, 2<sup>nd</sup> edition. Sinauer Associates, Sunderland, MA.

**Leslie matrix-** The equations used to project the population can be expressed more simply in matrix form known as the Leslie Matrix. If there are k age classes, the Leslie matrix is a k x k square and has the following form:

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & \Lambda & F_k \\ P_1 & 0 & 0 & \Lambda & 0 \\ 0 & P_2 & 0 & \Lambda & 0 \\ M & M & M & O & M \\ 0 & 0 & 0 & P_{k-1} & 0 \end{bmatrix}$$

The growth of the population can now be described as a simple matrix multiplication:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

Calculation of age specific survival and fertilities for the Leslie matrix using values from projection matrix example.

x	i	l(x)	b(x)	P <sub>i</sub> = l(i)/l(i-1)	F <sub>i</sub> = B(i)P <sub>i</sub>
0		1.0	0		
1	1	0.2	2	0.2	0.4
2	2	0.14	3	0.7	2.1
3	3	0.07	3	0.5	1.5
4	4	0	0	0	0

And the Leslie matrix is:

$$\mathbf{A} = \begin{bmatrix} 0.4 & 2.1 & 1.5 & 0 \\ 0.2 & 0 & 0 & 0 \\ 0 & 0.7 & 0 & 0 \\ 0 & 0 & 0.5 & 0 \end{bmatrix}$$

For many species (especially long-lived organisms) it is difficult to determine the age specific fecundity and survival for every age class in the population. In this case, it may be simpler to develop a **stage-based** model or **Lefkovitch matrix**. To parameterize the Lefkovitch matrix it is first you determine the number of distinct stages in the population, then you determine the survival and fecundity associated with each stage. For example with Spotted Owls, biologists have determined that survivorship and fecundity changes over the first three age classes. Thus, the Lefkovitch matrix can be parameterized with survivorship and fecundity values for juveniles, subadults, and adults. It is assumed that survivorship and fecundity remains constant once animals have reached the "adult stage". It is much simpler to parameterize this matrix then to attempt to estimate survivorship and fecundity for every age class in the population, which for Spotted Owls may include individuals 15 years of age or greater.

Following the notation of Caswell (2001) and assuming the census is conducted just after the birth pulse, the Lefkovitch matrix can be written as:

### Lefkovitch Matrix or Stage-based matrix

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 & \Lambda & F_k \\ G_1 & P_2 & 0 & \Lambda & 0 \\ 0 & G_2 & P_3 & \Lambda & 0 \\ M & M & M & O & M \\ 0 & 0 & 0 & G_{k-1} & P_k \end{bmatrix}$$

Where  $G_i$  is the probability of surviving (graduating) to the next stage class ( $P_i$  in Leslie matrix) and  $P_i$  is the probability of staying in the same stage class (P for staying put). Don't ask me why the mathematicians decided to change the notation for survival and use it for another parameter but they did!

In many species (such as the Spotted Owl), the probability of staying the same is 0 for all but the oldest stage in which case all but the last  $P_i$  terms are 0.

### Matrix multiplication

A matrix when right multiplied by a vector gives a vector with the same number of elements as the original vector. When right multiplying a matrix by a vector, turn the vector horizontally, multiply the corresponding vector element by the corresponding matrix element, and add the products. These sums are the values for the elements in the new vector. It is easy to confirm that this procedure produces the same equations as the projection matrix approach.

### Eigenvalues and eigenvectors

The dominant eigenvalue of the Leslie or Lefkovitch matrix is equal to lambda. The eigenvector associated with this eigenvalue gives the proportions in the stable age

distribution. Thus the values of lambda and the stable age distribution can be solved directly from the matrix.

### Sensitivity analysis

Once the demographic parameters are estimated for a population, sensitivity analyses can determine which parameters have the most influence on the growth rate of the population. There are two general ways that sensitivity can be measured.

**Sensitivity-** a measure of how the population growth rate ( $\lambda$ ) responds to small changes in a demographic parameter and is equal to the slope of the relationship between  $\lambda$  and the parameter.

**Elasticity-** a measure of the proportional sensitivity and is calculated as the product of the sensitivity and the parameter value divided by  $\lambda$ .

### Algebraic calculation of lambda

It is possible to solve for lambda algebraically specific numbers of stages and associated fecundity and survival. (See Noon and Sauer 1992, and Biles and Noon 1990. UMAP Journal 11.2:99-109)

If there are only three age classes and all breeding individuals have the same fecundity,  $\lambda$  can be determined directly by solving for x in the following second-order linear difference equation.

$$x^2 - P_3x - P_1P_2b = 0$$

The quadratic formula gives:

$$\lambda = \frac{P_3 + \sqrt{P_3^2 + 4P_1P_2b}}{2}$$

This formula is specific to the conditions stated above. For other situations, the difference equation must be solved. Although this approach is more direct than the Leslie or Levkovitch matrix approach, it is less general.

For instance, for a species that breeds at 1 yr, survivorship the first year differs from adult survival, and fecundity in the first year is the same as adult survival (such as many passerines) the difference equation approach gives:

$$\lambda = P + P_1b$$

where P is adult survival,  $P_1$  is first year survival, and b is fecundity.

## Spatially structured Population Models

Reading

Gotelli Ch. 4, Harrison 1991

**Metapopulation**- “a population of populations” (Levins 1970). A group of several local populations that are linked by immigration and emigration.

The simplest model assumes that we have  $n$  independent populations each with the same probability of extinction ( $p_e$ ) and no immigration or emigration. The regional persistence ( $P_x$ ) of this set of subpopulations is:

$$P_x = 1 - (p_e)^x$$

Now we will add immigration to the model and consider how it influences the persistence of the metapopulation. The proportion of occupied sites  $f$  is the difference between the rate of immigration  $I$  and the rate of extinction  $E$ :

$$\frac{df}{dt} = I - E$$

where  $f$  = fraction of sites occupied,  $I$  = immigration rate (proportion of sites successfully colonized /unit time),  $E$  = extinction rate (proportion of sites that go extinct/unit time). In the simplest case, the immigration rate is a function of the probability of local colonization  $p_i$  and the fraction of unoccupied sites  $(1-f)$  or:

$$I = p_i(1 - f)$$

and the extinction rate is a product of the probability of local extinction and the  $p_e$  and the fraction of occupied sites:

$$E = p_e(f)$$

Putting these two expressions together we get:

$$\frac{df}{dt} = p_i(1 - f) - p_e(f)$$

### Assumptions of simple metapopulation models

1. Homogeneous patches
2. No spatial structure
3. No time lags
4. Constant  $p_e$  and  $p_i$  – no correlation in  $p_e$  and  $p_i$  overtime
5. Regional occurrence ( $f$ ) affects local colonization ( $p_i$ ) and extinction ( $p_e$ ) (Except for basic island-mainland model).
6. Large number of patches

Gotelli considers four metapopulation models that make different assumptions about colonization and extinction processes.

**Island-Mainland Model-** both  $p_i$  and  $p_e$  are constants. A constant  $p_i$  implies a “propagule rain”- a continuous source of immigrants that could colonize an empty site:

$$\frac{df}{dt} = p_i(1-f) - p_e f = p_i - p_i f - p_e f$$

Setting the equation to 0 and solving for  $\hat{f}$ :

$$\begin{aligned} 0 &= p_i - p_i f - p_e f \Rightarrow \\ p_i f + p_e f &= p_i \Rightarrow \\ f(p_i + p_e) &= p_i \end{aligned}$$

Thus,

$$\hat{f} = \frac{p_i}{p_i + p_e}$$

⇒ some sites will be occupied as long as  $p_i$  is greater than 0.

**Internal Colonization Model-** Now assume that the only source of propagules is the set of occupied patches then:

$$p_i = if$$

where  $i$ =rate at which the probability of colonization of empty sites increases with each additional patch that is occupied (the slope of relationship). Each population contributes individuals to the pool of propagules and therefore  $p_i$  increases with  $f$ . assuming the local extinction rate is still independent then:

$$\frac{df}{dt} = i(f)(1-f) - p_e(f)$$

and the equilibrium solutions are:

$$\hat{f} = 0 \quad \text{or} \quad \hat{f} = 1 - \left( \frac{p_e}{i} \right)$$

⇒ if  $p_i > p_e$ , the metapopulation will persist, otherwise it will go extinct.

**Propagule Rain with Rescue Effect-** In the previous models we assumed that the rate of extinction was independent of fraction of occupied sites. Now we assume that the rate of extinction declines as  $f$  increases, in other words, populations have a better chance of being “rescued” from extinction as the proportion of occupied sites increases.

$$p_e = e(1 - f)$$

where  $e$  is a measure of the strength of the rescue effect, i.e. it measures how much  $p_e$  decreases with the addition of another occupied site. Combining this with constant immigration we get:

$$\frac{df}{dt} = p_i(1 - f) - ef(1 - f)$$

With the equilibrium solution:

$$f = \frac{p_i}{e}$$

⇒ The metapopulation will persist as long as  $p_i > 0$ .

**Internal Colonization and Rescue Effect Model-** Now assume that the rates of immigration and extinction both depend on the number of occupied sites:

$$\frac{df}{dt} = if(1 - f) - ef(1 - f)$$

⇒ There is no simple equilibrium solution to this equation. The equilibrium depends on the relative sizes of  $i$  and  $e$ . If  $i > e$  the proportion of occupied patches will increase until  $f=1$ . If  $i < e$  the metapopulation will crash. If  $i=e$   $f$  will not change and the system will be in a “neutral” equilibrium.

## Genetics of small populations

### Reading

#### Caughley 1994

**Locus**- location on the chromosome where the information for a particular gene can be found

**Allele**- specific genetic information found at the loci, usually denoted as A and a.  
In a sexually reproducing species, there are two alleles at each locus, one from the father, one from the mother. These alleles may be the same or different.

**Homozygous**- Two alleles at a locus are the same.

**Heterozygous**- Two alleles at a particular locus differ.

**Heterozygosity**- The proportion of loci in an individual that are heterozygous or the heterozygosity within the population.

**Electrophoresis** --technique for measuring differences in proteins at different loci.  
Different proteins at the same locus are thought to represent different alleles.

The 2 alleles (proteins) can be combined in an individual as

AA  
Aa  
aa

Hardy-Weinberg law implies these probabilities, i.e., random mating in a panmictic population.

Heterozygosity at a particular locus is estimated by:

$$h_j = 1 - \sum p_{ij}^2$$

where  $p_{ij}$  is frequency of allele  $i$  at loci  $j$  (provided the number of individuals measured at that locus is greater than 30).

For example, if  $\Pr(A) = 0.3$ ,  $p_{1j} = 0.3$  and  $p_{2j} = 0.7$ , so  $h_j = 0.42$ , which is the probability of have 2 unlike alleles at loci  $j$ . Homozygosity is the probability of 2 like alleles at loci  $j$ , equals  $1 - h_j$ .

Heterozygosity of the population can be estimated using the following equation:

$$\hat{H} = (1/L) \sum h_j$$

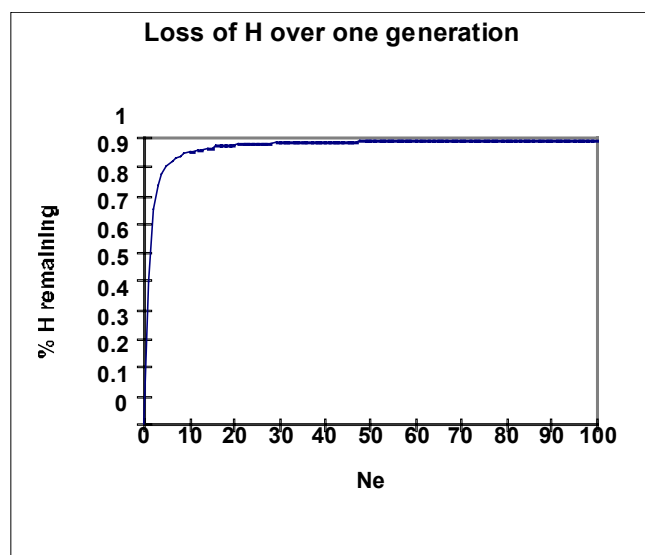
where  $L$  = no. of loci examined.  $H$  is the proportion of loci heterozygous in an average individual in the population.

In mammals, values of  $H$  vary from 0 to <0.18.

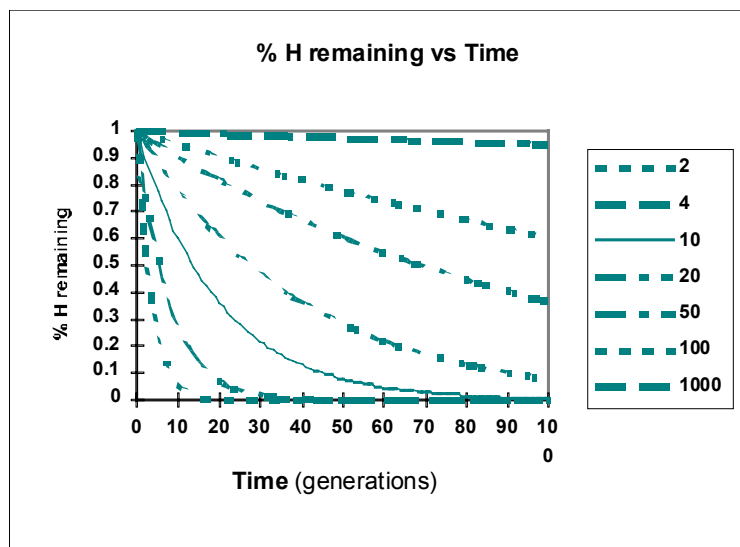
### Genetic drift

Allelic variation ultimately is produced by accumulation of genetic variation from mutation. Natural selection and genetic drift may act to maintain or decrease this variation. Selection may select for or against the maintenance of allelic variation depending on the contribution of each allele to the fitness of the individual. Genetic drift is the loss of allelic variation due to random processes during the formation of zygotes and mating. Genetic drift always acts to decrease genetic variation. The rate of decline is related to population size. Over  $t$  generations,  $H$  changes according to:

$$H_t = H_0(1 - (1/(2N)))^t$$



There is relatively little loss of heterozygosity in one generation except in very small populations. However, if population size remains low for several generations, the loss of heterozygosity can be substantial.



### Inbreeding

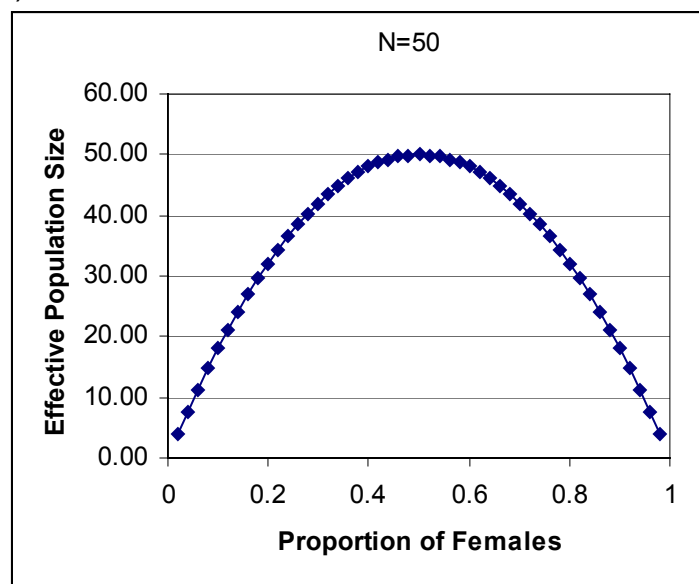
Inbreeding is breeding between close relatives. The chances of inbreeding increases as the population size declines. **Inbreeding depression**- decline in fitness due to loss of heterozygosity and the expression of deleterious recessive alleles.

### Effective population size $N_e$

Effective population size is size of an ideal population that loses genetic variation at the same rate as does the real population. In an ideal population the family size is distributed as a Poisson variate, the sex ratio is 50-50, generations do not overlap, mating is strictly at random, and the population is stable in size. The formulas given previously for loss of heterozygosity as a function of population size applies to the effective population size. Effective population size in terms of the sex ratio is given by:

$$\text{Sex ratios, } N_e = (4 N_m N_f)/(N_m + N_f)$$

where  $N_m$  is the number of breeding males and  $N_f$  is the number of breeding females.  $N_e$  is maximized when the number of breeding males is equal to the number of breeding females (see below).



Population Fluctuations- When populations fluctuate through time, all the genetic variation for all future populations is contained in only a few survivors (assuming the mutation rate is zero). The harmonic mean population size represents the effective population size for the population,

$$\frac{1}{N_e} = \frac{1}{t} \left( \frac{1}{N_1} + \frac{1}{N_2} + \dots + \frac{1}{N_t} \right)$$

## **Population Viability Analysis**

### **Reading**

**Caughley 1994, Gotelli Ch. 1 & 2**

**Population Viability Analysis-** The science of estimating the number of individuals needed to prevent a population from going extinct.

### **Goals of PVA**

1. How long?
2. What degree of certainty?

### **Factors to Consider**

1. Intrinsic rate of increase  $\lambda$
2. Demographic stochasticity
3. Environmental Stochasticity
4. Catastrophes
5. Genetic effects
6. Behavior (allege effect)
7. Metapopulation dynamics
8. Interactions between factors

### **Additional references**

Murphy, D. and B. R. Noon. 1992. A conservation strategy for the northern Spotted Owl. Ecological Applications. 2:

Soulé, M. E. (ed.) 1987. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

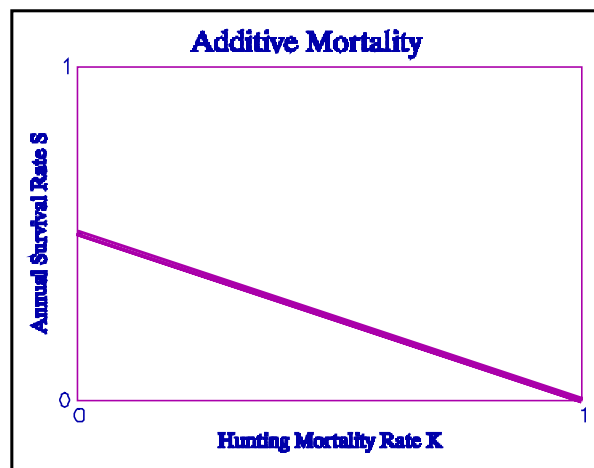
Soulé, M. E. (ed.) 1986. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Mass.

Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, J. Verner. 1990. Interagency scientific committee to address the conservation of the northern spotted owl. USDA Forest Service, USDI Bureau of Land Management, Fish and Wildlife Service, and National Park Service. Portland, Oregon. Govt. Printing Office. 791-171/20026. Washington, D.C.

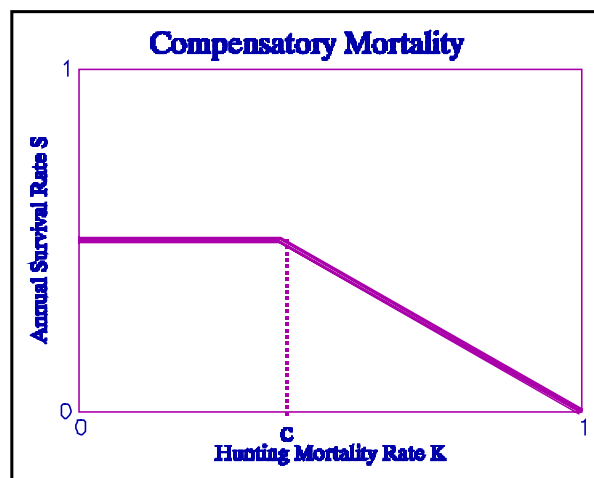
**Additive vs. compensatory mortality and MSY.**

Reading: Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory Mortality in waterfowl populations: a review of the evidence and implications for research and management. Trans. N. American Wildl. Nat. Res. Conf. 49:535-554.

Additive mortality is a case of density independence



Compensatory mortality is a case of density dependence operating on survival rate



### **Interspecific Competition**

Reading Gotelli Ch. 5, Wiens 1977

Up to this point we have focused on a single species or a single population and have discussed the factors that affect the growth of that population. However, species do not occur in a vacuum and certainly are affected by the species around them. There are a number of interactions that are recognized by ecologists.

- 1. Competition-** Two species that use the same limited resource of harm one another while seeking a resource.
- 2. Predation-** One species eats all or part of an animal species.
- 3. Herbivory-** One species eats all or part of a plant species.
- 4. Parasitism-** Two species live in an obligatory association in which the parasite depends metabolically on the host.
- 5. Disease-** An association between a pathogenic microorganisms and a host in which the host suffers physiologically.
- 6. Mutualism-** Two species live in close association with one another to the benefit of both.

### **Types of competitive interactions**

- 1. Exploitative or resource competition-** reduced survival and/or fecundity due to use of common limited resource.
- 2. Interference competition-** competition involving physical contact or conflict (even if the resource is not in short supply).

**Interspecific competition-** competition between two species.

**Intraspecific competition-** between different species.

**LOTKA-VOLTERRA COMPETITION EQUATIONS**

Recall the logistic growth equation:

$$dN / dt = r \left( \frac{K - N}{K} \right) N$$

Now let's include a term for the effect of one species on another (assuming the species effect each other equally), then:

$$dN / dt = r \left( \frac{K - N - N_2}{K} \right) N$$

But these effects may not be equal. To account for this we introduce competition coefficients that measure relative effect of the species on each other.

$\alpha$  = effect of species 2 on species 1 relative to the effect of 1 on 1.

$\beta$  = effect of species 1 on species 2 relative to the effect of 2 on 2.

The rate of change of species 1 now becomes:

$$dN_1 / dt = r_1 \left( \frac{K_1 - N_1 - \alpha N_2}{K_1} \right) N_1$$

and the rate of change in population size of species 2 becomes:

$$dN_2 / dt = r_2 \left( \frac{K_2 - N_2 - \beta N_1}{K_2} \right) N_2$$

Setting these equations equal to 0 and solving for the equilibrium solutions we get:

$$\hat{N}_1 = K_1 - \alpha N_2$$

and,

$$\hat{N}_2 = K_2 - \beta N_1$$

These equations lead to a variety of outcomes depending on the magnitudes of the competition coefficients and the relative carrying capacities of the species. This is easiest to see graphically.

**Graphical representation of Lotka-Volterra competition equations.**

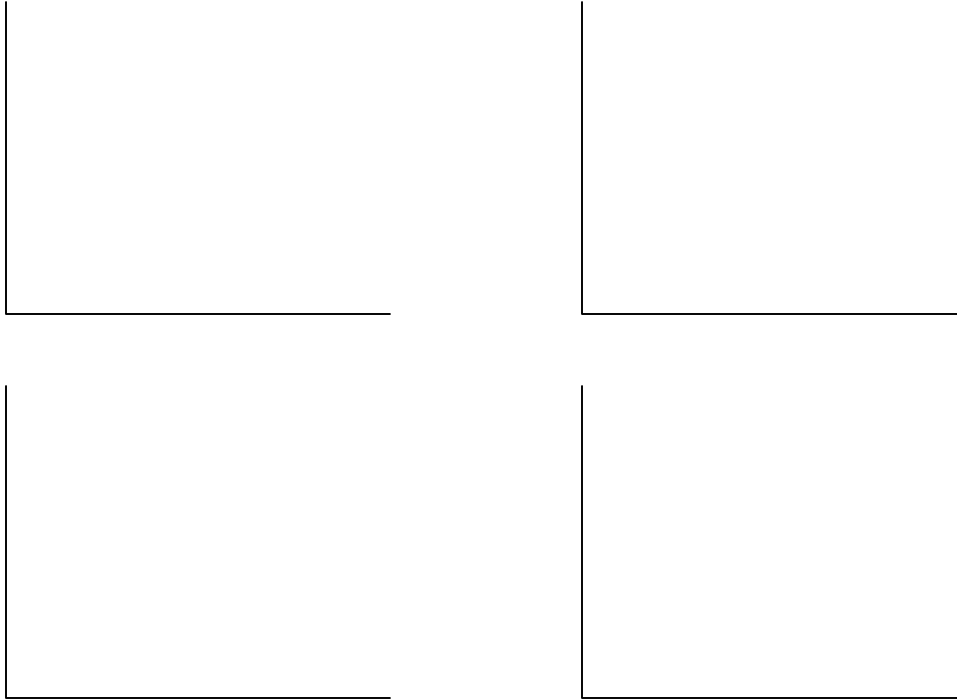
One of the most common ways of portraying the outcome of competitive interactions is to plot the equilibrium conditions when  $dN/dt=0$ , also known as the competitor isocline. For a single species this graph looks like this:



Now if we look at the second species, we may get a graph like this:



Put these two together to produce the "classic" competition isoclines.  
There are 4 graphs associated with the 4 possible outcomes of competition:



4 outcomes are:

1. Species 1 always wins, species 2 goes extinct. This occurs when  $K_2 < K_1/\alpha$  and  $K_2/\beta < K_1$  or  $\alpha < K_1/K_2$  and  $\beta > K_2/K_1$ .
2. Species 2 always wins, species 1 goes extinct. (derive the conditions yourself)
3. Both species coexist at a lower density. This occurs when  $K_2 < K_1/\alpha$  and  $K_1 < K_2/\beta$  or  $\alpha < K_1/K_2$  and  $\beta < K_2/K_1$  (i.e. each species affects the other less than it affects itself).
4. Unstable equilibrium, the outcome depends on the initial densities of the species.

### Assumptions

In addition to the assumptions of the logistic equation, three 3 additional assumptions are required for the L-V competition equations:

1. Resources available to the species are limited.
2. The competition coefficients are constant.
3. Linear relationships describe the competitive interactions adequately.

## Predator-Prey Interactions

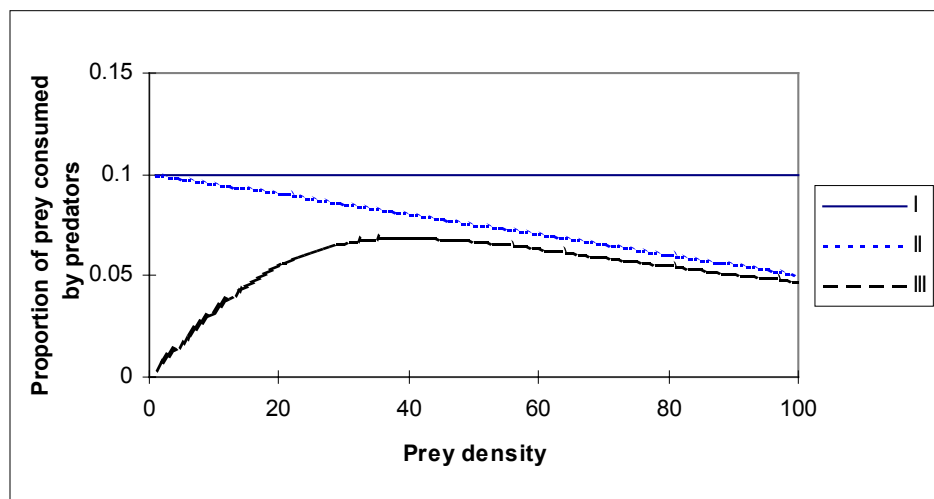
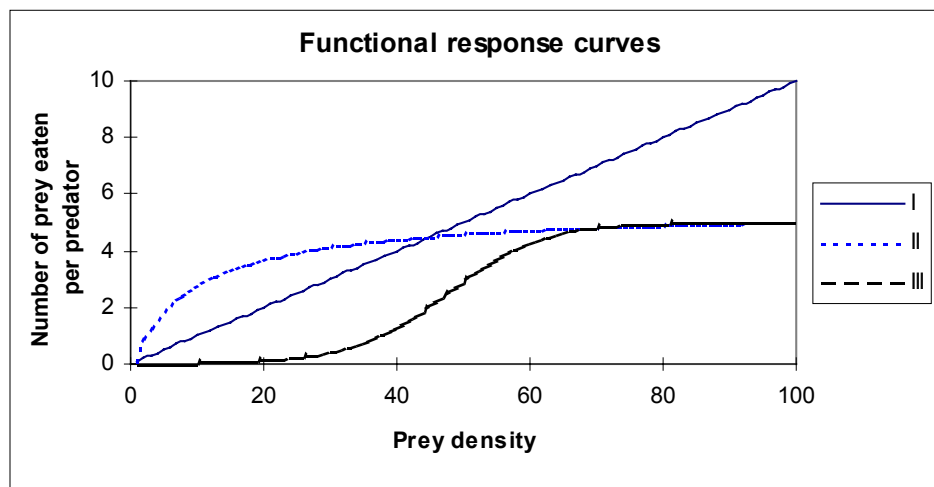
Gotelli Ch. 6

**Functional response-** change in the number of prey consumed by individual predators.

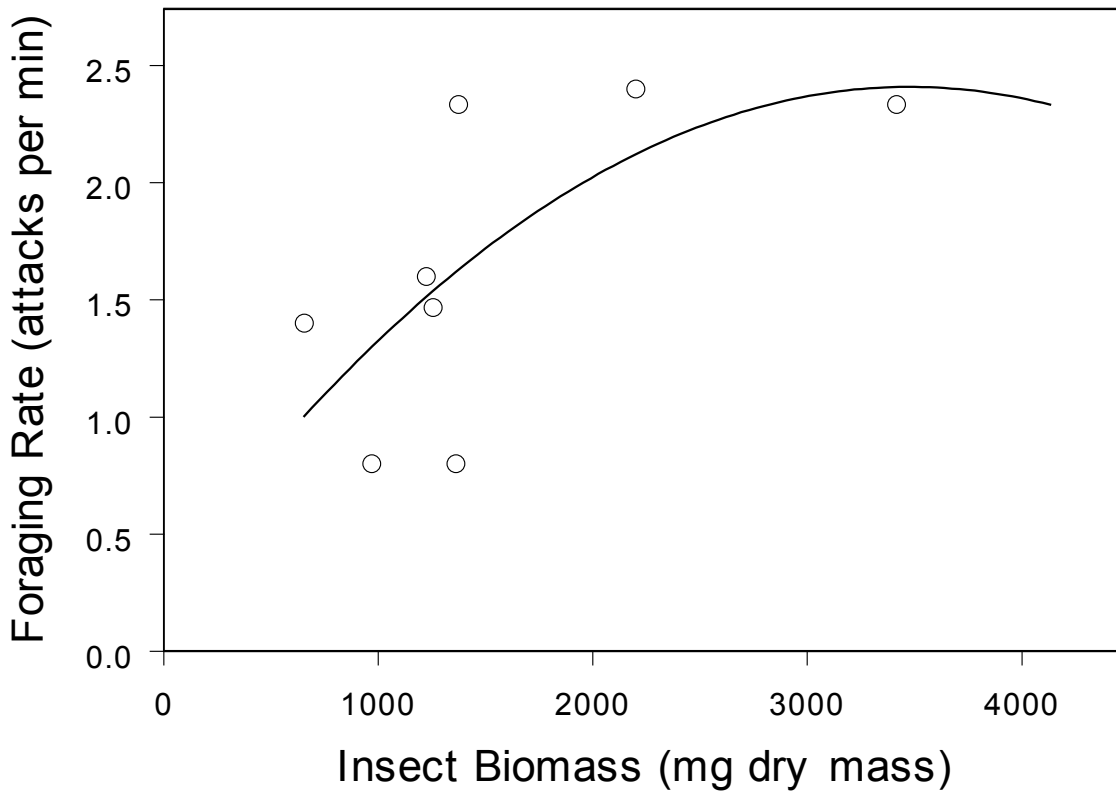
**Numerical response-** change in the density of predators in response to changing prey densities. This may occur in two ways:

- a. Demographic- changes in birth and death rates in response to changes in prey availability.
- b. Movement- immigration or emigration of individuals into a local population in response to changes in food availability.

**Total response-** changes in the total number of prey consumed by the predator population.



Below is an example of a functional response curve for the Olive-sided Flycatcher. Tim Meehan collected these data in Six Rivers National Forest in the summer of 2000. What type of functional response is this?



**Lotka-Volterra Predator-prey models**

The Lotka-Volterra predator-prey equations describe the interactions between one predator species and one prey population in an unlimited environment. The predator population is denoted by  $P$ , the prey (or victim) population by  $V$ .

Assume that the victim population increases exponentially in the absence of predators:

$$dV / dt = rV$$

The victim population is only limited by predators, thus:

$$dV / dt = rV - \alpha VP$$

$\alpha$  = the encounter rate or the proportion of prey caught per unit time per predator.

The predator population can be modeled by considering the birth rates and death rates separately:

$$dP / dt = bP - qP$$

where  $b$ =predator birth rate,  $q$ =predator death rate.

We assume that the birth rate of the predator is proportional to the number of prey thus:

$$b = \beta V$$

where  $\beta$  = the conversion efficiency, the rate at which victims (prey) are converted into predator. This is a function of search efficiency and metabolic efficiency. Thus the predator equation becomes:

$$dP / dt = \beta VP - qP$$

Now we solve for the equilibrium solution for the victim population:

$$\frac{dV}{dt} = rV - \alpha VP = 0 \Rightarrow r = \alpha P \Rightarrow P = \frac{r}{\alpha}$$

and the predator population:

$$\frac{dP}{dt} = \beta VP - qP = 0 \Rightarrow \beta V = q \Rightarrow V = \frac{q}{\beta}$$

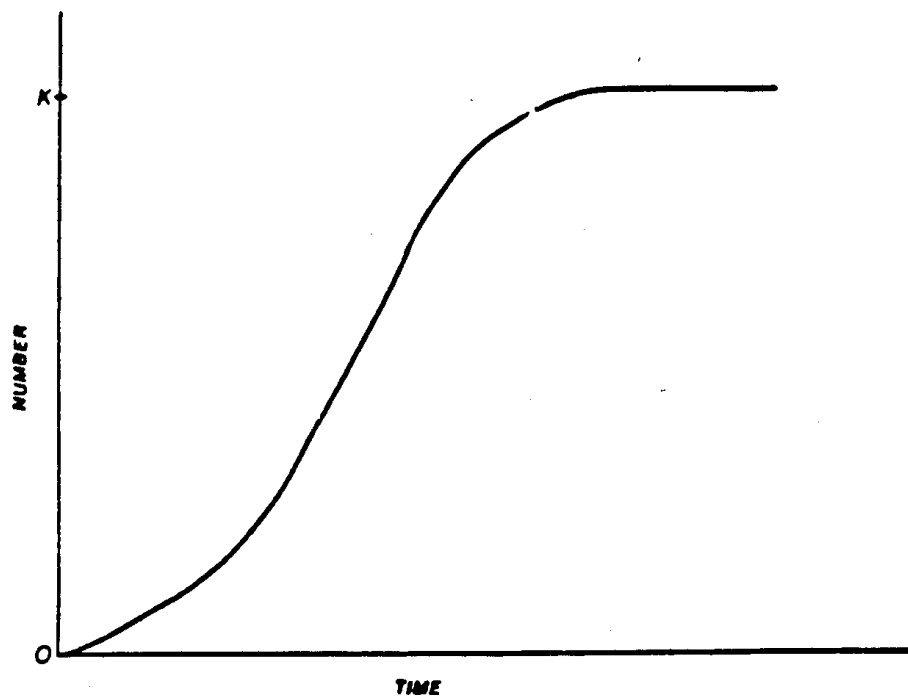
## AN INTRODUCTION TO PREDATOR-PREY INTERACTIONS

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In the absence of predators, prey populations will be regulated by other density-dependent limiting factors such as competition for food or transmission of disease and parasites. These limiting factors will set an upper limit or carrying capacity ( $K$ ) for the populations (Fig. 1).

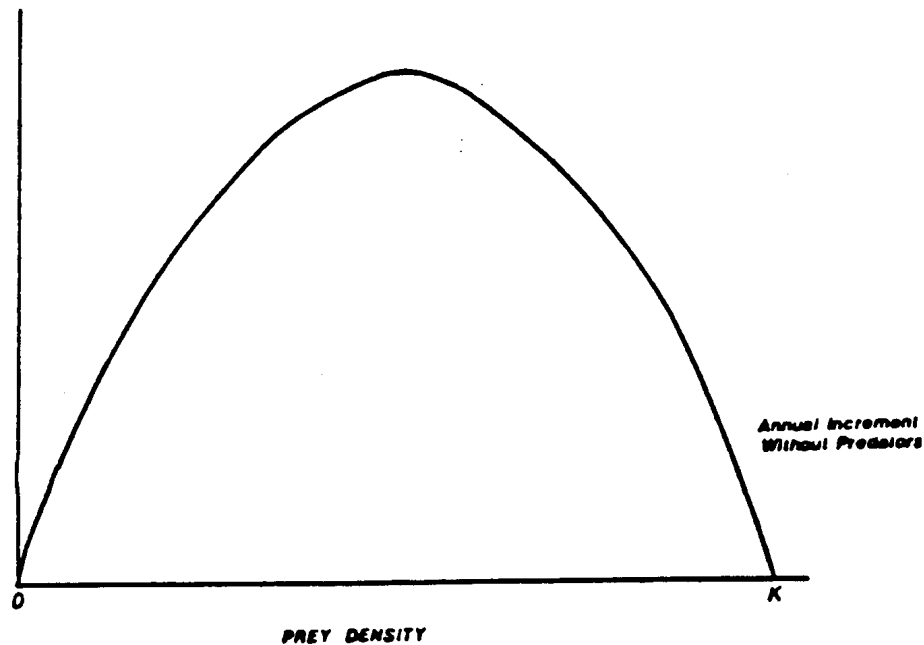
Figure 1.



The annual increment curve for this typical population growth pattern is a dome shaped curve (Fig. 2). Annual increment is the number of animals that are added to the population each year at different population densities. The annual increment is small at low populations because despite a high population growth rate, the number of reproducing animals is small. At high population numbers, near the carrying capacity, the annual increment is also small because despite the abundance of animals, the growth rate is close to zero due to the density-dependent effects of the limiting factors.

The maximum annual increment occurs at an intermediate population where there is a substantial breeding population and the effect of the limiting factors is still moderate.

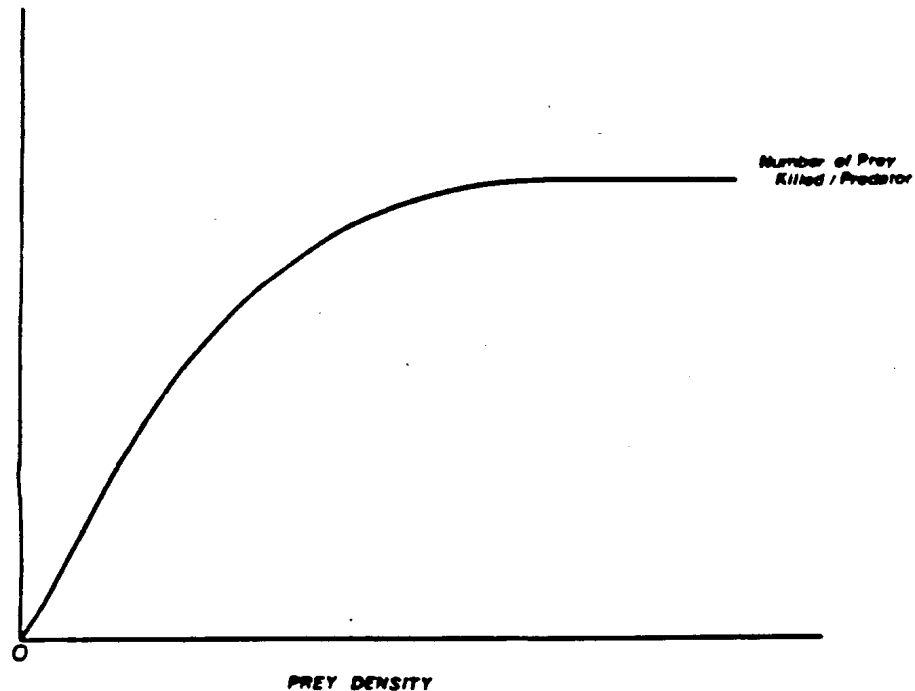
Figure 2.



Addition of predators to this system will remove some proportion of the prey population and thereby reduce both the annual increment and the natural equilibrium population. In this paper, I will explain the potential effects of predation on prey populations by removing the number of prey killed by predators from the annual increment that would be produced in the absence of predators. If the number killed by predators is less than the annual increment, the population will increase. If the number killed by predators is greater than the annual increment, the population will decline. The prey population will stabilize at any point where the number killed by predators is equal to the annual increment.

#### COMPONENTS OF THE PREDATION RATE

The number of prey killed by predators will be the product of the number of prey killed/predator times the number of predators. At low prey densities, the number of prey killed/predator will be small because prey are difficult to find. (Fig. 3) The number of prey killed/predator will increase as the prey density increases and prey become easier to find. However, the prey killed/predator will level off as each predator approaches its satiation point. This general relationship is called the functional response of predators to prey.

Figure 3.

In general, the number of predators will also increase in response to an increase in prey numbers (line a, Fig 4). This relationship is called the numerical response of predators to prey. However, various modifications of this general relationship are possible. The predator population may level off at an upper population size despite increasing prey numbers due to other limiting factors such as territoriality, disease or lack of other prey species (line b, Fig 4). In other predator-prey systems, the number of predators may not decline when the prey population declines because the predators have alternate sources of prey to sustain their populations (line c, Fig 4).

The predation rate (proportion of the prey population killed by predators) will be a function of both the functional response and the numerical response of the predators (Fig. 5). In general, as the prey population increases, the predation rate will increase due to the multiplicative effect of the increasing functional and numerical responses. Therefore, the predation rate is often density-dependent at low prey number (i.e., the rate of predation increases with increasing prey density). However, the predation rate will become constant (density-independent) if either the functional response or the numerical response level off at higher prey densities. If both the functional response and numerical response level off at high prey densities, the predation rate will decline with further increases in prey density (depensatory or inversely density-dependent predation rate).

Figure 4.

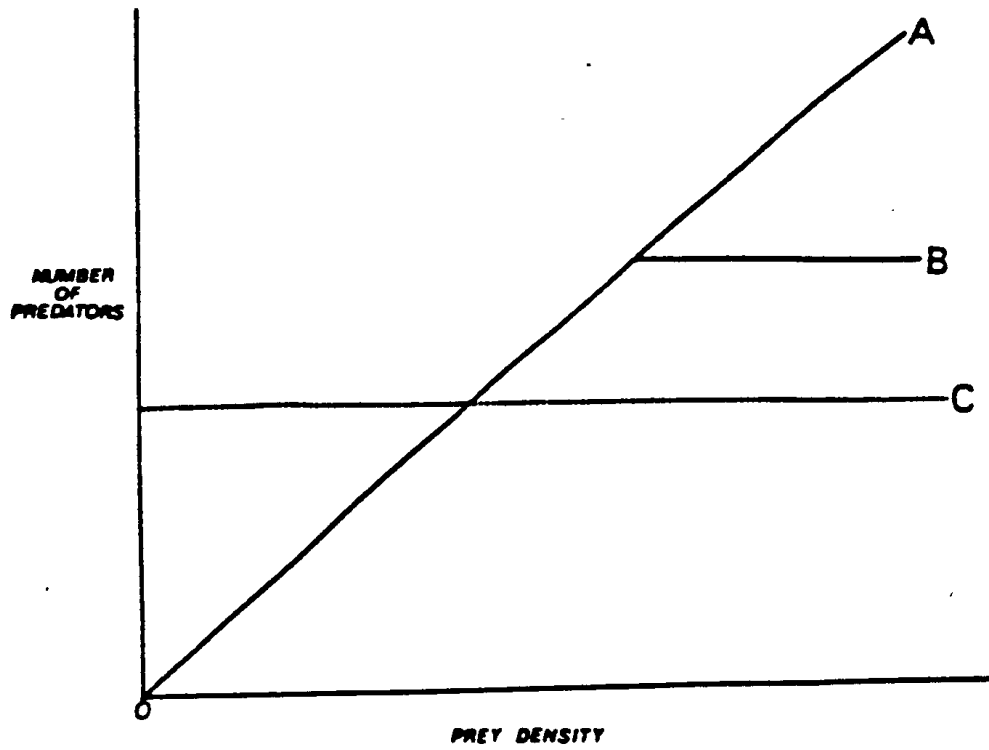
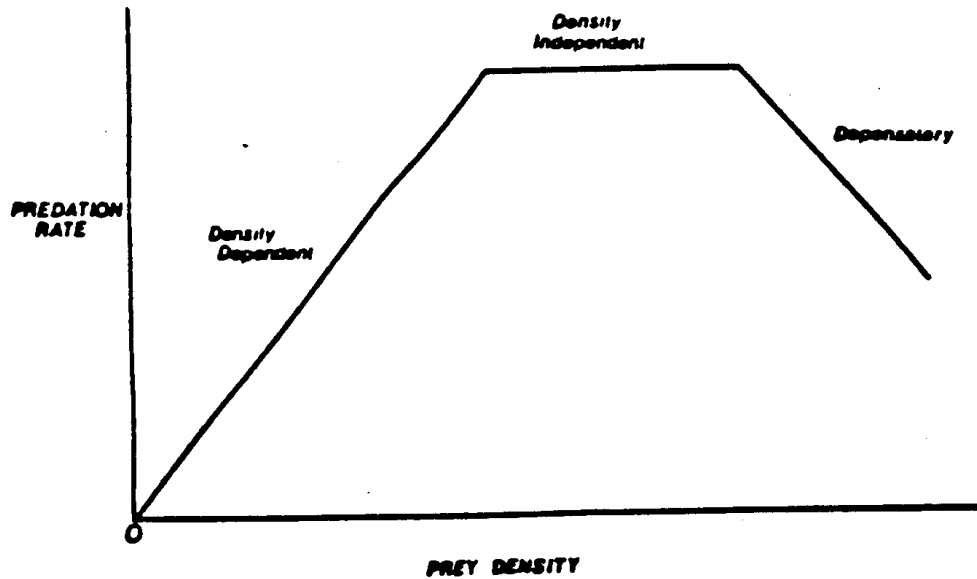
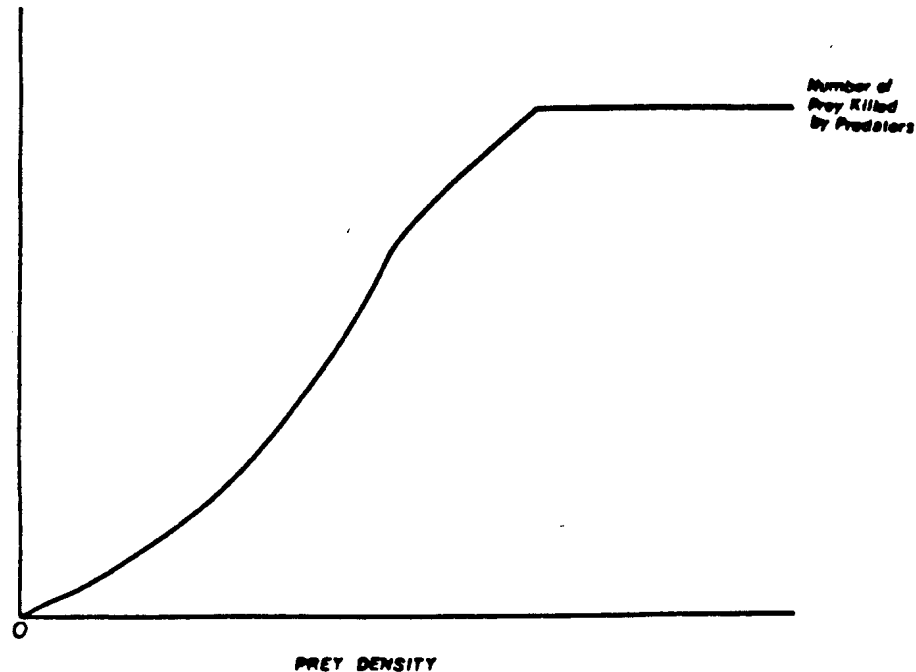


Figure 5.

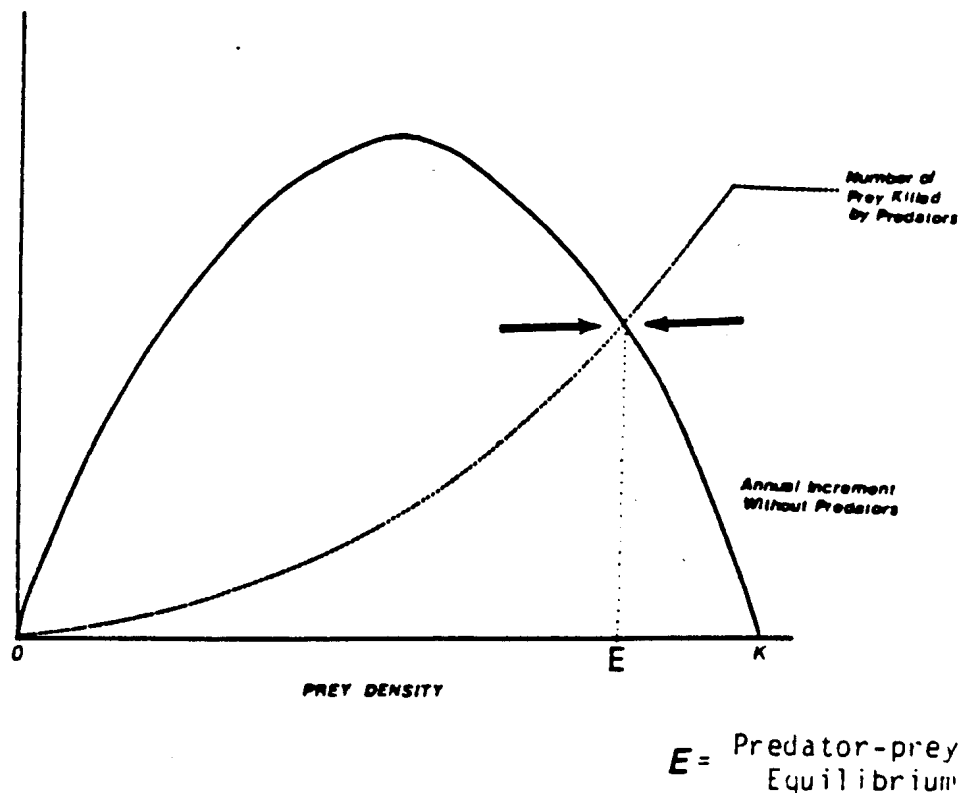
In terms of the number of prey killed (as opposed to the proportion killed), as the number of prey increase, the number killed by predators will increase exponentially due to the multiplicative effect of the functional response and the numerical response (Fig. 6). When either the functional or numerical response level off, the number of prey killed will begin to increase linearly with increasing prey numbers. If both the numerical response and functional response level off, the number of prey killed will remain constant with further increases in prey numbers.

Figure 6.

The effect of predation on the prey population can be evaluated by superimposing the graph of number killed by predators (Fig. 6) onto the annual increment curve for the prey population without predation (Fig. 2).

#### SIMPLE PREDATOR-PREY EQUILIBRIA

If the number of prey killed by predators increases slowly (relative to the annual increment curve) it will intersect the annual increment curve and establish a predator-prey equilibrium at a high prey density (Fig. 7) At prey numbers below the point of intersection, the annual increment of the prey exceeds the number killed by predators and the prey population will increase. At prey numbers above this point, the number killed by predators exceeds the annual increment so the prey population will decline to the equilibrium point.

Figure 7.

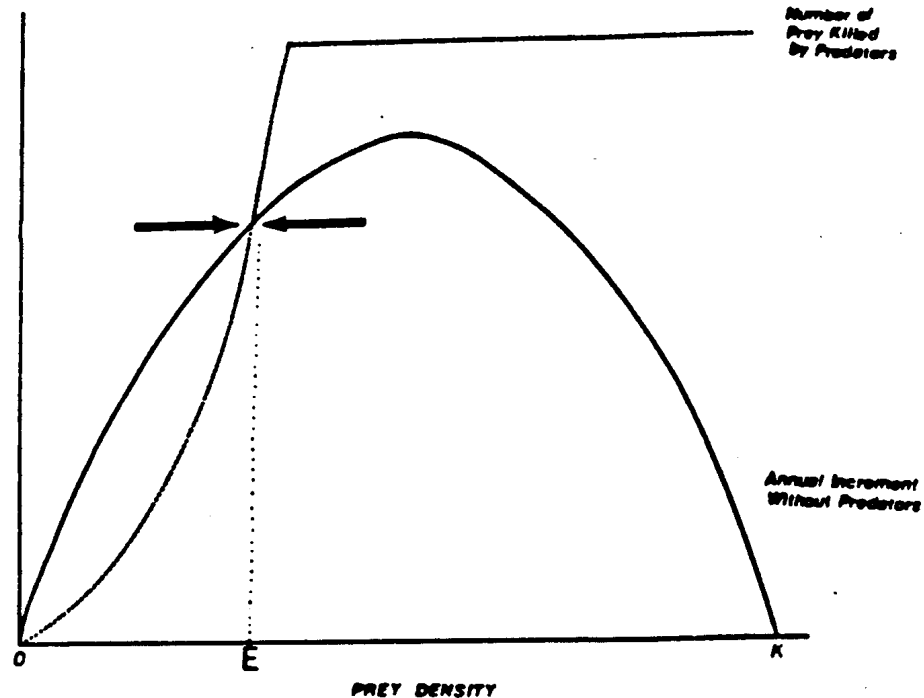
For low predator-prey equilibrium systems, predator control will be an effective means of increasing the prey population. Predator control can be used to reduce the numerical response of the predators and thereby establish a high predator-prey equilibrium as in Figure 7. However, predator control will have to be ongoing because if it is halted, the predators will increase and cause the prey population to decline back to the low equilibrium number.

In reality, the high and low equilibrium systems are points on a continuum. The full range of predator-prey equilibria, ranging from extinction to predators having almost no effect, are possible depending on the values for the numerical response, functional response and annual increment curve of the prey. Also, the relationships may change over time or even from year to year due to changes in the environment that affect these relationships. Time lags in predator responses to prey numbers will result in predator-prey cycles around the equilibrium point.

### MULTIPLE EQUILIBRIA AND PREDATOR PITS

If the maximum number of prey killed by predators levels off at a number less than the maximum annual increment of the prey population, a multiple equilibrium predator-prey system can occur (Fig. 9).

Figure 8.

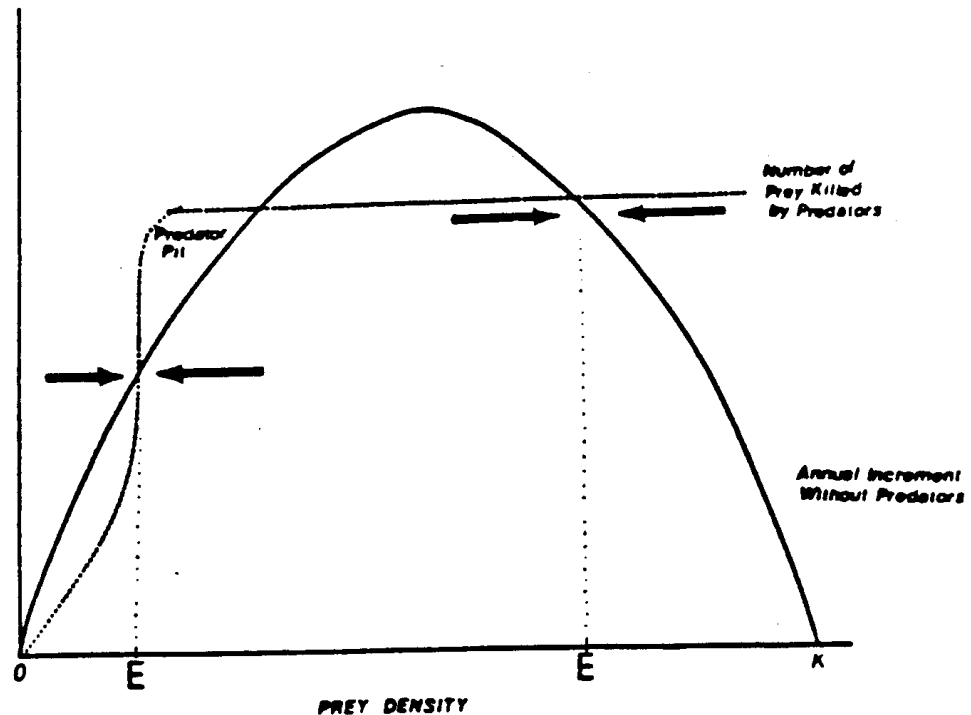


For a predator-prey system of this type, the annual increment and the equilibrium population are not greatly reduced by the predators. This situation will naturally occur when the prey have an effective anti-predator strategy such as use of escape terrain, migrations which lead to spatial separation between predator and prey or the ability to fight off the predator. It will also occur if some limiting factor other than prey availability such as disease, availability of other prey species or wolf control is reducing the numerical response of the predator to the prey. For wildlife populations that naturally exhibit high predator-prey equilibria, there is little justification for predator control because any gains in annual increment or prey populations will be minimal.

If predators are more effective at finding and killing the prey and/or if the number of predators increases rapidly in response to increased prey, the number of prey killed by predators will increase more quickly relative to the annual increment curve (Fig 8). This situation results in a predator-prey equilibrium at a low prey density, well below the number that could be sustained if predator numbers were reduced.

Low predator-prey equilibria will occur for prey species that do not have effective anti-predator strategies other than living at low densities and thereby making themselves difficult to find.

Figure 9.



This predator-prey system has both a low and a high stable equilibrium point. Between these two points is an unstable equilibrium. Between the lower equilibrium and the unstable equilibrium is a “predator pit”, a range of prey numbers where losses to predators exceed the annual increment. Prey populations below the lower equilibrium point will increase because the annual increment exceeds the losses to predators. Prey populations in the range of the predator pit will decline to the lower equilibrium because losses to predators exceed the annual increment. Prey populations between the predator pit and the upper equilibrium will increase to the upper equilibrium because the annual increment exceeds the losses to predators that have now leveled off. Prey populations above the upper equilibrium will decline and stabilize at the upper equilibrium point.

Therefore, if the prey population is low, the predators can keep them at low numbers. However, if the prey populations can be increased to a number above the predator pit,

the prey population will increase to the higher equilibrium population. Theoretically, predator control could be used to increase a prey population from the low equilibrium to a point above the predator pit and the prey population would then grow to the upper predator-prey equilibrium. Ongoing predator control would not be required because the upper equilibrium is stable.

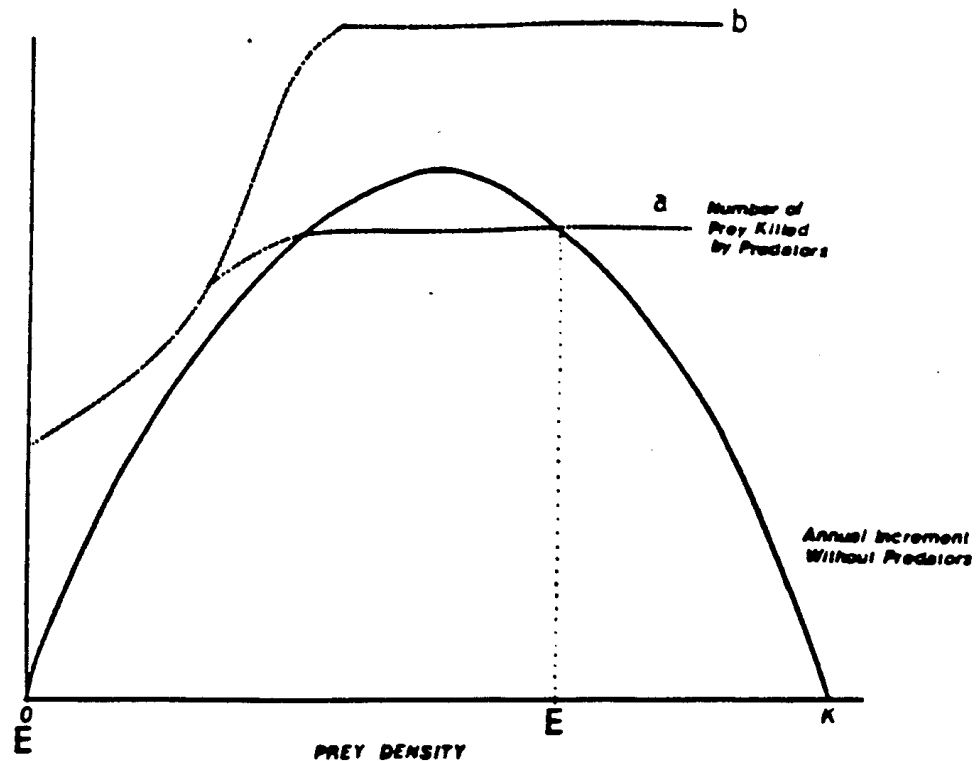
The prevalence of multi-equilibria predator-prey systems is debatable. Situations that appear to be a single low equilibrium system may actually be the lower equilibrium point of a multi-equilibrium system. Similarly, systems that appear to be a simple high predator-prey equilibrium may crash to a low equilibrium if the prey population is reduced into an unforeseen predator pit by hunting, severe weather or other limiting factors.

Multi-equilibrium systems are most likely to occur when the number of predators levels off due to limiting factors other than prey density. However, the only conclusive way to determine if a predator-prey system has several stable equilibria is to manipulate prey numbers and then allow the system to naturally equilibrate.

If predator control is to be used to increase a low prey population, the program should be designed to test if the system has a higher predator-prey equilibrium that is stable without ongoing predator control. After the prey population has increased, predator control should be stopped and the prey population monitored. If it is a single low-equilibrium system, the prey population will decline to low numbers and ongoing predator control would be required to maintain higher prey numbers. However, if it is a multi-equilibrium system, the prey population will stabilize at a higher number and ongoing predator control will not be necessary.

## PREDATOR PITS AND PREY EXTINCTIONS

If a predator population is sustained by several prey species, the number of predators and the predation rate may be maintained at levels that are sufficient to exterminate one or more of the prey species. Even though some of the prey species are declining to extinction, the predator numbers are sustained by the alternate prey species. The number killed by predators can exceed the annual increment of some of the prey species all the way to the point of extinction. This predator pit may be part of a predator-prey system that has a stable equilibrium at high prey densities (line a, Fig 10) or alternatively there may be no stable equilibrium in the system for that prey species (line b, Fig 10).

Figure 10.

The latter case will rarely be observed because the prey species will soon be extinct. However, the prey may be observed in the process of going extinct if the conditions leading to this situation have only recently been established by environmental changes such as colonization by a new alternate prey species. If the system does have a stable predator-prey equilibrium at higher prey densities, the existence of this predator pit may remain unknown unless the prey population is reduced into the predator pit by other limiting factors such as hunting or severe weather.

If a wildlife population is in a predator pit of this type, predator control is probably required to prevent the prey from going extinct. If the system has a stable equilibrium at higher prey densities, temporary predator control to boost the prey out of the predator pit will suffice. However, if there is not stable equilibrium, ongoing predator control will be required if the prey species is to be saved from extinction in the area.

## PREDATION AND HABITAT

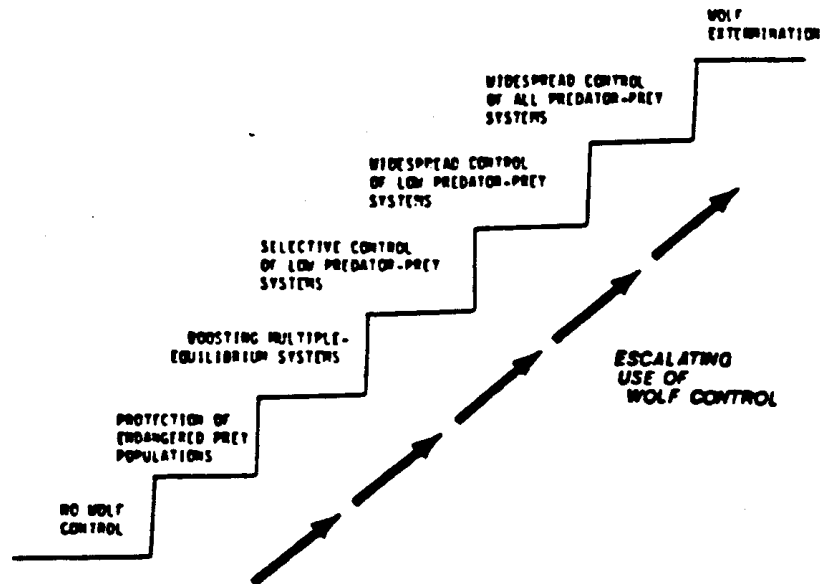
Changes in habitat characteristics can alter predator-prey systems in various ways:

1. Removal of escape terrain or escape cover can increase the predation rate resulting in a lower prey population.
2. Reducing the amount of suitable habitat can concentrate the prey into a smaller area leading to a higher predation rate and a reduced prey population.
3. Habitat changes that encourage the establishment or loss of alternate prey species may alter the dynamics of existing predator-prey systems.
4. Habitat changes that increase or decrease the productivity of prey species will affect the annual increment curve and the ability of the prey to sustain losses to predators.

Therefore, habitat protection and management may be as important as predator control as a means to manage some predator-prey systems.

## IMPLICATIONS FOR WOLF CONTROL

The controversy over use of wolf control for wildlife management often becomes polarized as a debate between those for and those against. However, given the variety of possible predator-prey interactions, the question should be "Under what conditions is wolf control justified?". There is a continuum of wolf control applications ranging from no control under any circumstances to extermination of the wolf (Fig. 11).

Figure 11.

Probably very few people support either of these extremes. Intermediate options, ranging from the most conservative to the most liberal application of wolf control for wildlife management include:

1. Wolf control to protect a prey species from local extinction. This control can be temporary if there is a stable predator-prey balance possible at higher prey numbers. However, wolf control will have to be ongoing if no such stable equilibrium point exists.
2. Wolf control to boost a multi-equilibria system from the low prey equilibrium to the high prey equilibrium. This wolf control can be temporary because once the prey population escapes the predator pit it can stabilize at the higher predator-prey equilibrium point without ongoing wolf control. Because the prevalence of multi-equilibrium systems is unknown, this application of wolf control should be approached experimentally.
3. Wolf control to increase prey populations that are naturally held at low densities by predators. Reducing the numerical response of the wolves can establish a predator-prey equilibrium at a higher prey density. Ironically, the number of

wolves that can be maintained at this higher equilibrium may be greater than what is present at the natural low predator-prey equilibrium. Therefore, it may be possible to use wolf control to actually maintain higher wolf populations in the long term. However, ongoing wolf control is required to maintain this higher equilibrium. If wolf control is stopped, the wolves will increase and reduce the prey populations to the lower equilibrium points.

A further management decision associated with this option is whether it is going to be restricted to selected areas that contain high priority prey populations or if its application is going to be widespread.

4. Widespread wolf control to increase all prey populations. Since this approach would include areas that have naturally high predator-prey equilibrium systems, the benefits of this approach would be minimal in many areas.