The Opportunity for Sexual Selection

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The Current View of Sex Differences

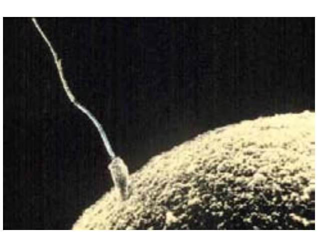
Males and females are ***defined*** by differences in energetic investment in gametes.

In most sexual species, females produce ***few, large ova***, whereas males produce ***many, tiny sperm***.

Parental Investment Theory

(Bateman 1948; Williams 1966; Trivers 1972; Emlen & Oring 1977; Maynard Smith 1977; Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Reynolds 1996; Ahnesjö et al. 2001; Alcock 2005)

•Predicts that gamete dimorphism ***initiates*** sexual selection.



•The few, large ova of females are a ***limited resource*** for which males must compete.

•Males are will be ***more competitive*** in mate acquisition, ***less discriminating*** in mate choice, and ***less parental*** toward offspring than females.

An Alternative View,

Sex differences are NOT due to differences in initial parental investment.

Instead, sex differences are due to sex differences in ***fitness variance***.

i.e., in ***selection intensity***

To Understand

Whether and to what extent the sexes may become distinct,

It is necessary to measure the mean and the ***variance in fitness*** for males and females.

Measuring the Mean and Variance in Offspring Numbers

$N_{Ototal} = 5$

$N_{\text{♀}}=5;$

Measuring the Mean and Variance in Offspring Numbers

Females	Males
1	1
2	2
3	3
4	4
5	5

$N_{Ototal} = 5$

$N_{\text{♀}}=5$; $O_{\text{♀}}= 1$;

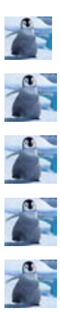
Measuring the Mean and Variance in Offspring Numbers

Females	Males
1	1
2	2
3	3
4	4
5	5

$N_{Ototal} = 5$

$N_{\text{♀}}=5$; $O_{\text{♀}}= 1$;
$V_{O\text{♀}}= 0.$

Measuring the Mean and Variance in Offspring Numbers



Females	Males
1	1
2	2
3	3
4	4
5	5

$N_{Ototal} = 5$

$N_{\text{♀}}=5$; $O_{\text{♀}}= 1$;
$V_{O\text{♀}}= 0.$

$N_{\text{♂}}=5$;

Measuring the Mean and Variance in Offspring Numbers

$N_{Ototal} = 5$

$N_{♀}=5;\quad O_{♀}= 1;$
$V_{O♀}= 0.$

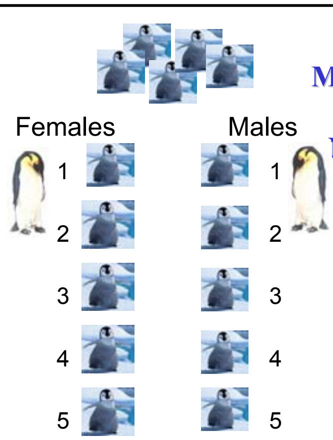
$N_{♂}=5;\quad O_{♂}= 1;$

Measuring the Mean and Variance in Offspring Numbers

$N_{Ototal} = 5$

$N_{♀}=5;\quad O_{♀}= 1;$
$V_{O♀}= 0.$

$N_{♂}=5;\quad O_{♂}= 1;$
$V_{O♂}= 0.$

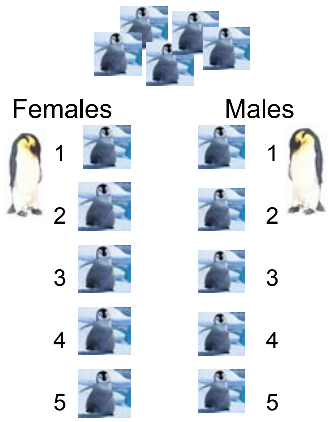


Measuring the Mean and Variance in Offspring Numbers, *By Sex*

$N_{Ototal} = 5$

$N_{♀}=5;\quad O_{♀}= 1;$
$V_{O♀}= 0.$

$N_{♂}=5;\quad O_{♂}= 1;$
$V_{O♂}= 0.$



If each female produces 1 ovum…

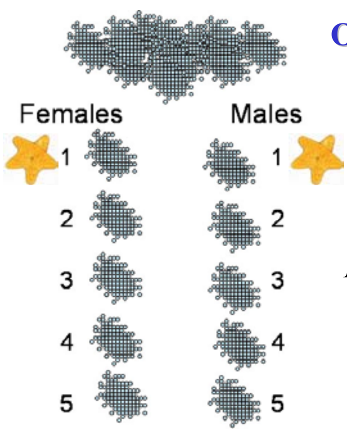
$N_{Ototal} = 5$

$N_♀ = 5$; $O_♀ = 1$;

$V_{O♀} = 0$.

$N_♂ = 5$; $O_♂ = 1$;

$V_{O♂} = 0$.



Or if each female produces 10^5 ova…

$N_{Ototal} = 5 \times 10^5$

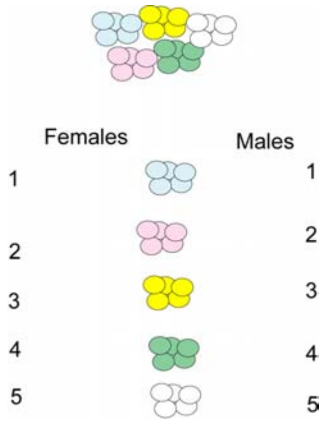
$N_♀ = 5$; $O_♀ = 10^5$;

$V_{O♀}$ » 0.

$N_♂ = 5$; $O_♂ = 10^5$;

$V_{O♂}$ » 0.

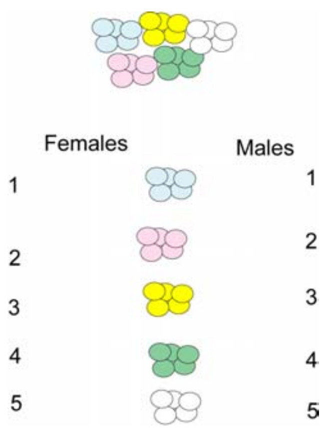
This is Why



The Mean and Variance in Offspring Numbers

$N_{Ototal} = 25$

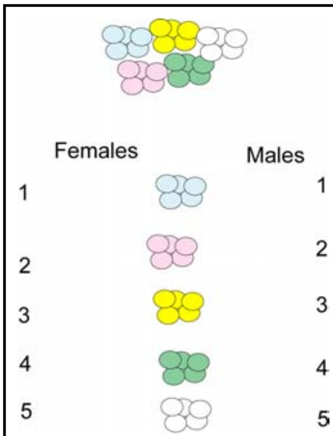
$N_{♀}=5$;



The Mean and Variance in Offspring Numbers

$N_{Ototal} = 25$

$N_{♀}=5$; $O_{♀}= 5$;

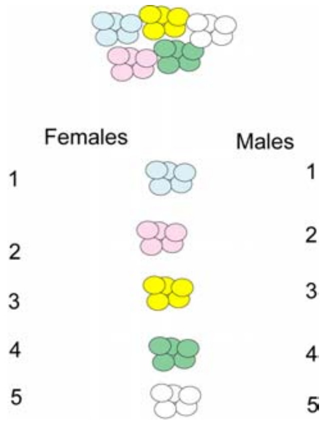


The Mean and Variance in Offspring Numbers

$N_{Ototal} = 25$

$N_{♀}=5$; $O_{♀}= 5$;

$V_{O♀}= 0$.

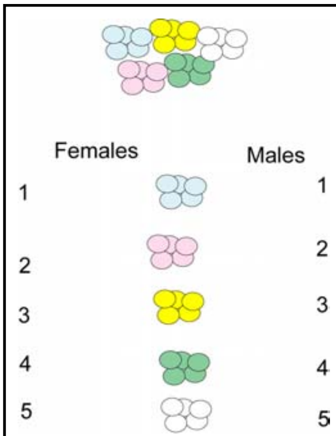


The Mean and Variance in Offspring Numbers

$N_{Ototal} = 25$

$N_{♀}=5$; $O_{♀}= 5$; $V_{O♀}= 0$.

$N_{♂}=5$;

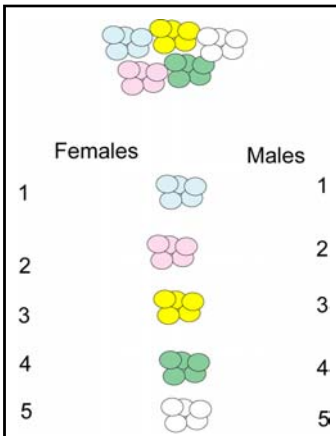


The Mean and Variance in Offspring Numbers

$N_{Ototal} = 25$

$N_{♀}=5$; $O_{♀}= 5$; $V_{O♀}= 0$.

$N_{♂}=5$; $O_{♂}= 5$;



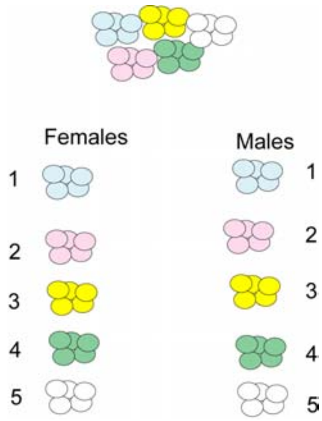
The Mean and Variance in Offspring Numbers

$N_{Ototal} = 25$

$N_{♀}=5$; $O_{♀}= 5$; $V_{O♀}= 0$.

$N_{♂}=5$; $O_{♂}= 5$; $V_{O♂}= 0$.

The Mean and Variance in Offspring Numbers, *by Sex*

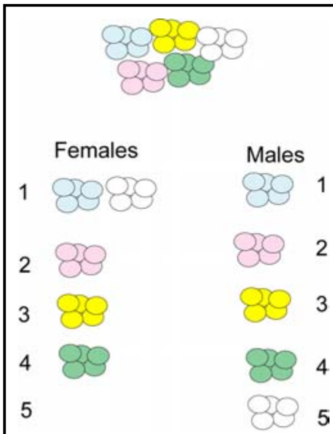


$N_{Ototal} = 25$

$N_{\text{♀}}=5$; $O_{\text{♀}}= 5$; $V_{O\text{♀}}= 0$.

$N_{\text{♂}}=5$; $O_{\text{♂}}= 5$; $V_{O\text{♂}}= 0$.

If One Female Mates Twice...

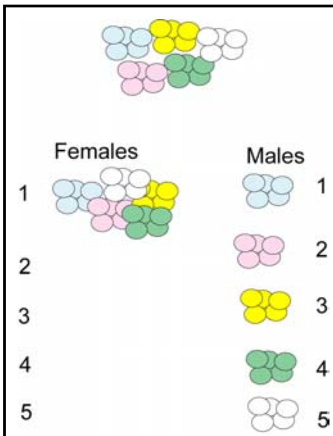


$N_{Ototal} = 25$

$N_{\text{♀}}=5$; $O_{\text{♀}}= 5$; $V_{O\text{♀}}= 10$.

$N_{\text{♂}}=5$; $O_{\text{♂}}=5$; $V_{O\text{♂}}= 0$.

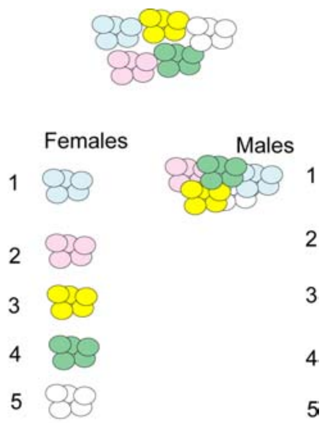
If One Female Mates Five Times...



$N_{Ototal} = 25$

$N_{\text{♀}}=5$; $O_{\text{♀}}= 5$; $V_{O\text{♀}}= 20$.

$N_{\text{♂}}=5$; $O_{\text{♂}}=5$; $V_{O\text{♂}}= 0$.



If One Male Mates Five Times...

$N_{Ototal} = 25$

N=5; $O_{♀}$= 5; $V_{O♀}$= 0.

N=5; $O_{♂}$=5; $V_{O♂}$= **20**.

This Means That:

The **variance** in offspring numbers in one sex can ***far exceed*** the **variance** in offspring numbers in the other sex.

Males (or females) with ***no*** mates will produce ***no*** offspring at all.

Thus, unsuccessful males (or females) produce ***fewer*** offspring than the average female.

This Is Why:

Sexual selection is one of the most powerful evolutionary forces known,

It produces such rapid changes in phenotype.

What Do We Measure?

The variance in fitness; is proportional to the strength of selection.

The sex difference in the variance in fitness; its magnitude determines whether and to what degree the sexes will diverge.

What Tools Do We Use?

The Mean and Variance in Fitness

The Opportunity for Selection

Analysis of Variance

The Mean and Variance in Fitness

Consider a population in which,

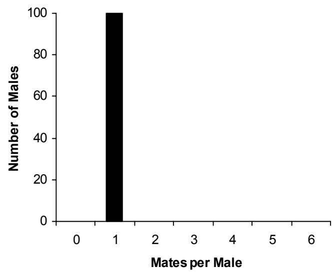
$N_{males} = 100$

$N_{females} = 100$

Sex ratio = $R = N_{females} / N_{males} = 1$

Females mate once, males can mate more than once.

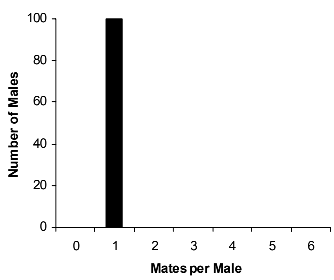
Case 1: Monogamy
The Classes of Mating Males, k_i



Males can be divided into a series of mating classes, k_i.

Thus, k_0 males do not mate, k_1 males mate once, k_2 males mate twice, and so on.

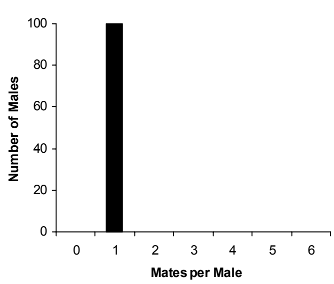
The Number Males in Each Mating Class, m_i



The value of each m_i depends on how variable males are in their mating success.

Here, $m_1 = 100$, all other mating classes = 0.

The Average Male Mating Success, M

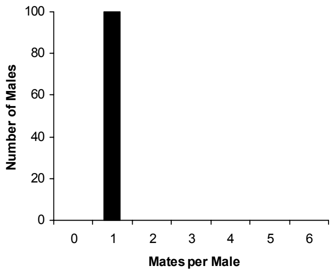


$M = \Sigma [k_i m_i] / \Sigma m_i$

Or,

$[(0)(0) + (1)(100) + (2)(0) + (3)(0) + (4)(0) + (5)(0) + (6)(0)] / 100 = 1.$

The Average Mating Success of Mating Males, H

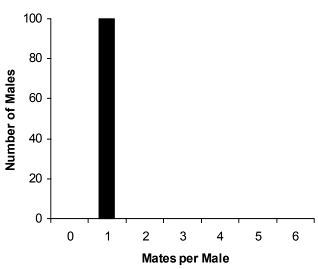


$H = \Sigma\,[k_i\, m_i]\,/\,[\Sigma\,(m_i) - m_0]$

Or,

$[(0)(0) + (1)(100) + (2)(0) + (3)(0) + (4)(0) + (5)(0) + (6)(0)]\,/\,[100 - 0] = 1.$

The Variance in Male Mating Success, V_M

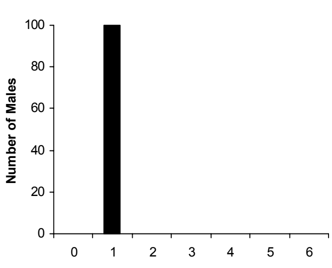


$V_M = [\Sigma(k_i^2\, m_i)/\, \Sigma m_i] - [\Sigma(k_i\, m_i)/\, \Sigma m_i]^2$

Or,

$\{[(0)^2(0) + (1)^2(100) + (2)^2(0) + (3)^2(0) + (4)^2(0) + (5)^2(0) + (6)^2(0)]/100\} - \{[(0)(0) + (1)(100) + (2)(0) + (3)(0) + (4)(0) + (5)(0) + (6)(0)]/100\}^2 = 1 - 1 = 0$

With Monogamy,



All individuals have one mate.

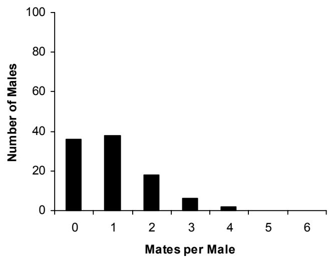
Thus,

$R = N_{females}\, /\, N_{males}$ **$= M = H$**

$= 1$,

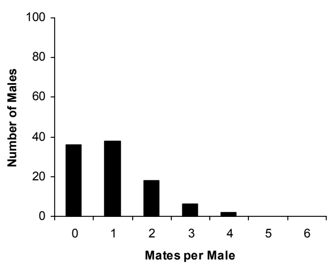
and **$V_M = 0$**

Case 2: Random Mating
The Classes of Mating Males, k_i



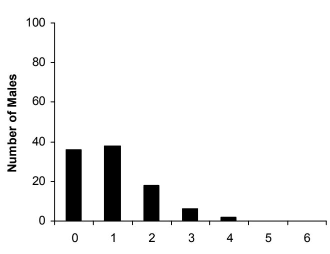
There are still 7 classes of mating males, but the distribution of males among mating classes has ***changed***.

The Number Males in Each Mating Class, m_i



With random mating, some males mate more than once; some do not mate at all. Thus, m_0=36, m_1=38, m_2=18, m_3=6, m_4=2, m_5=0, m_6=0.

The Average Male Mating Success, M

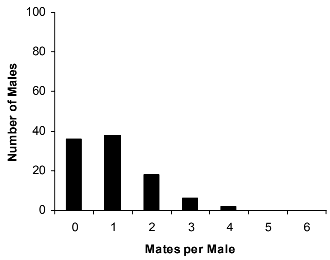


$M = \Sigma\,[k_i\, m_i] \,/\, \Sigma\, m_i$

Or,

[(0)(36) + (1)(38) + (2)(18) + (3)(6) + (4)(2) + (5)(0) + (6)(0)] / 100 = **1**.

The Average Mating Success of Mating Males, H

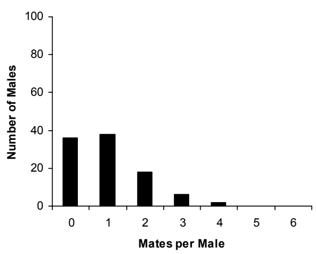


$\boldsymbol{H} = \Sigma\, [k_i\, m_i]$ $/\, [\Sigma\, (m_i) - m_0]$

Or,

$[(0)(36) + (1)(38) + (2)(18) + (3)(6) + (4)(2) + (5)(0) + (6)(0)]\, /\, [100 - 36] =$ **1.56**.

The Variance in Male Mating Success, V_M

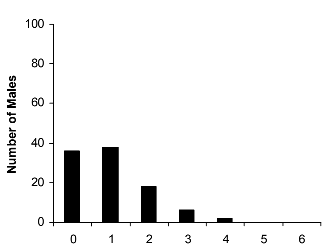


$V_M = [\Sigma(k_i^2\, m_i)/\, \Sigma m_i] - [\Sigma(k_i\, m_i)/\, \Sigma m_i]^2$

Or,

$\{[(0)^2(36) + (1)^2(38) + (2)^2(18) + (3)^2(6) + (4)^2(2) + (5)^2(0) + (6)^2(0)]/100\} - \{[(0)(36) + (1)(38) + (2)(18) + (3)(6) + (4)(2) + (5)(0) + (6)(0)]/100\}^2 = 1.$

With Random Mating,



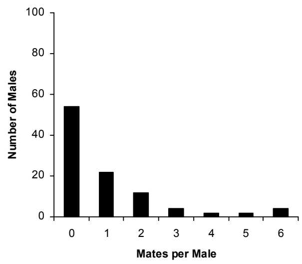
By chance, some males are excluded from mating.

Thus, $\boldsymbol{R = M = 1}$,

but $\boldsymbol{H > M}$.

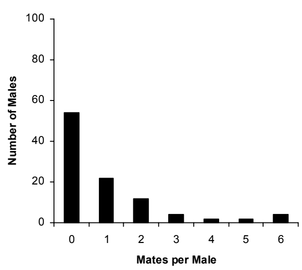
And because the distribution is wider, $\boldsymbol{V_M = 1}$.

Case 3: Polygyny
The Classes of Mating Males, k_i



Again, there are 7 classes of mating males, but the distribution of males in each class is even ***more extreme***.

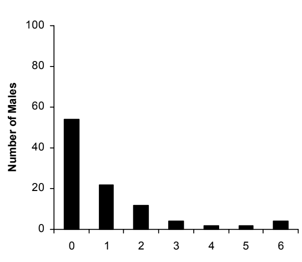
The Number Males in Each Mating Class, m_i



Now, each of the mating classes contains males, but, $\boldsymbol{m}_0$=54, $\boldsymbol{m}_1$=22, $\boldsymbol{m}_2$=12, $\boldsymbol{m}_3$=4, $\boldsymbol{m}_4$=2, $\boldsymbol{m}_5$=2, $\boldsymbol{m}_6$=4.

$\boldsymbol{N}_{males} = \boldsymbol{N}_{females}$ = 100, so $\boldsymbol{R}$ = 1.

The Average Male Mating Success, M

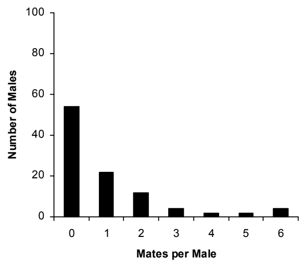


$\boldsymbol{M} = \Sigma\ [k_i\, m_i] / \Sigma\ m_i$

Or,

[(0)(54) + (1)(22) + (2)(12) + (3)(4) + (4)(2) + (5)(2) + (6)(4)] / 100 = **1**.

The Average Mating Success of Mating Males, H

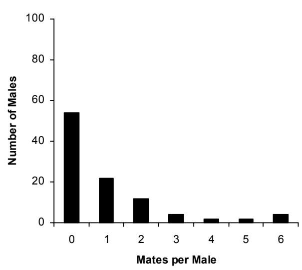


$\boldsymbol{H} = \Sigma\, [k_i\, m_i] \;/\; [\Sigma\,(m_i) - m_0]$

Or,

$[(0)(54) + (1)(22) + (2)(12) + (3)(4) + (4)(2) + (5)(2) + (6)(4)] \;/\; [100 - 54] =$ **2.17**.

The Variance in Male Mating Success, V_M

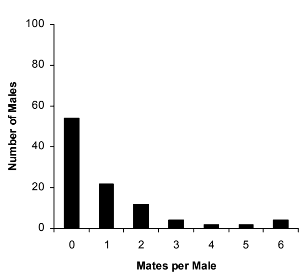


$\boldsymbol{V_M} = [\Sigma(k_i^2\, m_i)/\, \Sigma m_i] - [\Sigma(k_i\, m_i)/\, \Sigma m_i]^2$

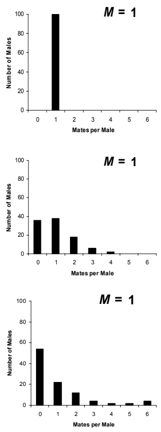
Or,

$\{[(0)^2(54) + (1)^2(22) + (2)^2(12) + (3)^2(4) + (4)^2(2) + (5)^2(2) + (6)^2(4)]/100\} - \{[(0)(54) + (1)(22) + (2)(12) + (3)(4) + (4)(2) + (5)(2) + (6)(4)]/100\}$ = **2.32**.

With Polygyny,



Even *more* males are excluded from mating ($\boldsymbol{m_0}$=54). Again, $\boldsymbol{R = M = 1}$**.** But $\boldsymbol{H >> M}$**,** and because the distribution of male mating success is wider, V_M = **2.32**.



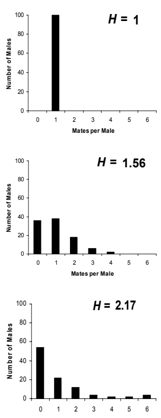
In General

When $N_{males} = N_{females}$,
$\boldsymbol{R = M = 1}$, regardless of the distribution of females with males.

This is true because the ratio,

$N_{females} / N_{males}$

equals the sex ratio, *as well as* the average number of mates per male.

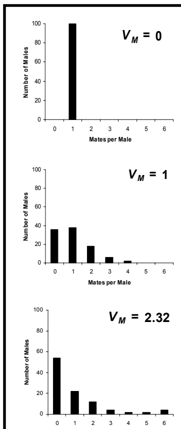


In General

If some males mate *more than once*, other males will be *excluded* from mating. Thus, $\boldsymbol{H > M}$**,** except with monogamy.

This is true because average harem size, $\boldsymbol{H}$, equals $N_{females}$ divided by the number of *mating* males.

As $\boldsymbol{m}_0$ gets larger, so does $\boldsymbol{H}$ because *fewer* males mate.



In General

As $\boldsymbol{H}$ increases, so does the variance in mate numbers, V_M.

As $\boldsymbol{m}_0$ increases, ***fewer*** males contribute to the next generation.

Thus, the greater the variance in fitness, the stronger selection becomes.

Why? THE ZERO CLASS GETS INCREASINGLY LARGE!!!

The Opportunity for Selection: What is it and What does it measure?

$$I = V_W/W^2 = V_w$$

Compares the fitness of breeding parents ***relative*** to the population before selection.

The variance in relative fitness, V_w, places ***an upper limit*** on the total phenotypic change per generation.

An Upper Bound Because,

Heritability (h^2) is usually < 1.

The correlation between the variance in relative fitness and phenotypic change, i.e., Cov(ΔZ, V_w) is usually < 1.

By chance, bad things happen to good genes and vice versa.

How is $I_♂$ Measured?

$$W_♂ = \Sigma_♂ O_i / N_♂$$

where O_i the brood size of the *i*-th male, who may have his brood with > 1 female.

$$V_♂ = \Sigma_♂ (W_♂ - O_i)^2 / N_♂$$

$$I_♂ = V_♂ / (W_♂)^2$$

How is $I_♀$ Measured?

$$W_♀ = \Sigma_♀ O_j / N_♀$$

where O_j the brood size of the j-th female who may have her brood with >1 male.

$$V_♀ = \Sigma_♀ (W_♀ - O_j)^2 / N_♀$$

$$I_♀ = V_♀ / (W_♀)^2$$

How are $I_♂$ and $I_♀$ Related?

***First*: Every offspring has one mother and one father**

$$\Sigma_♂ o_i = \Sigma_♀ o_j$$

$$W_♂ = R W_♀$$

Where $R = N_♀ / N_♂$

Like an ANOVA: The Distribution of Females with Males

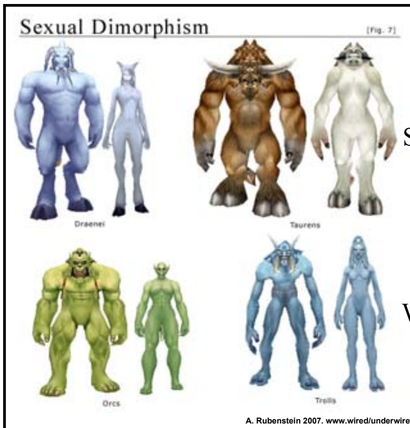
N Mates	Frequency	Mean # of Offspring	Variance in Offspring #
0	p_0	$0O$	$0V_O$
1	p_1	$1O$	$1V_O$
2	p_2	$2O$	$2V_O$
3	p_3	$3O$	$3V_O$
4	p_4	$4O$	$4V_O$
.	.	.	.
k	p_k	kO	kV_O
$N_{♀♀}$	1	$N_{♀♀}O$	$N_{♀♀}V_{O♀♀}$

This Means That:

The **variance** in offspring numbers in one sex can ***far exceed*** the **variance** in offspring numbers in the other sex.

Males (or females) with ***no*** mates will produce ***no*** offspring at all.

Thus, unsuccessful males (or females) produce ***fewer*** offspring than the average female.



This Is Why:

Sexual selection is one of the most ***powerful*** evolutionary forces known;

Why it produces such ***rapid*** changes in phenotype.

As in ANOVA,

$$V_{total} = V_{within} + V_{among}$$

= The ***average of the variances*** in offspring numbers within the classes of males who mate

\+

The ***variance of the averages*** in offspring numbers among the classes of mating *and* nonmating males

$$V_{\text{♂}} = \Sigma\, p_j\, (jV_{\text{♀}}) + \Sigma\, p_j\, (jW_{\text{♀}} - RW_{\text{♀}})^2$$

$$= RV_{\text{♀}} + W_{\text{♀}}^2 V_{mates}$$

How are $I_{♂}$ and $I_{♀}$ Related?

***Third*: Apply these definitions,**

Recall that $RW_{♀}$ = average number of offspring/male.

Dividing $V_{♂}$ by $[RW_{♀}]^2$ gives

$$V_{♂} / [RW_{♀}]^2 = [RV_{♀} + W_{♀}^2 V_{mates}] / [RW_{♀}]^2$$

which gives

$$I_{♂} = (1/R)I_{♀} + I_{mates}$$

Conventional and Reversed Sex Roles

For species with ***conventional*** sex roles

$$I_{♂} = (1/R)I_{♀} + I_{mates}$$

For species with ***reversed*** sex roles

$$I_{♀} = (R)I_{♂} + I_{mates}$$

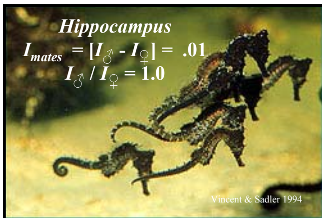
The Sex Difference in the Strength of Selection, ΔI

$$\Delta I = \{ I_{♂} - I_{♀} \} = I_{mates}$$

When $I_{♂} > I_{♀}$, sexual selection modifies ***males***

When $I_{♀} > I_{♂}$, sexual selection modifies ***females***

When $\Delta I = 0$, either there is ***no*** sexual selection
Or sexual selection is ***equally strong***
in both sexes



Hippocampus

$I_{mates} = [I_♂ - I_♀] = .01$

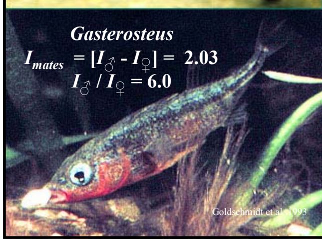
$I_♂ / I_♀ = 1.0$

Syngnathus

$I_{mates} = [I_♂ - I_♀] = -.88$

$I_♀ / I_♂ = 5.4$

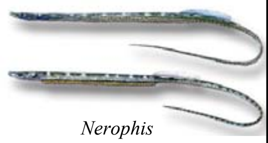
Berglund et al. 1989



Gasterosteus

$I_{mates} = [I_♂ - I_♀] = 2.03$

$I_♂ / I_♀ = 6.0$



Nerophis

$I_{mates} = [I_♂ - I_♀] = -1.04$

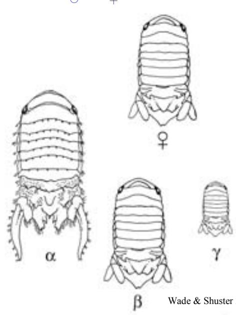
$I_♀ / I_♂ = 7.4$

Berglund et al. 1989

Paracerceis

$I_{mates} = [I_♂ - I_♀] = 2.8$

$I_♂ / I_♀ = 20.4$



Wade & Shuster 2004

Thermosphaeroma

$I_{mates} = [I_♂ - I_♀] = 1.5$

$I_♂ / I_♀ = 4.5$

The Opportunity for Selection

Crow (1952, 1964)

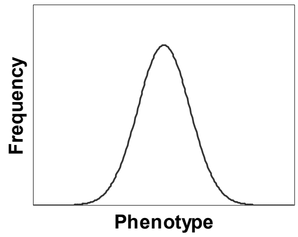
$$I = V_W/W^2$$

The fitness of breeding parents *relative* to the population before selection.

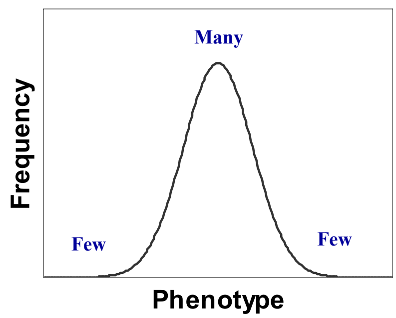
The variance in fitness, V_W, places *an upper limit* on the change in mean fitness from one generation to the next.

Phenotypic Distributions

Most populations of characteristics can be described by a bell-shaped (i.e, normal) curve.



Phenotypic Distributions

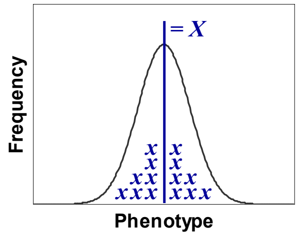


The Average

A measure of central tendency

Calculated as:

$$X = \sum x_i / N$$
$$= \sum p_i x_i$$



Phenotype

The mean phenotype in the population before selection, *Z*, is

$$Z = \int z p(z) dz$$

z = individuals with phenotypic value, z
$p(z)$ = the frequency of such individuals in the population

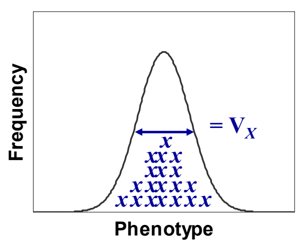
The Variance

A measure of the width of the distribution.

Calculated as:

$$V_X = (\sum x_i^2)/N - X^2$$

$$= \sum p_i (x_i - X)^2$$



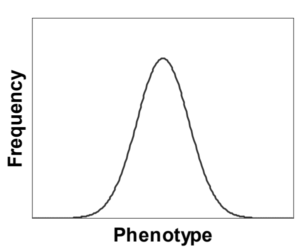
What Causes the Variation?

1. Variation in environmental conditions during development.

a. Differences in food, temperature, disease.

b. Maternal effects.

c. Variation in current conditions.

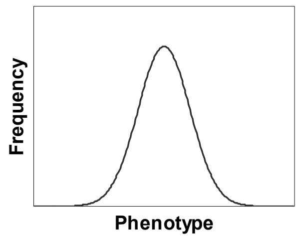


What Causes the Variation?

2. Genetic Variation, factors inherited from parents and which to contribute to phenotypic variation in future generations.

a. Several components to genetic variation.

b. The part that makes offspring resemble their parents is ***additive genetic variance***.



Heritability

The tendency for a character to be inherited by progeny is its *heritability*

1. $h^2 = 1$, character is completely heritable.
2. $h^2 = 0$, character is not heritable.

Fitness

We can define FITNESS as the ability of an individual to leave viable progeny.

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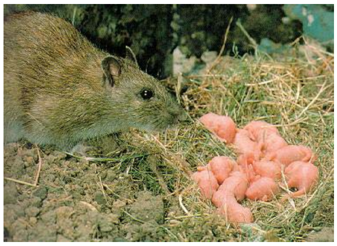
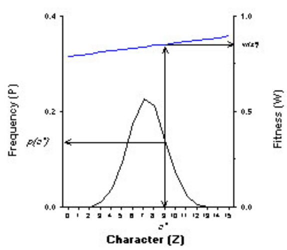
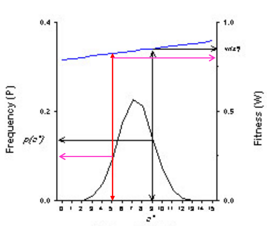


Fitness Function

The relationship between a phenotypic character (z) and fitness (w).



The Strength of Selection



the slope of the function shows how strongly selection is operating.

$p' = p(z)w(z)$

So,

$p' = p(z)w(z)$

$>$

$p' = p(z)w(z)$

Fitness

The mean fitness of the population before selection, W, is

$$W = \int W(z)p(z)dz.$$

$W(z)$ = fitness of an individual with phenotypic value, z
$p(z)$ = the frequency of such individuals in the population

Relative Fitness

The relative fitness, $w(z)$, for individuals with phenotype z is the ratio of individual fitness to the population mean fitness

$$w(z) = W(z)/W$$

Selection

The distribution of phenotypes changes from $p(z)$ before selection, to $p'(z)$ after selection. These two distributions are related by relative fitness, $w(z)$, so that

$$p'(z) = w(z)p(z)$$

The Change in Mean Fitness

The mean fitness of the breeding parents, W', changes as well to

$$W' = \int W(z)p'(z)dz$$

and because $p'(z) = w(z)p(z)$ and $w(z) = W(z)/W$, by substitution,

$$W' = \int [W^2(z)/W]p(z)dz$$

The Difference in Fitness

Thus, the difference in fitness, ΔW, between breeding parents and the unselected population is

$$\Delta W = W' - W$$

$$= \int [W^2(z)/W]p(z)dz - \int W(z)p(z)dz$$

The Variance in Fitness

$$\Delta W = \int [W^2(z)/W]p(z)dz - \int W(z)p(z)dz$$

can be rewritten as

$$[\int W^2(z)p(z)dz - \int W^2]/[W]$$

$$= V_W/W,$$

where V_W is the variance in fitness in the unselected population.

The *Relative* Change in Mean Fitness

The ***relative*** change in mean fitness as a result of selection, $\Delta W/W$, is thus equal to

$$\Delta W/W = V_W/W^2$$

This is the Opportunity for Selection.

The Opportunity for Selection

Crow (1958, 1962)

$$I = V_W/W^2 = V_w$$

The fitness of breeding parents *relative* to the population before selection.

The variance in relative fitness, V_w, places *an upper limit* on the change in mean fitness from one generation to the next.

The Covariance Between Phenotype and Relative Fitness

$$\Delta Z = Cov(z, w[z])$$

measures the change in the average phenotype that results from the relationship between phenotype and fitness.

As with W, this expression is usually less than one.

The Relationship Between ΔZ and V_w

The average fitness as well as the average phenotype may change as a result of selection

$$Cov(z, w[z]) \,/\, (V_Z\, V_w)^{1/2}$$

measures the product moment correlation between phenotype and fitness.

Unless a perfect correlation exists, this expression too is less than one.

Hence, the variance in relative fitness, V_w, places an *upper bound* not only on the change in mean fitness itself, but also on the standardized change in the mean of ***every other*** phenotypic trait.

It was for this reason, that Crow (1958, 1962) defined I, the "opportunity for selection," as

$$I = V_W/W^2 = V_w.$$