Mate Choice and Sexual Selection

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The Presumed Importance of Female Mate Choice:

Mate choices influence female fitness through *direct selection* on females and through *indirect selection* on progeny

What is Direct Selection?

Selection on females that arises from variance in fitness ***among females*** due to differences in offspring numbers produced by different females.

What is Indirect Selection?

Selection on females that arises from variance in fitness ***among offspring*** due to mate choices made by different females.

Direct Selection on Choosy Females Is Presumed To:

Constrain sexual selection.

Mitigate sexual conflict.

Allow assessment of male resource or phenotypic quality.

Indirect Selection on Choosy Females Is Presumed To:

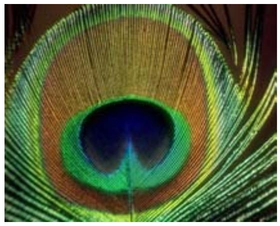
Constrain sexual selection.

Mitigate sexual conflict.

Allow assessment of male genetic quality.

These Hypotheses Assume That:

Total selection on females is strong enough to counteract the effects of sexual selection on males.



Two Questions:

When ***can*** total selection on females constrain sexual selection on males?

When do the effects of male quality influence female fitness ***most***?

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 Opportunity for Selection.
- Analysis of Variance.

The Opportunity for Selection

Crow (1958, 1962)

$$I = V_W/W^2$$

Compares 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.

The *Opportunity* for Selection

Places an *upper limit* on phenotypic change because:

Heritability (h^2) is usually less than 1.

The correlation between phenotypic change and fitness variance, i.e., the relationship between ΔZ and V_w is usually less than 1.

How Can We Measure $I = V_W/W^2$ In a Natural Population?

Begin with:

The Mean and Variance in Offspring Numbers Among Females

$$O = \Sigma\, o_i \,/\, N_{females}$$

where x_i the brood size of the i-th female

$$V_O = \Sigma\, p_k (O - o_i)^2$$

Where p_k = the proportion of females with brood size k

Next:

The Mean and Variance in Offspring Numbers Among Males

Average Male Mating Success

$= N_{females} / N_{males}$

= the Sex Ratio (***R***)

O = Average Offspring/Female

RO = Average Offspring/Male

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	$N_{♀♀}O$	$N_{♀♀}V_{O♀♀}$

A Key Point

The mean and variance in offspring numbers for each mating class of males equals the products, jO and $jV_{Ofemales}$ respectively,

where

j = harem size ; O = average offspring/female,

$V_{Ofemales}$ = variance in offspring/female

This Means That:

The mean and variance in offspring numbers among males will ***far exceed*** the mean and variance in offspring numbers among females.

Males with no mates will produce no offspring at all; thus unsuccessful males produce ***fewer*** offspring than the average female.

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	$N_{♀♀}O$	$N_{♀♀}V_{O♀♀}$

As in ANOVA,

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

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

+

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

$$V_{males} = \Sigma\, p_j\, (jV_{Ofemales}) + \Sigma\, p_j\, (jO\text{-}RO\,)^2$$

$$= RV_{Ofemales} + O^{\,2}V_{mates}$$

The *Total* Opportunity for Selection on Males and Females

(Wade 1979; Wade & Arnold 1980)

Recall that ***RO*** = average number of offspring/male;
dividing V_{males} by $[RO]^2$ gives

$$V_{males} / [RO]^2 = [RV_{Ofemales} + O^{\,2}V_{mates}\,] / [RO]^2$$

which gives

$$I_{males} = (1/R)I_{females} + I_{mates}$$

I_{mates} Equals the *Sex Difference* in the Opportunity for Selection

$$I_{males} = 1/R\,(I_{females}) + I_{mates}$$

when $R = 1$,

$$I_{males} - I_{females} = I_{mates}$$

In general, the ***sex difference*** in the opportunity for selection is due to ***differences in mate numbers*** between the sexes.

Conventional and Reversed Sex Roles

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

$$I_{♂} = (1/R)I_{♀} + I_{mates}$$

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

$$I_{♀} = (R)I_{♂} + I_{mates}$$

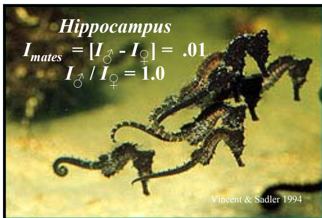
The Sex Difference in the Strength of Selection, ΔI

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

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

$I_{mates} = [I_{♂} - I_{♀}] = .01$

$I_{♂} / I_{♀} = 1.0$

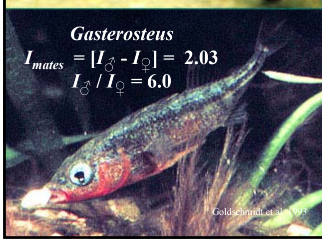
Vincent & Sadler 1994

Syngnathus

$I_{mates} = [I_{♂} - I_{♀}] = -.88$

$I_{♀} / I_{♂} = 5.4$

Berglund et al. 1989

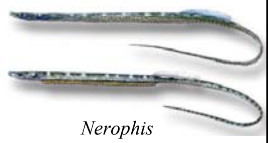


Gasterosteus

$I_{mates} = [I_{♂} - I_{♀}] = 2.03$

$I_{♂} / I_{♀} = 6.0$

Goldschmidt et al. 1993



Nerophis

$I_{mates} = [I_{♂} - I_{♀}] = -1.04$

$I_{♀} / I_{♂} = 7.4$

Berglund et al. 1989

Shuster 1981

Thermosphaeroma

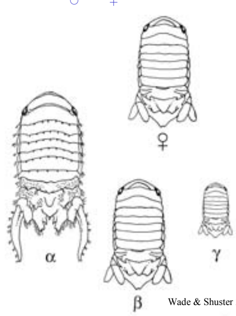
$I_{mates} = [I_{♂} - I_{♀}] = 1.5$

$I_{♂} / I_{♀} = 4.5$

Paracerceis

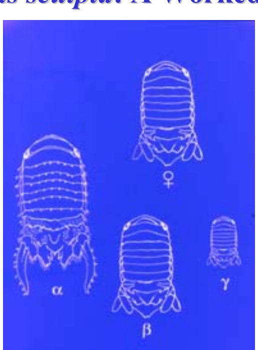
$I_{mates} = [I_{♂} - I_{♀}] = 2.8$

$I_{♂} / I_{♀} = 20.4$

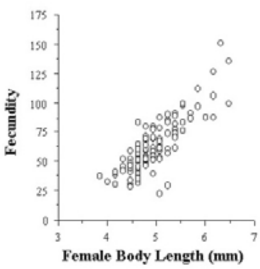


Wade & Shuster 2004

Paracerceis sculpta: A Worked Example



Calculating the Variance in Offspring Numbers for Females (N=825)



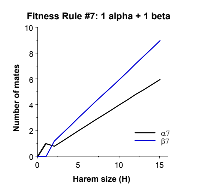
$O_{\text{♀}} = 62.1$

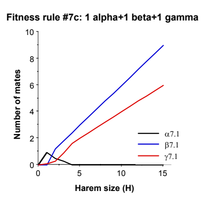
$V_{O\text{♀}} = 521.7$

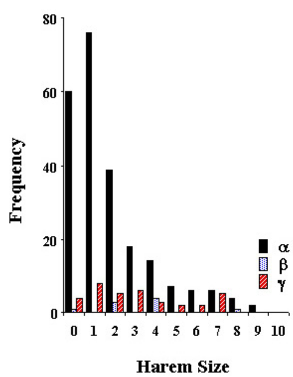
$I_{\text{♀}} = V_{O\text{♀}} / O_{\text{♀}}^2$

$= .14$

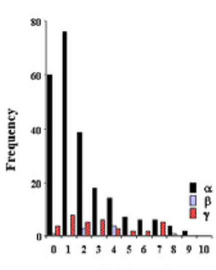
Some Rules for Assigning Male Mating Success







Calculating the Variance in Offspring Numbers for Each Morph



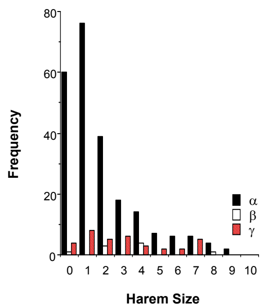
$V_{O\text{♂}total} = V_{O\text{♂}within} + V_{O\text{♂}among}$

For the *k*-th male morph,

$V_{O\text{♂}k} =$

$\Sigma\,\Sigma\, p_{jk}(j_k V_{O\text{♀}}) + \Sigma\,\Sigma\, p_{jk}(j_k O_{\text{♀}} - m_k O_{\text{♀}})^2$

Calculating the Variance in Offspring Numbers for All Males (N=555)



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

$= 24{,}488.0 + 20.6$

$(RO_{♀})^2 = (92.6)^2 = 8{,}567.1$

$\boldsymbol{I_{♂total} = 2.86}$

$I_{♂among} = .002$

From Shuster & Wade 1991

How Much of Total Selection is Sexual Selection?

$I_{♂} = V_{O♂} / (RO)^2 = 2.86$

$I_{♀} = V_{O♀} / O^2 = .14$

$I_{♂} - I_{♀} = (1/R\text{-}1)\, I_{♀} + I_{mates}$

$I_{mates} = 2.77$

$I_{mates} / I_{♂} = .97$

$I_{♂} / I_{♀} = 20.4$

This Means That:

Sexual selection in *P. sculpta* is *so strong* that direct selection on female fecundity is *very small* by comparison.

Conclusion I:

When can direct selection on females constrain sexual selection on males?

When sexual selection is *weak*.

Question Two:

When do the effects of ***male quality*** influence female fitness ***most***?

The Sex Difference in the Opportunity for Selection

Recall that,

$$I_{males} - I_{females} = I_{mates}$$

To assess the effects of direct selection on females vs. sexual selection on males, we must measure $I_{females}$.

Recall That:

Direct selection on females affects the variance in offspring numbers among individuals.

Thus, $I_{females}$ can be understood by investigating selection on female life history.

Three Components of Female Life History:

The number of times a female mates:

Monandry vs. Polyandry

The number of reproductive episodes in a female's lifetime:

Semelparity vs. Iteroparity

The duration of female reproductive competence:

Uniseasonal vs. Multiseasonal Iteroparity

The Effect of Monandry on I_{mates}

When a female mates *once* and produces only *one clutch* of offspring, she awards her *entire* reproductive output to a single male.

The Effect of Polyandry on I_{mates}

When a female mates *more than once*, she *partitions* her clutch into several sub-clutches, equal in number to the number of sires.

The Overall Effects of Polyandry on I_{mates}

Males sire *fewer* progeny with each female; because each mating male sires only a fraction of the offspring of each mate he secures, the variance in mate numbers among males is *reduced*.

The Effect of Semelparity on I_{mates}

When a female produces only *one clutch* of offspring, no variance exists *within females* in the number of offspring produced; all of the variance exists *among females*.

The Effect of Iteroparity on I_{mates}

When a female produces *more than one clutch*, the variance in offspring numbers can be partitioned into *within-* and *among-female* components.

The Overall Effects of Iteroparity on I_{mates}

Multiple reproductive episodes by females *erode* I_{mates} because as clutch number increases, I_{mates} becomes a smaller fraction of the total variance in offspring numbers.

This Means That:

I_{mates} is eroded *least* in monandrous, semelparous species, and is eroded *most* in polyandrous, iteroparous species.

The Opportunity for Selection on Female Life History

Wade (1987)

$$I_{clutches} = V_{clutches} / X^2_{clutches}$$

$I_{clutches}$ is the opportunity for selection on females arising from multiple matings and from multiple reproductive events.

Both tendencies simultaneously ***decrease*** the variance in fitness among males and ***increase*** the variance in fitness among females.

The Total Opportunity for Selection

Wade (1987)

$$I_{males} = 1/R\,(I_{females} - I_{clutches}) + I_{mates}$$

$I_{clutches}$ equals the opportunity for selection on females, owing to variance among females in the number of clutches produced.

I_{mates} equals the sex difference in the opportunity for selection.

When the sex ratio, *R*, is assumed to equal 1

$$I_{males} - I_{females} = I_{mates} - I_{clutches}$$

How Can We Measure $I_{clutches}$ in a Natural Population?

Measuring the Variance in Offspring Numbers Among Females

Approach 1: Two Factor ANOVA

Identifies main effects of male and female parents as well as effects of parental interactions on offspring numbers.

Measuring the Variance in Offspring Numbers Among Females

Approach 2: Nested ANOVA

The effects of males and females are not considered fixed, but instead represent a ***random*** selection from the breeding population.

Table 4.1. Breeding design for females that mate more than once and produce more than one clutch of offspring with each mate; sperm are not stored after the last oviposition with each mate.

Females (a=3)	F_1			F_2			F_3		
Males (b=3)	M_{11}	M_{12}	M_{13}	M_{21}	M_{22}	M_{23}	M_{31}	M_{32}	M_{33}
Clutches (n=3)	C_{111}	C_{121}	C_{131}	C_{211}	C_{221}	C_{231}	C_{311}	C_{321}	C_{331}
	C_{112}	C_{122}	C_{132}	C_{212}	C_{222}	C_{232}	C_{312}	C_{322}	C_{332}
	C_{113}	C_{123}	C_{133}	C_{213}	C_{223}	C_{233}	C_{313}	C_{321}	C_{333}
Sire sums ΣC_{ijk}	C_{11}	C_{12}	C_{13}	C_{21}	C_{22}	C_{23}	C_{31}	C_{32}	C_{33}
Sire means C_B	C_{B11}	C_{B12}	C_{B13}	C_{B21}	C_{B22}	C_{B23}	C_{B31}	C_{B32}	C_{B33}
Dam means C_A	C_{A1}			C_{A2}			C_{A3}		

Grand mean (C_{AB}) = $(1/nab)\ \Sigma^a\Sigma^b\Sigma^n C_{ijk}$

SS_{among} (among groups) = $nb\ \Sigma^a\ (C_A - C_{AB})^2$

SS_{sires} (sires within dams) = $n\ \Sigma^a\Sigma^b\ (C_B - C_A)^2$

SS_{within} (within dams) = $\Sigma^a\Sigma^b\Sigma^n\ (C_{ijk} - C_B)^2$

Sources of Variance in Offspring Numbers:

Vwithin = variance in clutch size within females (SS_{within} divided by $ab(n - 1) = MS_1$)

Vsires = variance in clutch size due to individual mating males (SS_{sires} divided by $a(b-1) = MS_2$)

Vamong = variance in clutch size among females (SS_{among} divided by $(a - 1) = MS_3$)

MS_3 / MS_2 = the effect of individual females on offspring numbers

MS_2 / MS_1 = the effect of individual sires on offspring numbers

The Variance Components of $V_{females}$

$$V_{females} = V_{clutch\ number} + V_{sires\ within\ females} + V_{clutch\ size}$$

$V_{clutch\ number}$ = the variance in offspring numbers arising from females' production of multiple clutches of offspring.

$V_{sires\ within\ females}$ = the variance in offspring numbers arising from the effects of multiple sires.

$V_{clutch\ size}$ = the variance in average number of offspring per clutch, calculated across all females, i.e., the *among-female* component of variance in offspring numbers.

The Variance Components of $V_{females}$

$V_{clutch\ number} + V_{sires\ within\ females}$ = the variance in offspring numbers, averaged across all females, that is, the *within-female* component of variance in offspring numbers.

If $V_{clutches} = V_{clutch\ number} + V_{sires\ within\ females}$,

then because ,

$$V_{females} = V_{clutch\ number} + V_{sires\ within\ females} + V_{clutch\ size}$$

$$V_{females} = V_{clutches} + V_{clutch\ size}, \text{ or}$$

$$V_{clutch\ size} = V_{females} - V_{clutches}$$

The Relationship of $V_{females}$ to $I_{clutches}$

$$V_{clutch\ size} = V_{females} - V_{clutches}$$

Then if each of these terms is divided by the square of the grand mean in offspring per female,

$$I_{clutch\ size} = I_{females} - I_{clutches}$$

Recall that the total opportunity for selection is,

$$I_{males} = 1/R\ (I_{females} - I_{clutches}) + I_{mates}$$

This Means That:

Nested ANOVA provides a method for measuring the effects of multiple sires and multiple breeding episodes on $I_{females}$ that is consistent with Wade (1987).

However, Recall That:

$$I_{males} = 1/R\,[I_{females} - (I_{clutch\ number} + I_{sires\ witin\ females})] + I_{mates}$$

If the effects of male "quality" lie ***within*** $I_{sires\ within\ females}$, which lies ***within*** $I_{clutches}$, then in most species,

$$I_{sires\ within\ females} < I_{clutches} < I_{females} < I_{mates}$$

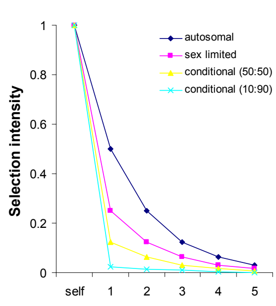
Indirect Selection (↑ $I_{sires\ within\ females}$)   *Direct Selection* (↑ $I_{clutches}$)   *Total selection on females* (↑ $I_{females}$)

Indirect Selection Occurs Across Generations

The intensity of indirect selection ***diminishes*** by ½ with each generation.

Indirect selection intensity on sex limited traits is ***further*** diminished.

Indirect selection on conditional traits is diminished ***further still***.



When Female Mate Choice Occurs:

Few males produce each generation; I_{mates} becomes ***extremely large***

compared to the opportunity for selection on females, $I_{females}$.

When this happens, $I_{clutches}$ and $I_{sires\ within\ females}$ become ***extremely small***.

Conclusion II:

When do the effects of male quality influence female fitness ***most***?

When sexual selection is ***negligible***.

Sexual Selection in Humans

Sex-differences in ***genetic drift*** creates different patterns of genetic diversity for genes inherited through each sex.

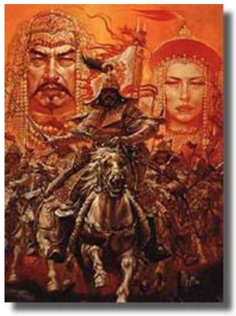
Prediction: Genetic diversity will ***decrease*** with ***increasing*** selection intensity.

Test: Y chromosome and mitochondrial sequence divergence in *Homo sapiens*

An Example of Low Y-Chromosome Diversity

Nearly 8% of the men living in the region formerly controlled by the Mongol Empire

Share the same 1,000 year old Y-chromosome haplotype originating in Mongolia.



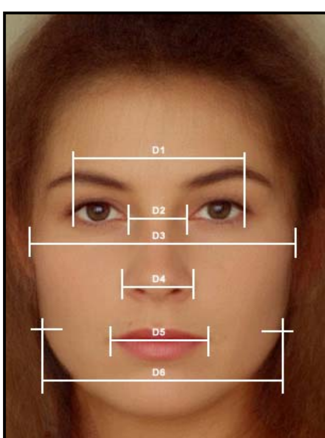
This is approximately 1.0% of the world's human population.

For Other Human Populations:

Sexual selection represents an average of 54.8% (range 28.4% to 77.7%) of all selection

Wade & Shuster 2004

Sexual selection in human populations has the potential to be *very strong*.



Facial Symmetry Indicates 'Genetic Quality?'

But recall that selection on 'quality' is strongest when $I_{mates} = 0$.

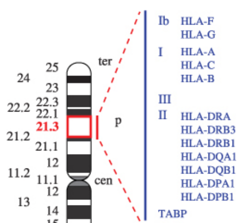
Adaptive benefits in this context may be ***unlikely*** to the extent to which human populations have experienced sexual selection.

Is Facial Symmetry *Really* Attractive

Not all symmetrical faces are "beautiful."

A possible explanation is that human facial perception is tuned to "directional symmetry" which provides information in social situations.

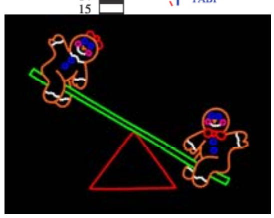
Major Histocompatibility Complex (MHC) Loci



Sequence variability appears to be involved in olfactory mate attraction in fish, mice, humans; choices favor ***heterozygosity***.

Interpretation: particular combinations may be 'uniquely compatible'.

However, such ***balancing selection*** is unlikely to generate directional change.



In General:

Male quality will be ***least important*** to females when I_{mates} is extremely large compared to $I_{clutches}$; at such times, female preferences are likely to be ***arbitrary***.

Male quality will be ***most important*** when I_{mates} and $I_{clutches}$ are approximately equal in magnitude; such mating systems may be ***unstable***.