The Quantitative Paradox of Sexual Selection

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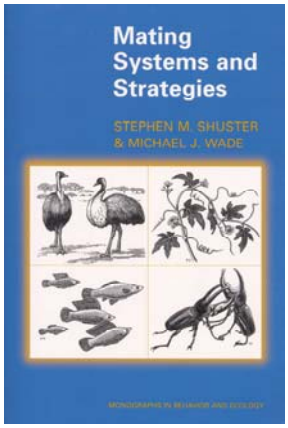
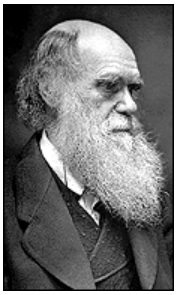
Northern Arizona University



Sexual Selection
Darwin's Two Questions:



- Why do males and females in the *same species* differ from one another, with male characters more exaggerated than those of females?
- Why do the males of *related species* exhibit greater differences in morphology than females of the same, related species?

The First Question

- Is a ***micro-evolutionary*** one.
- The pattern is seen ***within species*** of most taxa.
- Indicates that selection acts to differentiate the sexes.
- Males are affected more than females.

The Second Question

- Is ***macro-evolutionary*** one.
- The pattern is observed ***across species***, within genera or families of most taxa.
- Large differences in male phenotype among closely related taxa are the signature of a *rapid* and *powerful* evolutionary force.

Phenotypic Differences Between the Sexes

- Are ***not*** associated with essential reproductive physiology.
- Are ***not*** associated with development of male and female gametes.
- Exaggerated plumage, coloration, behavior, and morphology of males are correlated with but are ***not*** necessary for reproduction.

Yet These Differences Are So Marked That The Exaggerated Traits of Males *Define* Many Species.

Male-Female Differences

- Only male **big horn sheep** (*Ovis canadensis*; Hogg and Forbes 1997), possess massive coiled horns; female horns are short, uncoiled pegs.

Male-Female Differences

- Only male **red-winged blackbirds** (*Aegelaius phonecius phonecius*; Searcy 1979; Weatherhead & Robertson 1979), are black with red epaulets on the wings, females are inconspicuous and dull brown in color.

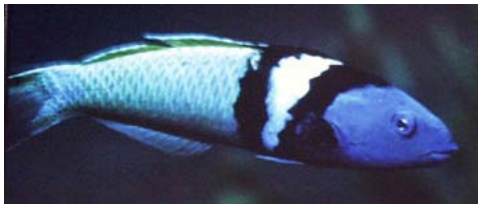
Male-Female Differences

- Only male **satin bowerbirds** (*Ptilonorhynchus violaceus;* Borgia 1986) build elaborate bowers in which to court and mate with females.

Male-Female Differences

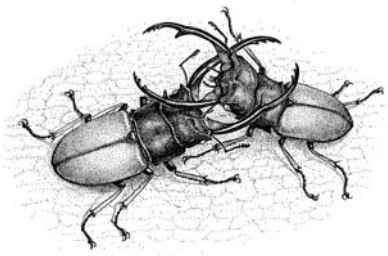
- In the **bullfrog**, *Rana catesbania* (Howard 1984), it is only the male, which makes the deep call from which the species gets its common name; female bullfrogs are silent.

Male-Female Differences



- Only males have blue heads in **blue head wrasse** (*Thallasoma bifasciatum* Petersen et al. 2001).

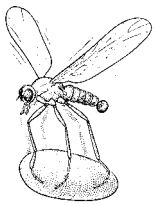
Male-Female Differences



- Only male **stag beetles** (*Lucanus cervus;* Price 1997) possess enlarged, antler-like mandibles.

Male-Female Differences

- In **balloon flies** (*Hilara santor*; Downes 1970), only the males carry balloons of silk as nuptial gifts for females .



"Trivial" Male Characters

- Darwin saw no obvious functional relationship between the exaggerated traits of males and the physical environment.
- In fact, Darwin considered sexual selection ***weak***.

Darwin on Sexual Selection

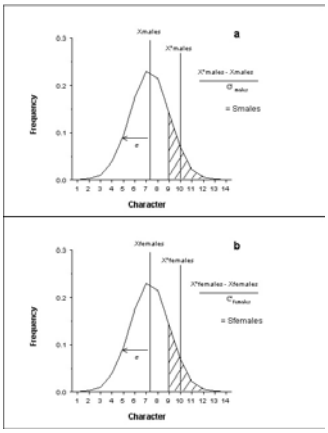
sexual selection "…*depends, not on a struggle for existence, but on a struggle between males for possession of the females; the result is not death of the unsuccessful competitor, but few or no offspring.* ***Sexual selection is, therefore, less rigorous than natural selection***" (1859, p. 88).

Conflict

- How can sexual selection appear to be one of the most ***powerful*** evolutionary forces known,
- Yet Darwin himself considered sexual selection ***less rigorous*** than natural selection?

The Micro-evolutionary Predictions

- Suggest that Darwin was right.
- Single-sex selection, sex-limited expression, age-limited expression and viability selection experiments **all** predict that sexual selection will be ***slow*** and ***weak.***



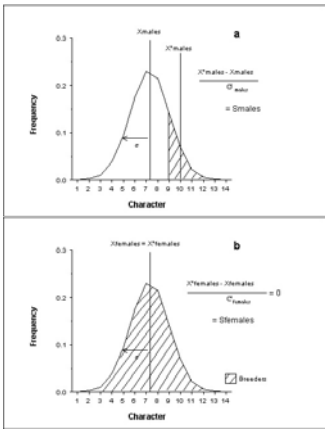
Selection on Both Sexes

Selection is as strong in males as it is in females, thus,

$$S_{males} = S_{females}$$

or,

$$S_{total} = (S_{males} + S_{females})/2$$



Single Sex Selection

Selection acts *only* on males; females breed at random with respect to the character.

Thus,

$$S_{total} = (S_{males} + 0)/2$$

Conspicuous Male Divergence in Traits

- The taxonomic pattern stands in sharp contrast with the expectation of a slow evolutionary response to single sex selection.
- This contrast is even starker when considering the ***sex limited expression*** of male phenotypes.

Sex-Limited Expression of Traits

- Sex-limited expression is an evolved property of a species' developmental genetic system.
- In general, genetic correlations between the sexes produce a phenotypic response ***in both sexes*** when selection occurs in only one sex.

Wilson's Bird of Paradise (*Diphyllodes respublica*)

Male AND female heads are blue and featherless

Spanish Fighting Bulls

•Bravery and fighting tactics of males are assessed in females.

•Brave, noble females tend to have brave, noble brothers and sons for the ring.

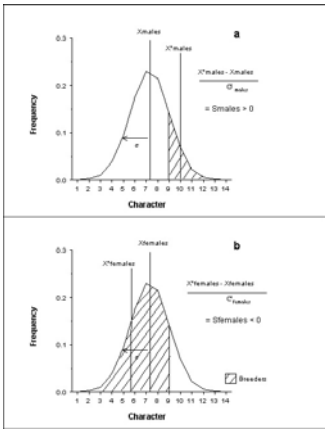
Male Nipples

•The fitness advantage females gain by having nipples and breasts is clear; and may be large.

•The optimal expression of nipples in males may therefore be displaced because of this advantage in females.

Selection for Modifier Alleles

- Genetic correlations between the sexes must be modified for *sex-limited expression* to occur, as exists when male phenotypes become exaggerated.
- Modifier genes act to reduce the genetic correlation in trait expression between the sexes.
- ***This makes total selection weaker and makes trait evolution even slower***.



Disruptive Selection in Both Sexes

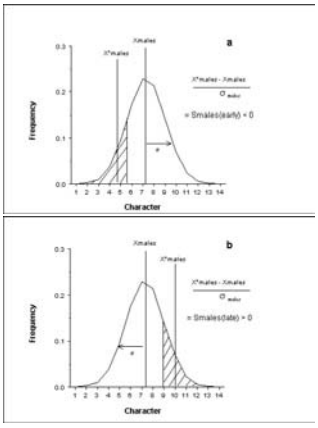
Exaggerated traits, when favored in males, are *selected against* in females;

thus,

$S_{total} = (S_{males} - S_{females})/2$

Sex-Limited Expression of Traits

- Sex-limited expression is an evolved property of a species' developmental genetic system.
- In general, genetic correlations between the sexes must be modified for sex-limited expression to occur.
  - ***This takes time***.



Disruptive Selection in Males

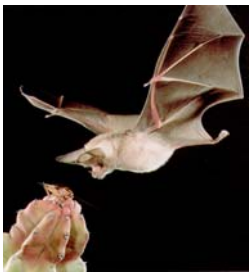
Selection in opposite directions within male life cycles weakens its overall effect;

thus,

$S_{males(early)} < 0$, and $S_{males(late)} > 0$

Viability Selection on Males

- Exaggerated male traits make males more conspicuous to predators. Calling male crickets expend much energy in calling and suffer increased predation by bats.



Viability Selection on Males

- Male lampyrid beetles (Lloyd 1975) encounter a sex-specific risk of predation, often from heterospecific "femme-fatales" that mimic the signals of receptive females and eat the responding males.

Viability Selection on Females

- In sage grouse, females may suffer increased predation in their attempts to mate with particular males (Höogland & Alatalo 1998).

Viability Selection on Females

- In yellow dungflies (*Scatophaga stercoraria*) females may be injured or killed by the mating attempts of males (Parker 1970)

The Sex Specific Selection Differentials for an Exaggerated Male Trait

	Viability	Reproduction	Total Selection Differential
Males	$S_{early} < 0$	$S_{late} > 0$	S_{males}
Females	$S_{early} < 0$	$S_{late} < 0$	$S_{females} < 0$

*A selection differential greater than zero indicates that the trait enhances this component of fitness and is favored by selection while a negative selection differential (< 0) indicates the opposite.

A Poor Fit

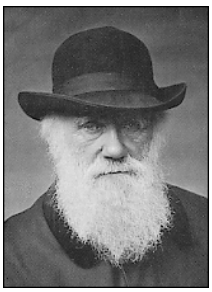
- The macro-evolutionary pattern suggests that selection for exaggerated characters in males is ***rapid*** and ***strong***.

- Darwin, micro-evolutionary theory, and studies of selection all predict that selection acting only on one sex will be ***slow*** and ***weak***.

The Quantitative Paradox of Sexual Selection

How can sexual selection be strong enough to counter the opposing forces of male and female viability selection?

Darwin's Two Components of Sexual Selection



Male Combat

Female Mate Choice

Male-Male Combat: winners mate, losers do not

Female Choice: chosen males mate, not chosen do not.

Current Approaches to the Study of Sexual Selection

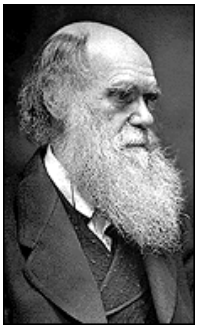
- Identify the context of selection.
- Measure the degree to which traits are modified by selection.
- Speculate on the intensity of selection.

These Approaches *Do Not* Address the Quantitative Paradox

Identifying the mechanism of sexual selection is ***not the same*** *as identifying its evolutionary effect;*

To do this, we must ***measure the actual intensity*** *of sexual selection*

Intensity of Sexual Selection



"If each male secures two or more females, many males would not be able to pair."

C. Darwin, 1871, p. 266.

Instantaneous Calculation:

$N_{donuts} = 10$

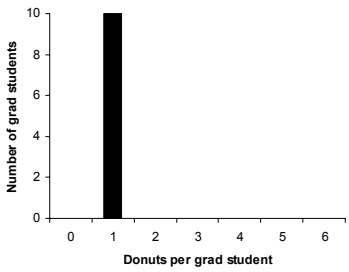
$N_{gradstudents} = 10$

$\boldsymbol{R_d}$ = (10 donuts/10 students) = 1

Therefore, the average number of donuts per student eating donuts,

$\boldsymbol{D} = \boldsymbol{R_d} = 1.$

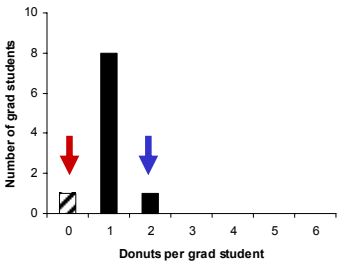
When $R_d = D = 1$



Each grad student is able to secure a donut.

Life is good.

But if One Student Takes *Two*…



One student ***must*** go without.

D now equals the number of donuts, N_{donuts}, ***divided*** by the number of students who ***secure donuts***, or

$$D = N_{donuts} / (N_{students} - N_{students\ without\ donuts}).$$

Notice,

$N_{donuts} = 10$

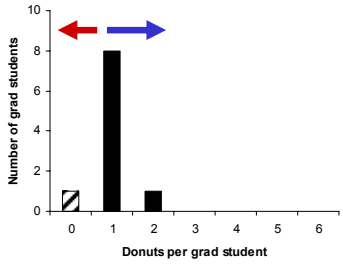
$N_{gradstudents} = 10$

R_d = (10 donuts/10 students) = 1

But ***D*** *increases* from 1 per student, to 1.111 per student

[= 10 donuts / (10-1) students].

Also Notice,



There are now 2 kinds of students.

Those who ***get*** donuts.

And those who ***don't***.

If We Let,

p_d = fraction of students ***with*** donuts (= 9/10 = .9).

$(1 - p_d) = p_0$, the fraction of students ***without*** donuts (= 1/10 = .1).

$p_d + p_0 = .9 + .1 = 1.$

Three Relationships

1. The ***distribution*** of donuts over ***all*** students, R_d, can be expressed as,

$$R_d = N_{donuts}/N_{students}$$

Or as,

$$R_d = p_d\,(D) + p_0\,(0)$$

It is Easy to See That

$$R_d = p_d(D) + p_0(0)$$

Because $p_0(0) = 0$,

$p_d(D) = .9(1.111) = 1$

as it should.

Relationship #2

Because $p_d = (1 - p_0)$, we can rewrite $R_d = p_d(D)$ as,

$$p_0 = 1 - (R_d / D).$$

This expression shows how the fraction of students without donuts, p_0, is related to R_d and D.

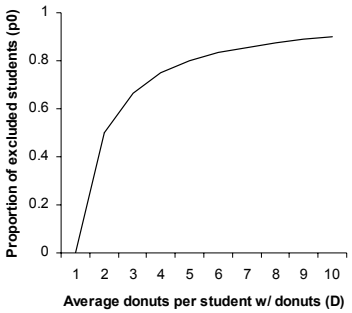
Relationship #3

If the ratio of donuts to students, R_d, remains at 1, this equation simplifies to

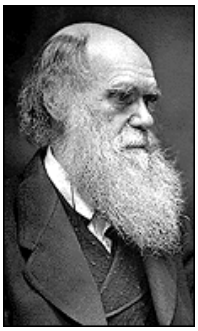
$$p_0 = 1 - (1 / D)$$

What does this mean?

Graphically, $p_0 = 1-(1/D)$



Intensity of Sexual Selection



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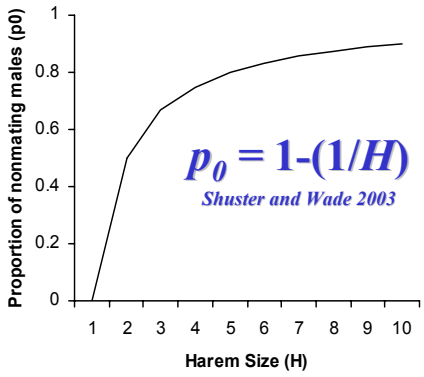


Sexual Selection is a Powerful Evolutionary Force Because:

For every male who sires young with with several females, there must be several males who ***fail to reproduce at all***.

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 Current View of Sex Differences

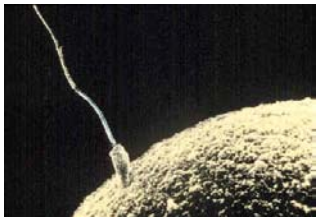
Males and females are ***defined*** by differences in energetic investment in gametes.

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.

Sex Role Reversal

Males become ***more parental***, females become ***more aggressive*** and showy.

Both sexes ***retain*** their sexual identities in gamete size and sexual physiology.

How is this possible if parental investment is ***causal***?

Moreover,

Sex differences in parental investment ***fail to explain*** the details of male parental care.

In sticklebacks, male care **enhances** a male's ability to mate.

In seahorses, male care **reduces** male mating opportunities.

How is this possible if parental investment is ***causal***?

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***.

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.