Sexual Selection and Mating Systems

In the Light of Evolution III: Two Centuries of Darwin
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Outline

1. Darwin’s contributions
2. Existing emphases in plant and animal mating systems
3. Quantitative approaches
4. Combining and improving methodologies
5. Conclusions
Sexual Dimorphism and Sexual Differences: 1859

http://www.juliezickefoose.com/blog/uploaded_images/manakinsfinalbright-762279.jpg

http://www.dargate.com/219_auction/all_images/1850.jpg
Darwin’s Observations On Sexual Differences

• Focused mainly on the contexts in which sexual selection occurred
  • Male-male combat
  • Female mate preferences
• An emphasis that persists to this day.
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).
Is There A 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 Cause of Sexual Selection

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

(Darwin 1871, p. 266).
Visualizing the Process
Wade 1979; Shuster and Wade 2003

When each male mates once, all males are equally successful.

When some males mate more than once, other males are excluded from mating at all.
Sexual Selection Creates Two Classes of Males

If \( p_S \) equals the fraction of males in the population who mate, and \( p_0 \) \((= 1 - p_S)\) equals the fraction of males that do not mate,

\[
H = \frac{N_{females}}{(1 - p_0)}
\]
Graphically, $p_0 = 1 - (1/H)$

Shuster & Wade 2003; Wade & Shuster 2004
Sexual Selection is a Powerful Evolutionary Force Because:

For every male who sires young with $k$ females, there must be $k-1$ males who fail to reproduce at all.

Shuster & Wade 2003
Darwin on Animal Mating Systems

Sexual Selection is NOT Ubiquitous in Animals

“In many cases, special circumstances tend to make the struggle between males particularly severe.”

(Darwin 1871, p. 208).
Darwin’s Grasp of Animal Mating Systems

The “special circumstances” in which reproduction occurs within individual species.

It is here that sexual differences arise - or do not.
Selfing is NOT Ubiquitous in Plants

“Various hermaphrodite plants have become heterostyled, and now exist under two or three forms; and we may confidently believe that this has been effected in order that cross-fertilisation should be assured.”

(Darwin 1877, p. 266).
Darwin’s Grasp of Plant Mating Systems

Certain physical structures of flowers prevent or allow selfing.

It is here that floral differences arise - or do not.
Since Darwin

Two Descriptions of Mating Systems:

In terms of the *genetic relationships* that exist between mating male and female elements (Plants)

In terms of the *numbers of mates* per male or per female (Animals)
Plant Mating Systems

Darwin 1877; Wright 1922; Fisher 1941; Clegg 1980; Lande & Schemske 1985; Holsinger 1991; Barrett and Harder 1996; Vogel and Kalisz 2002

A focus on *deviations from random mating* and their associated genetic consequences.

Differences in mating system identified in terms of *floral morphology*.
A Summary of Plant Mating Systems

Perfect Flowers (hermaphroditic)

Imperfect Flowers

After R. Cronn
Sexual Selection in Plants?

Shuster & Wade 2003

"Male plants compete with one another through pollen production and pollen tube growth on the female stigmatic surface in a manner analogous to sperm competition between males within multiply inseminated females in insects. However, this kind of male--male competition through pollen does not necessarily result in greater variance in male than in female reproductive success."

http://www.spps.kvl.dk
http://news.bbc.co.uk
Animal Mating Systems


• Parental Investment Theory:
  Gamete dimorphism *initiates* sexual selection.

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

  • The *intensity of sexual selection* on males depends on the degree to which females are rare.
The Environmental Potential for Polygamy (EPP)

Emlen & Oring 1977

The degree to which the social and ecological environment allows males to monopolize females as mates.

However, EPP is difficult to define and quantify among species.

Fig. 2. Graphic representation of the environmental potential for polygamy (indicated by the perpendicular height of the shaded area) and its relation to the spatial distribution of resources and temporal availability of receptive mates.

from Emlen & Oring 1977
The Operational Sex Ratio
Emlen & Oring 1977

\[ OSR = \frac{N_{\text{mature males}}}{N_{\text{receptive females}}} \]

A reproductive competition coefficient.

\( OSR > 1 \) = females are rare, competition for mates is intense.

\( OSR < 1 \) = females are abundant, competition for mates is relaxed.
Evolutionary Interpretations
Biases in OSR are presumed to have significant consequences


Reversal of sex roles: (Emlen & Oring 1977; Smith 1984; Berglund et al. 1989; Forsgren et al. 2004; Andersson 2005; Simmons & Kvarnemo 2006)


Mate guarding/mating duration (McLain 1981; Sillen-Tullberg 1981; Jormalainen 1998; Gao & Kang 2005)

Family sex ratio adjustment McLain & Marsh 1990; Lopez & Dominguez 2003; Warner & Shine 2007;

Aggressive behavior Grant et al. 2000; Grant & Foam 2002;

Changes in oviposition rate Spence & Smith 2005;

Female body temperature: (Alsop et al. 2006)

Population declines: (Stifetten & Dale 2006)
Measuring OSR


Considers the effect of certain receptive individuals at a particular time and in a particular place, on the intensity of sexual selection.
Problems with Leaving Certain Individuals Out

The justification for this is that only certain individuals reproduce at any time;

Including everyone could bias estimates of competition intensity.

Specifically, leaving individuals out causes errors in estimates of actual selection.
When Losers are Ignored

A significant fraction of the *among-group* component of fitness variance goes unrecognized. This creates 2 kinds of errors:

1. The **average fitness** of the population is **overestimated**
2. The **variance in fitness** for the population is **underestimated**
And, the Stronger Sexual Selection Becomes,

Because as fewer males mate, more of the male population is excluded from mating altogether. 

The larger the possible error!
A Better Approach

Measure Selection Directly

If traits under selection are known,

Measure the standardized covariance between phenotype and fitness – slope of this line is $\beta$.

Bateman gradients

Phenotypic Correlations

What happens when *particular* individuals in a population mate with other *particular* individuals?

When particular traits become associated between the sexes, *genetic correlations* may arise between male and female mating phenotypes.

After Bakker 1993
Genetic Correlations

Fisher 1930; Lande 1981; Kirkpatrick 1982; Bakker 1993

Relative fitness

0.5

Choosy females

Nonchoosy females

Dull males

Bright males
Other Genetic Correlations

Shuster & Wade 2003

Relative fitness

0.5

0

Solitary females

Grouped females

Nonaffiliative males

Affiliative males
Selection On Specific Traits?
The Opportunity for Selection

(Crow 1958, 1962; Wade 1979)

\[ I = \frac{V_w}{W^2} = V_w \]

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

The variance in relative fitness, \( V_w \), provides an empirical estimate for selection’s strength.

\[ I_\varnothing = \frac{V_o\varnothing}{(O\varnothing)^2} \quad I_\varnothing = \frac{V_o\varnothing}{(O\varnothing)^2} \]
The Sex Difference in the Strength of Selection, $\Delta I$

Shuster & Wade 2003

$$\Delta I = \{ I_\bullet - I_\circ \} = I_{mates}$$

When $\Delta I > 0$, sexual selection modifies *males*

When $\Delta I < 0$, sexual selection modifies *females*

When $\Delta I = 0$, either there is *no* sexual selection

Or sexual selection is *equally strong* in both sexes
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.

However, 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*?
**Hippocampus**

\[ \Delta I = [I_\sigma - I_\varphi] = 0.01 \]

\[ I_\sigma / I_\varphi = 1.0 \]

Vincent & Sadler 1994

**Syngnathus**

\[ \Delta I = [I_\sigma - I_\varphi] = -0.88 \]

\[ I_\varphi / I_\sigma = 5.4 \]

Berglund et al. 1989

**Gasterosteus**

\[ \Delta I = [I_\sigma - I_\varphi] = 2.03 \]

\[ I_\sigma / I_\varphi = 6.0 \]

Goldschmidt et al. 1993

**Nerophis**

\[ \Delta I = [I_\sigma - I_\varphi] = -1.04 \]

\[ I_\varphi / I_\sigma = 7.4 \]

Berglund et al. 1989
Quantify Offspring Numbers in Males and Females?
Sexual Selection and the Spatio-Temporal Distribution of Matings

c.f. Shuster & Wade 2003

Does OSR reliably estimate the intensity of competition?
Consider: Equal sex ratio (5 males: 5 females).
5 male territories, 5 females with variable receptivity

<table>
<thead>
<tr>
<th>Patches w/ males</th>
<th>Intervals w/ females-&gt;</th>
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</thead>
<tbody>
<tr>
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<td>5</td>
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<tr>
<td>(N_j)</td>
<td>0</td>
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</table>

\(\sum \) 0
Possible Measurements:

\[ \text{N}_j = N_{females} \text{ in each interval} \]

\[ \text{N}_i = N_{females} \text{ in each row} \]

\[ K(t) = N_{males} \text{ in all territories} \]

\[ R = N_{females}/N_{males} \]

\[ R_O = N_{males}/N_{females} = \text{OSR} \]

\[ R(t) = N_i/K(t) = R \text{ at each interval} \]

\[ R_O(t) = K(t)/N_i = R_O \text{ at each interval} \]

\[ \sum R_O(t) = \text{the sum of the individual instantaneous OSRs} \]

\[ \sum R(t) = \text{the sum of the individual instantaneous Rs} \]
**Scenario 1:**

### Intervals w/ females->

<table>
<thead>
<tr>
<th>Patches</th>
<th>1</th>
<th>2</th>
<th>3</th>
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<th>Ni.</th>
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<tr>
<td>w/ males</td>
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\[ \Sigma = 5 \]

<table>
<thead>
<tr>
<th>Nj</th>
<th>1</th>
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<th>1</th>
<th>1</th>
<th>1</th>
<th>1</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>K(t)</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
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<tr>
<td>R(t)</td>
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<td>0.20</td>
<td>0.20</td>
<td>0.20</td>
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<td>1.00</td>
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<tr>
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<td>5</td>
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<td>25.00</td>
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<tr>
<td>1/Nfemales(t)</td>
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</table>
## Scenario 2:

### Intervals w/ females->

<table>
<thead>
<tr>
<th>Patches</th>
<th>w/ males</th>
<th>Ni.</th>
<th>Nj</th>
<th>K(t)</th>
<th>R(t)</th>
<th>Ro(t)</th>
<th>1/Nfemales(t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
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<td>1</td>
<td>5</td>
<td>0.20</td>
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<td>3</td>
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<td>3</td>
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Note: The table represents the number of intervals where females are present, with males present in the same interval.
Scenarios 1 and 2 are *clearly distinct* in the number of males that mate. Yet their instantaneous OSRs \([R_0(t)]\) *are identical!* Also, while \(\Sigma R(t)=R=R_0=1\), \(\Sigma R_0(t) = 25\). Each \(R_0(t)\) *overestimates* the overall effect of competition among males.

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**But there is a Problem...**

<table>
<thead>
<tr>
<th>Patches w/ males</th>
<th>Intervals w/ females</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>(N_i)</th>
<th>1/(N_{females(t)})</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
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</tbody>
</table>

\[N_j\]  
\[K(t)\]  
\[R(t)\]  
\[R_0(t)\]  
\[\Sigma R(t) = 25\]
A Solution: Partitioning Variance Components

\[ V_{total} = V_{within} + V_{among} \]

= The *average of the variances* within the classes (groups)
  + The *variance of the averages* among the classes (groups)
<table>
<thead>
<tr>
<th>Patches w/males</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
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</thead>
<tbody>
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<td>N_j</td>
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<td>(R_t)</td>
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<td>Ro(t)</td>
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<td>Vti</td>
<td>0.16</td>
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<tr>
<td>I_{mates}(t)</td>
<td>4</td>
<td>4</td>
<td>4</td>
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<td>4</td>
</tr>
<tr>
<td>(R_t)/R)²</td>
<td>0.04</td>
<td>0.04</td>
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<td>0.04</td>
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</tr>
</tbody>
</table>

\[ I_{mates} = I_{\text{sex ratio}} + \left( I_{mates(t)} - I_{mates(k)} \right) \]

---

A Solution!

Shuster & Wade 2003
pp. 94-100

\[ \frac{N_{\text{females}}}{N_{\text{males}}} = R \]

\[ I_{mates} = \frac{V_{mates}}{R^2} \]
What Does It Mean?

The total opportunity for sexual selection

The opportunity for sexual selection caused by temporal variation in the *sex ratio* (a better ‘OSR’)

The opportunity for sexual selection caused by temporal variation in the availability of females minus

The opportunity for sexual selection caused by spatial variation in the availability of females
Quantify Mating Success?
The mean crowding of females on resources defended by males can be expressed as,

\[ m^* = m + \left( \frac{V_m}{m} \right) - 1 \]

In this context, \( m^* \) represents the number of other females the average female experiences on her resource patch.

\[ t^* = t + \left( \frac{V_t}{t} \right) - 1 \]
Spatial Distribution of Mates

\[ m^* = m + [(V_m / m) - 1] \]

\( m^* = \text{large} \)

\( m^* = \text{small} \)

Shuster & Wade 2003
Temporal Distribution of Mates

\[ t^* = t + \left( \frac{V_t}{t} - 1 \right) \]

Shuster & Wade 2003
m*, t* and I_{mates} (= ∆I)

The relationship between \( m^* \) and \( I_{mates} \) is **proportional**.
At \( m^*_{max} \) one or a few males could defend and mate with *all* of the females in the population.

Conversely, the relationship of between \( t^* \) and \( I_{mates} \) is **reciprocal**.
At \( t^*_{max} \), the ability of one or a few males to mate with multiple females is *reduced*. 
The $\Delta I$ Surface

Shuster & Wade 2003
Dynamic Evolution of Mating Systems

When $m^*$ is low and $t^*$ is high:

Males are likely to *seek out, remain with*, and provide *parental care* for isolated, synchronously receptive females

*Persistent Pairs*

Shuster & Wade 2003
If Females Become More Spatially Aggregated:

$m^*$ is moderate to high, $t^*$ is high:

Males are expected to defend *individual females*, but breeding will occur in *large aggregations*.

Mass Mating
**Polygamy Occurs When**

The mean spatial crowding of matings, $m^*$, and the mean temporal crowding of matings, $t^*$ are both moderate.
If Male Traits Attract the Attention of Females…

Then $m^*$ increases and the $t^*$ decreases.

And sexual selection can become intense…
The $\Delta I$ Surface

$m^*$ vs $t^*$

Shuster & Wade 2003
The Ecology and Phenology of Plant Mating Systems

- Outcrossers
- Dioecy
- Animal pollinated
- Spatial crowding m*
- Temporal crowding t*
- Wind pollinated
- Heterostyly
- Selfers
- Mating Systems
- Dioecy
- Animal pollinated
- Wind pollinated
- Heterostyly
- Selfers
How are Plant and Animal Mating Systems Related?

The effects of $m^*$ and $t^*$ may be more moderate in plants than in animals.
Summary

Why not to use the same quantitative methods for studying plant and animal mating systems?

Population genetics rigor and emphasis on genetic parentage data from plants.

Spatio-temporal data and quantitative genetic approaches to selection from animals.