Sexual Selection and Mating Systems

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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

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

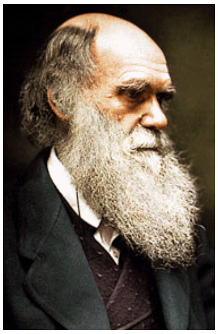
"*…depends, not on a struggle for existence, but on a struggle between males for possession of the females; the result is not death of the unsuccessful competitor, but few or no offspring.*

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"

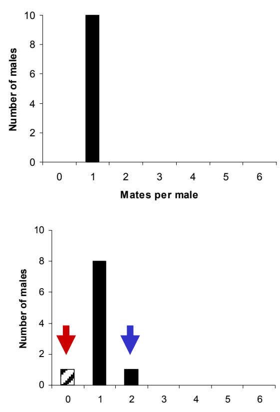
(Darwin 1871, p. 266).

Visualizing the Process

Wade 1979; Shuster and Wade 2003

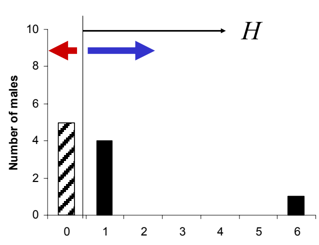
When each male mates once, all males are ***equally successful***.

When some males mate ***more than once***, other males are excluded from mating ***at all***.



Sexual Selection Creates Two Classes of Males

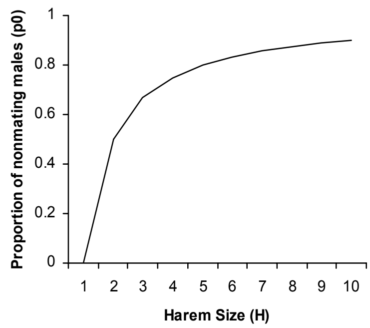
If p_S equals the fraction of males in the population who ***mate***, and p_0 (= $1 - p_S$) equals the fraction of males that ***do not mate***,



$$H = N_{females} / (1 - p_0)$$

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 with k females, there must be k-1 males who ***fail to reproduce at all***.

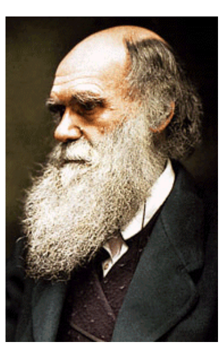
Shuster & Wade 2003

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).

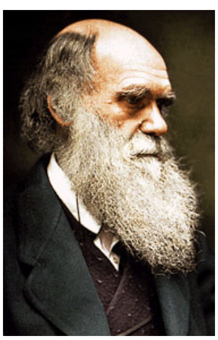


Darwin's Grasp of Animal Mating Systems

The "***special circumstances***" in which reproduction occurs within individual species.

It is here that sexual differences arise - **or do not**.

Darwin on Plant Mating Systems



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

Sexual Selection in Plants?

Shuster & Wade 2003

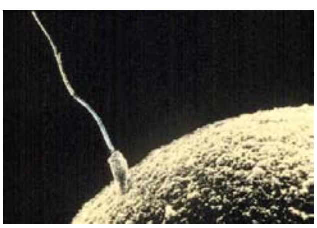
$\neq$

However, this kind of male-male competition through pollen does not necessarily result in greater variance in male than in female reproductive success."

Animal Mating Systems

(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)

•**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.

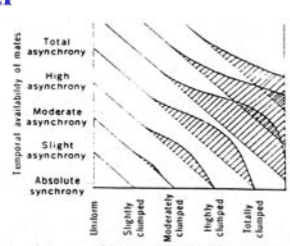


Fig. 2. Graphic representation of the environmental potential for polygamy (indicated by the perpendicular height of the shaded area) and its relation to the spatial distribution of resources and temporal availability of receptive mates.

from Emlen & Oring 1977

The Operational Sex Ratio

Emlen & Oring 1977

$OSR = N_{mature\ males} / N_{receptive\ females}$

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

Variance in mating success: (Positive effect: Emlen 1976; Balshine-Earn 1996; Kvarnemo et al. 1995; Jann et al. 2000; Jones et al. 2001; Foellmer & Fairbairn 2005; Negative effect: Shuster et al. 2001; No effect: Cerchio et al. 2005;

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

Avoidance of sperm competition (Positive: Møller 1989; Møller & Briskie 1995; Hosken 1997; Bateman 1997; Pitnick & Karr 1996; Negative: Pen & Weissing 1999; Kemp & Macedonia 2007)

Mate selection and choosiness: (Rosenqvist 1993; Berglund 1994; Kokko & Monahagn 2001)

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;

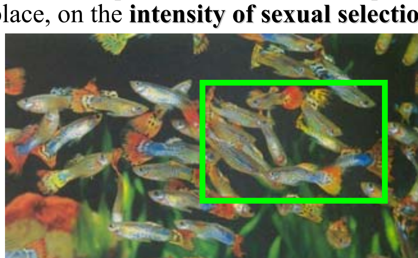
Female body temperature: (Alsop et al. 2006)

Population declines: (Stifetten & Dale 2006)

Measuring OSR

(Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Parker & Simmons 1996; Ahnesjö et al. 2001; Forsgren et al. 2004)

Considers the effect of *certain receptive* individuals at a *particular* time and in a *particular* place, on the **intensity of sexual selection**.



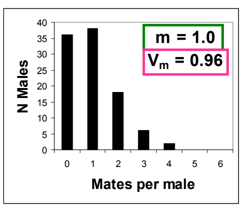
Problems with Leaving Certain Individuals Out

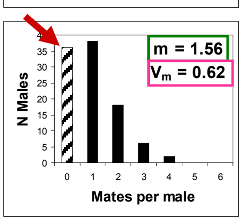
The justification for this is that only *certain* individuals reproduce at any time;

Including everyone *could bias* estimates of competition intensity.

Specifically, leaving individuals out **causes errors** in estimates of ***actual selection***.

When Losers are Ignored



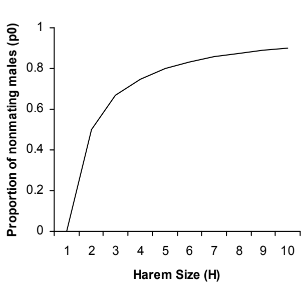


A significant fraction of the ***among-group*** component of fitness variance ***goes unrecognized.***

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,



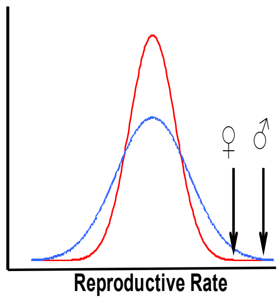
The ***larger the possible error!***

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

A Similar Problem Exists for Potential Reproductive Rates

Only ***a fraction*** of the actual population is considered in most measurements – Those with the ***largest potential values***

Under most circumstances, ***few if any*** individuals may achieve this rate.

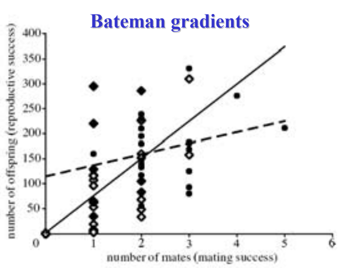


A Better Approach

Measure Selection Directly

If traits under selection are known,

Measure the standardized covariance between phenotype and fitness – slope of this line is β.

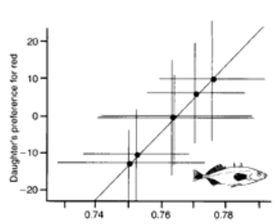


Jones, Arguello & Arnold 2002 *Proc. Roy. Soc. Lond. B: Biol. Sci.*

Phenotypic Correlations

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

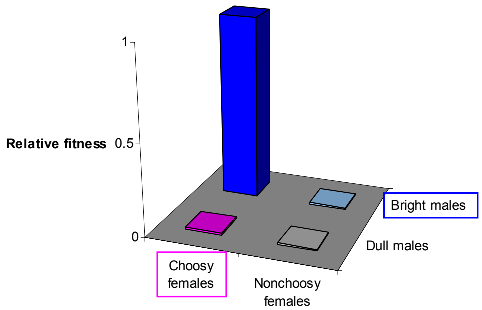
When particular traits become associated between the sexes, ***genetic correlations*** may arise between male and female mating phenotypes.



After Bakker 1993

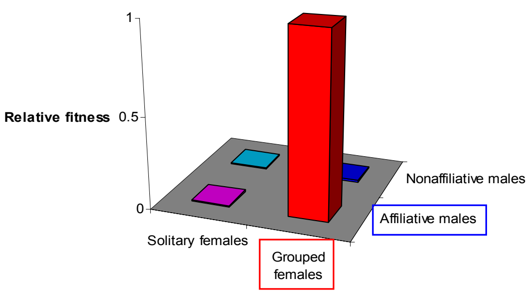
Genetic Correlations

Fisher 1930; Lande 1981; Kirkpatrick 1982; Bakker 1993



Other Genetic Correlations

Shuster & Wade 2003



Selection On Specific Traits?

The Opportunity for Selection

(Crow 1958, 1962; Wade 1979)

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

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

The **variance in relative fitness**, V_w, provides an empirical estimate for selection's strength.

$$I_{\text{♂}} = V_{O\text{♂}}/(O_{\text{♂}})^2 \qquad I_{\text{♀}} = V_{O\text{♀}}/(O_{\text{♀}})^2$$

The Sex Difference in the Strength of Selection, ΔI

Shuster & Wade 2003

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

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

Parental Investment and Animal Mating Systems

(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)

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***.

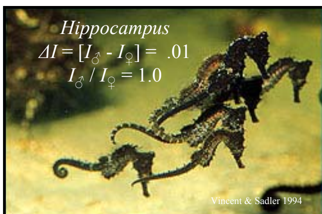
However,

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***?

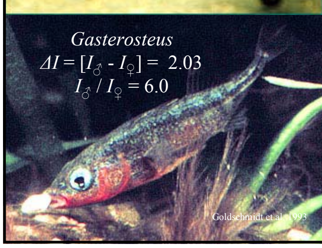


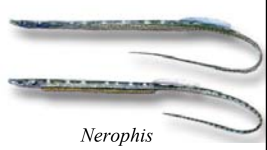
Syngnathus

$\Delta I = [I_♂ - I_♀] = -.88$

$I_♀ / I_♂ = 5.4$

Berglund et al. 1989





Nerophis

$\Delta I = [I_♂ - I_♀] = -1.04$

$I_♀ / I_♂ = 7.4$

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

Intervals w/ females->

Patches w/males	1	2	3	4	5		$N_{i.}$
1	0	0	0	0	0		0
2	0	0	0	0	0		0
3	0	0	0	0	0		0
4	0	0	0	0	0		0
5	0	0	0	0	0		0
						Σ	0
$N_{.j}$	0	0	0	0	0	0	

Possible Measurements:

Intervals w/ females->

Patches w/ males	1	2	3	4	5		$N_{i.}$
1	1	0	0	0	0		1
2	1	0	0	0	0		1
3	1	0	0	0	0		1
4	1	0	0	0	0		1
5	1	0	0	0	0		1
						Σ	5
$N_{.j}$	5	0	0	0	0	5	
K(t)	5	5	5	5	5		
R(t)	1.00	0.00	0.00	0.00	0.00	1.00	
Ro(t)	1					1.00	
$1/N_{females}(t)$	0.2						

$\mathbf{N_{.j}} = N_{females}$ in each interval

$\mathbf{N_{i.}} = N_{females}$ in each row

$K(t) = N_{males}$ in all territories

$\boldsymbol{R} = N_{females}/N_{males}$

$\boldsymbol{R_O} = N_{males}/N_{females} =$ **OSR**

$\boldsymbol{R}(t) = N_{i.}/K(t) = \boldsymbol{R}$ at each interval

$\boldsymbol{R_O}(t) = K(t)/N_{i.} = \boldsymbol{R_O}$ at each interval

$\Sigma\, \boldsymbol{R_O}(t)$ = the sum of the individual instantaneous OSRs

$\Sigma\, \boldsymbol{R}(t)$ = the sum of the individual instantaneous Rs

Scenario 1:

Intervals w/ females->

Patches w/ males	1	2	3	4	5		$N_{i.}$
1	1	1	1	1	1		5
2	0	0	0	0	0		0
3	0	0	0	0	0		0
4	0	0	0	0	0		0
5	0	0	0	0	0		0
						Σ	5
$N_{.j}$	1	1	1	1	1	5	
K(t)	5	5	5	5	5		
R(t)	0.20	0.20	0.20	0.20	0.20	1.00	
Ro(t)	5	5	5	5	5	25.00	
$1/N_{females}(t)$	1	1	1	1	1		

Scenario 2:

	Intervals w/ females->						
Patches w/ males	1	2	3	4	5		$N_{i.}$
1	1	0	0	0	0		1
2	0	1	0	0	0		1
3	0	0	1	0	0		1
4	0	0	0	1	0		1
5	0	0	0	0	1		1
						Σ	5
$N_{.j}$	1	1	1	1	1	5	
K(t)	5	5	5	5	5		
R(t)	0.20	0.20	0.20	0.20	0.20	1.00	
Ro(t)	5	5	5	5	5	25.00	
$1/N_{females}(t)$	1	1	1	1	1		

Scenario 1

	Intervals w/ females->						
Patches w/ males	1	2	3	4	5		$N_{i.}$
1	1	1	1	1	1		5
2	0	0	0	0	0		0
3	0	0	0	0	0		0
4	0	0	0	0	0		0
5	0	0	0	0	0		0
						Σ	5
$N_{.j}$	1	1	1	1	1	5	
K(t)	5	5	5	5	5		
R(t)	0.20	0.20	0.20	0.20	0.20	1.00	
Ro(t)	5	5	5	5	5	25.00	
$1/N_{females}(t)$	1	1	1	1	1		

Scenario 2

	Intervals w/ females->						
Patches w/ males	1	2	3	4	5		$N_{i.}$
1	1	0	0	0	0		1
2	0	1	0	0	0		1
3	0	0	1	0	0		1
4	0	0	0	1	0		1
5	0	0	0	0	1		1
						Σ	5
$N_{.j}$	1	1	1	1	1	5	
K(t)	5	5	5	5	5		
R(t)	0.20	0.20	0.20	0.20	0.20	1.00	
Ro(t)	5	5	5	5	5	25.00	
$1/N_{females}(t)$	1	1	1	1	1		

But there is a Problem…

Scenarios 1 and 2 are ***clearly distinct*** in the number of males that mate.

Yet their instantaneous OSRs [R_O(t)] *are identical!*

Also, while Σ**R**(t)=**R**=$\mathbf{R_O}$= 1, Σ$\mathbf{R_O}$(t) = 25.

Each R_O(t) ***overestimates*** the overall effect of competition among males.

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)

Patches w/males	Intervals w/ females-> 1	2	3	4	5		$N_{i.}$	$N_{i.}/T$	V(k)	$I_{mates}(k)$
1	1	1	1	1	1		5	1	0.00	0
2	0	0	0	0	0		0	0	0.00	
3	0	0	0	0	0		0	0	0.00	
4	0	0	0	0	0		0	0	0.00	
5	0	0	0	0	0		0	0	0.00	
						Σ	5			
$N_{.j}$	1	1	1	1	1	5	1			
K(t)	5	5	5	5	5					
(R_t)	0.20	0.20	0.20	0.20	0.20	1.00				
Ro(t)	5	5	5	5	5	25.00				
Vti	0.16	0.16	0.16	0.16	0.16					
$I_{mates}(t)$	4	4	4	4	4					
$(R(t)/R)^2$	0.04	0.04	0.04	0.04	0.04					
$^*I_{mates}(t)$	0.16	0.16	0.16	0.16	0.16					

A Solution !

Shuster & Wade 2003
pp. 94-100

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

$$I_{mates} = V_{mates}/R^2$$

$$I_{mates} = I_{sex\ ratio} + ({}^*I_{mates(t)} - {}^*I_{mates(k)})$$

What Does It Mean?

$$I_{mates} = I_{sex\ ratio} + ({}^*I_{mates(t)} - {}^*I_{mates(k)})$$

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 in Space and Time

Lloyd 1967; Wade 1995; Shuster & Wade 2003

The mean crowding of females on resources defended by males can be expressed as,

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

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

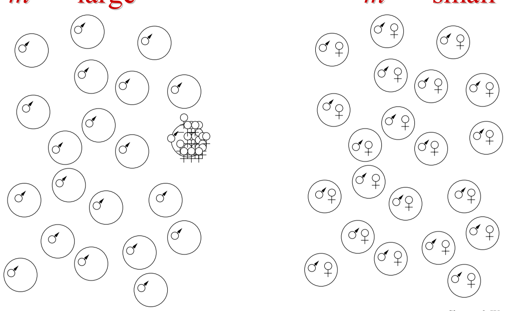
$$t^* = t + [(V_t / t) - 1]$$

Spatial Distribution of Mates

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

m^* = large

m^* = small



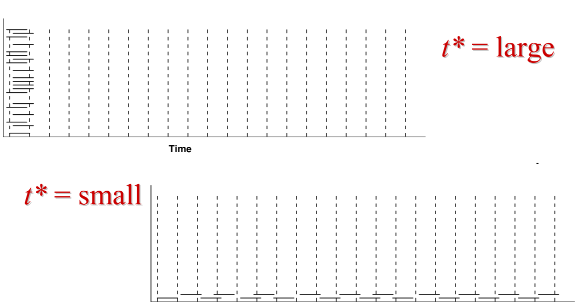
Shuster & Wade 2003

Temporal Distribution of Mates

$t^* = t + [(V_t / t) - 1]$

t^* = large

t^* = small



Shuster & Wade 2003

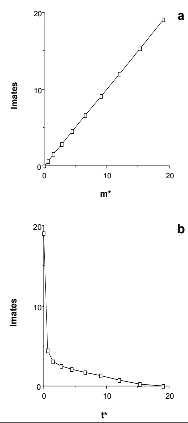
m^*, t^* and I_{mates} (= ΔI)

The relationship between m^* and I_{mates} is ***proportional***.

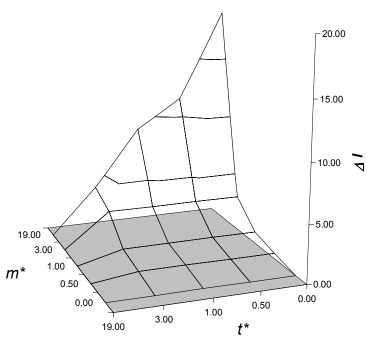
At m^*_{max} one or a few males could defend and mate with *all* of the females in the population.

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*.

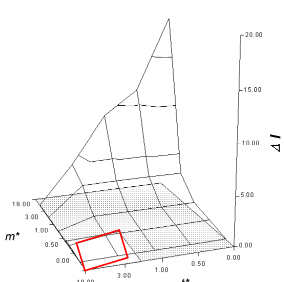


The ΔI Surface



Shuster & Wade 2003

Dynamic Evolution of Mating Systems



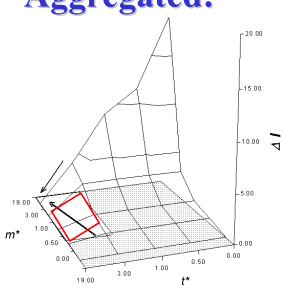
When m^* is low and t^* is high:

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

Persistent Pairs

Shuster & Wade 2003

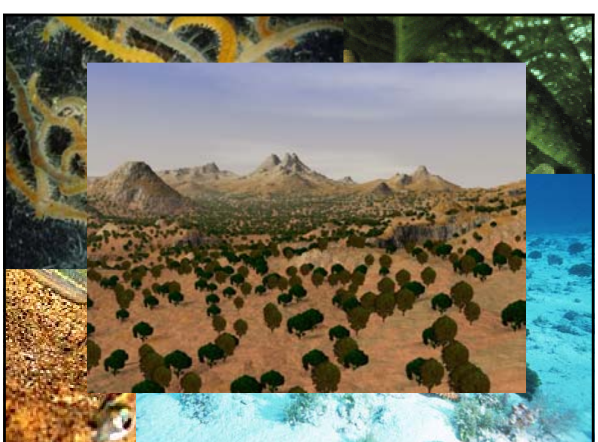
If Females Become More Spatially Aggregated:



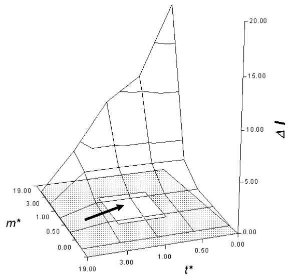
m^* is moderate to high, t^* is high:

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

Mass Mating

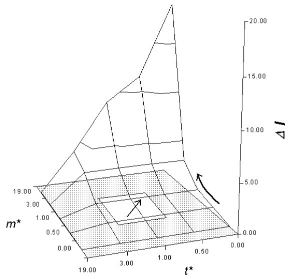


Polygamy Occurs When



The mean spatial crowding of matings, ***m****, and the mean temporal crowding of matings, ***t**** are both ***moderate***.

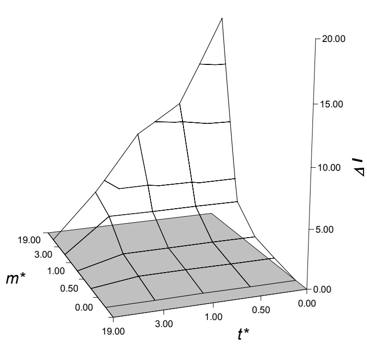
If Male Traits Attract the Attention of Females…



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

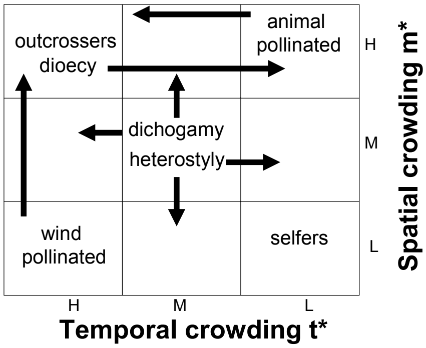
And ***sexual selection*** can become ***intense***…

The *ΔI* Surface

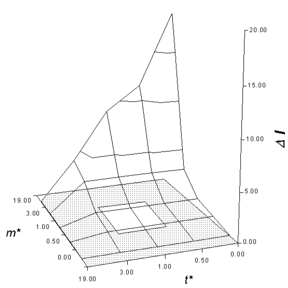


Shuster & Wade 2003

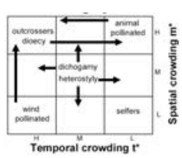
The Ecology and Phenology of Plant Mating Systems



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.