# The Operational Sex Ratio, the Potential Reproductive Rate, and the Opportunity for Sexual Selection

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# **Objectives**

1. Definitions of OSR/PRR.

2. What do they *really* measure?

3. Do better measures exist?

# What Is The Definition of OSR?

Originally defined by S.T. Emlen 1976 as: "*the ratio of potentially receptive males to receptive females at any time.*"

A measure of the ***level of competition*** for mates, and therefore, of the ***intensity of sexual selection.***

# 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.

# However,

This definition has *not remained consistent* among researchers.

**3 primary variants of the original concept of OSR:**

1. Changes in the *ratio* itself.

2. Changes in how individuals *are (or are not)* included in estimates.

3. Changes that attempt to incorporate the effects of *parental investment*.

**OSR is widely presumed to predict/induce evolutionary responses by populations**

# Changes In Ratio

## The "Operational Sex Ratio" has been expressed in several ways

Ratio of potentially receptive males to females at any time (Emlen 1976)

Ratio of sexually active males to fertilizable females at any time (Emlen & Oring 1977, and most others).

Reciprocal of the sex ratio ($R_O=1/R=N_{males}/N_{females}$; Shuster & Wade 2003)

Number of males and females ready to mate (Nyman et al. 2006)

Ratio of matured females to males (Yamamoto & Edo 2006)

Fertilizable females to sexually active males at any given time (Forbes et al. 2005; Prohl 2006).
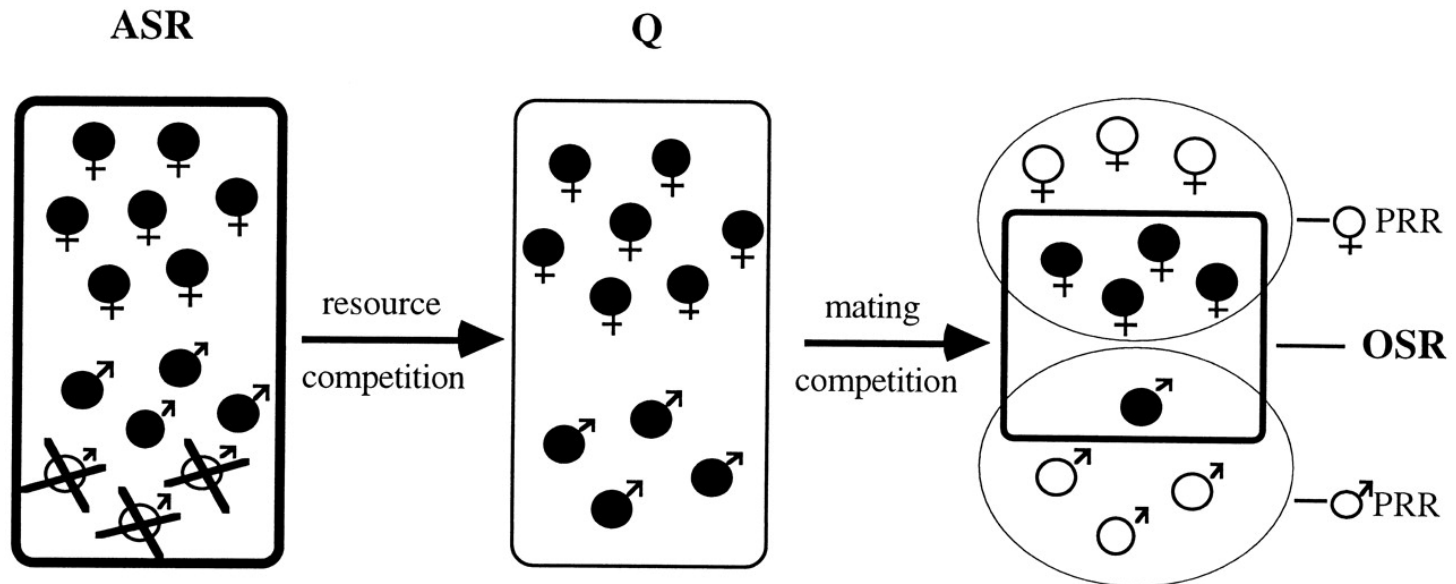
The relative number of members of each sex willing (or able) to mate at any given time (Kemp & Macedonia 2006)

# Changes in Personnel

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

A change in emphasis from *all* individuals that are *potentially* receptive,

To one that includes only *certain receptive* individuals at a *particular* time and in a *particular* place



ASR    Q

resource competition

mating competition

♀ PRR

OSR

♂ PRR

Ahnesjö, Kvarnemo & Merilaita 2001. Behav. Ecol. 12:397-401

# Changes In Emphasis

**The focus on parental care in sexual selection theory has also influenced the changing view of what OSR is.**

"*The cost of a single breeding attempt, which in iteroparous organisms can be measured as the probability of death as a consequence of the current breeding attempt, has a strong, direct effect on choosiness and well as consistent relationships with both OSR and PRR.*"

(Kokko & Monahagn 2001)
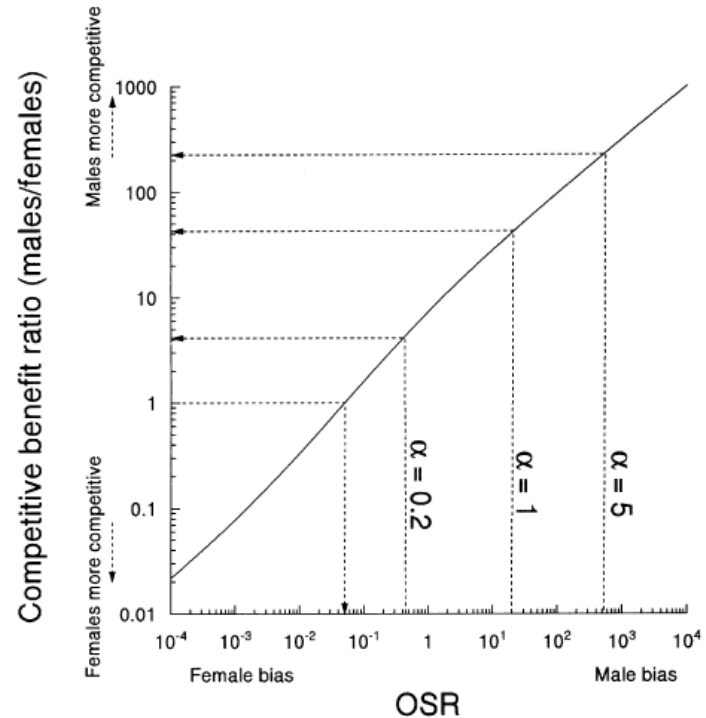
# Evolutionary Interpretations

## 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)

# Summary 1

The definition of OSR has *changed* somewhat since 1976.

Working definitions of OSR have attempted *to improve the fit* between theory and observation.

Evolutionary predictions from observed biases in OSR are now *common*.

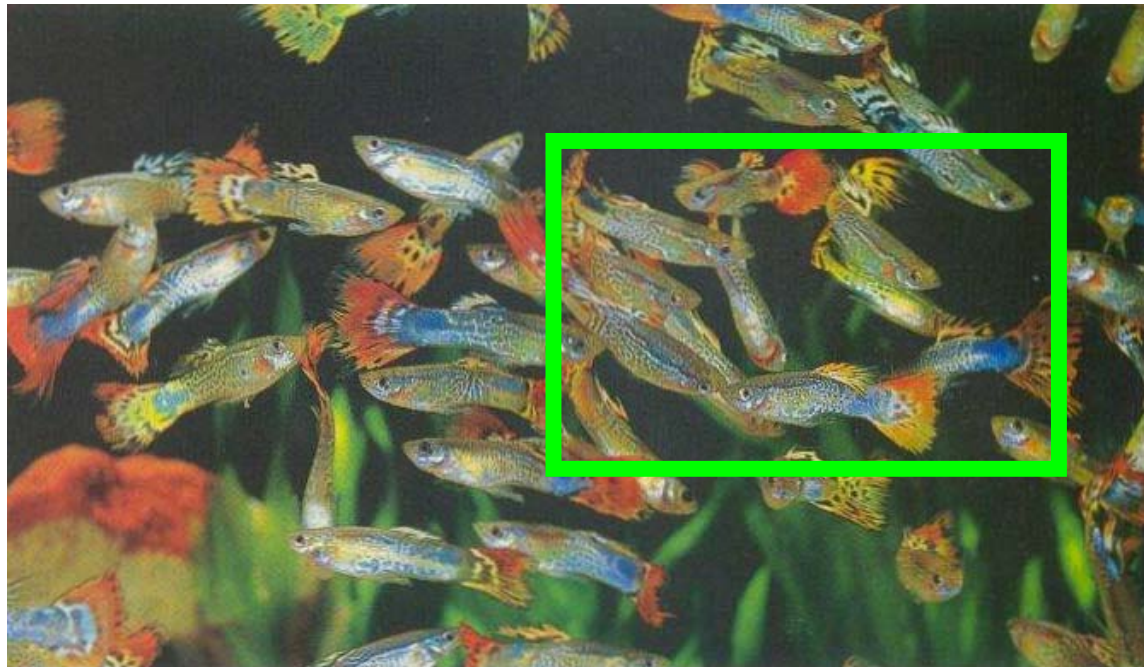# Objectives

1. Definitions of OSR/PRR.

2. What do they *really* measure?

3. Do better measures exist?

# Measuring OSR/PRR

(Clutton-Brock & Vincent 1991Clutton-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*.

# The Cause of Sexual Selection
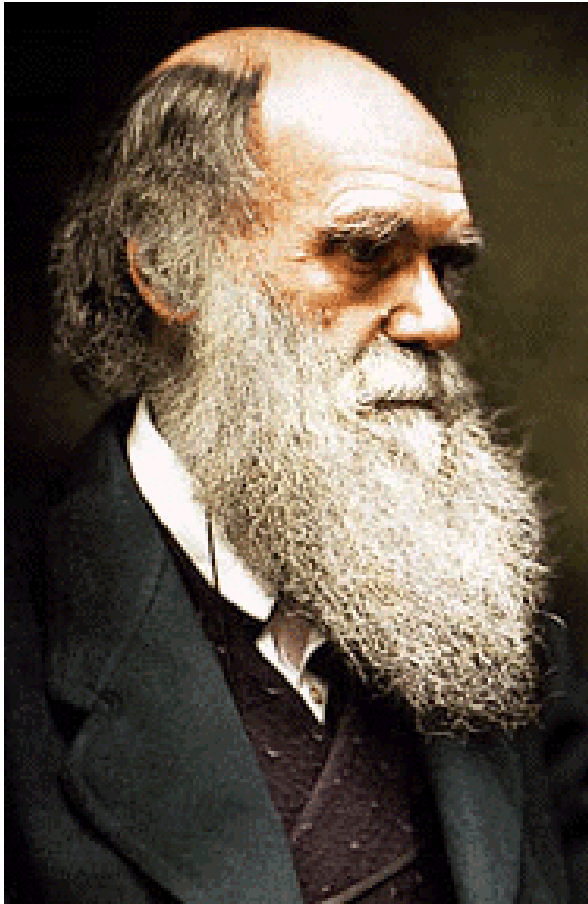
*"If each male secures two or more females, many males would not be able to pair"* (Darwin 1871, p. 266).

# For Harems, $p_0 = 1-(1/H)$

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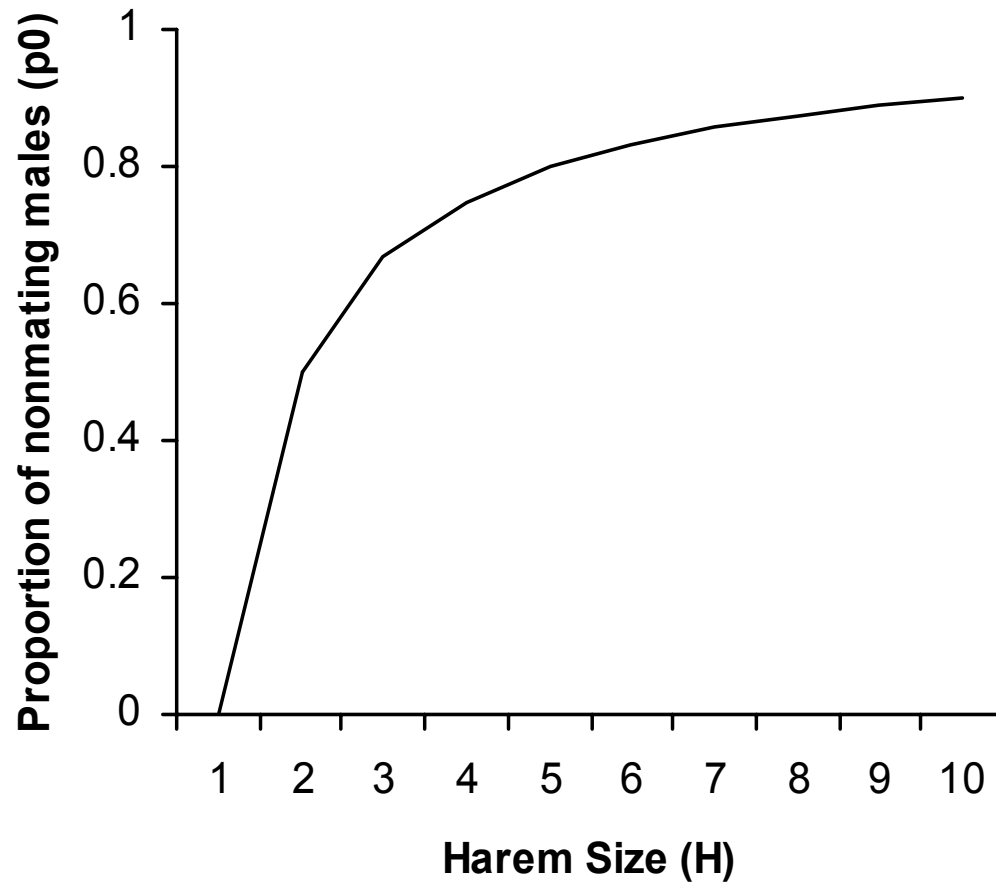
# **Sexual Selection is a Powerful Evolutionary Force Because:**

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

# 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*
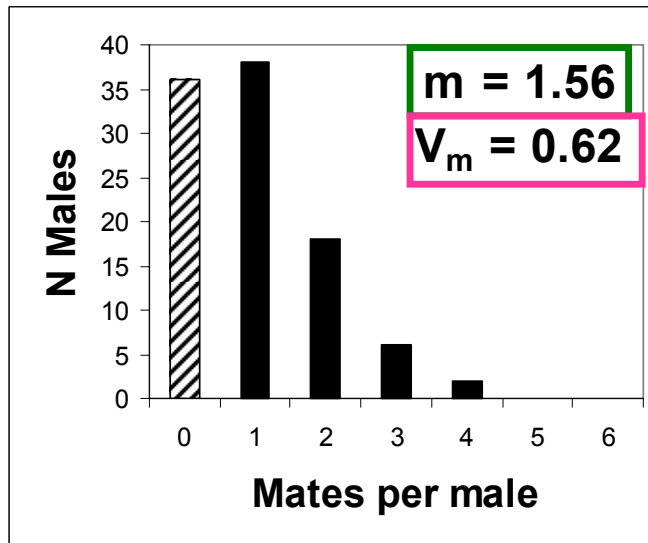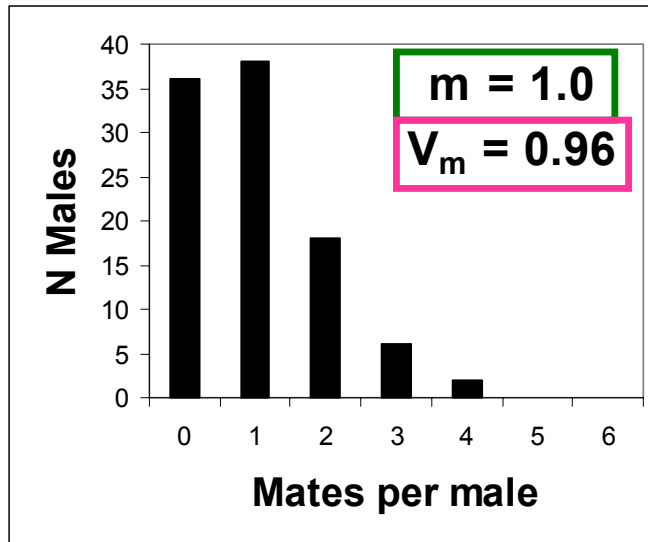
# And, the Stronger Sexual Selection Becomes,
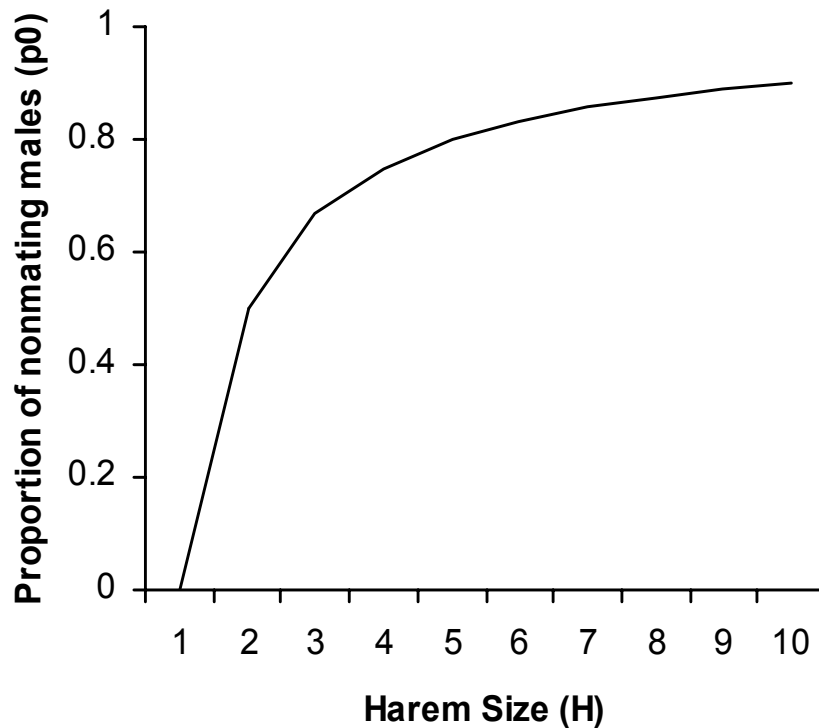
The *larger the possible error!*

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



Graph: x-axis "Harem Size (H)" ranging from 1 to 10, y-axis "Proportion of nonmating males (p0)" ranging from 0 to 1.

# 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.
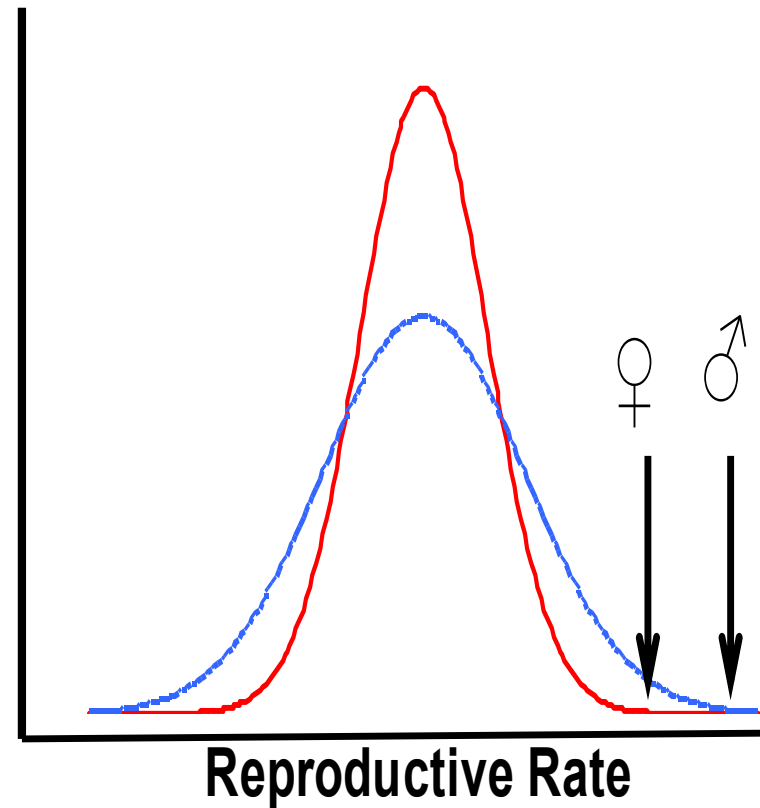
**Reproductive Rate**

# Do OSR/PRR Really Measure What We Think They Measure?

**Does OSR reliably estimate the intensity of competition?**

Consider: Equal sex ratio (5 males: 5 females).

5 male territories, 5 females with variable receptivity

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**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 |

c.f. Shuster & Wade 2003

# Possible Measurements:
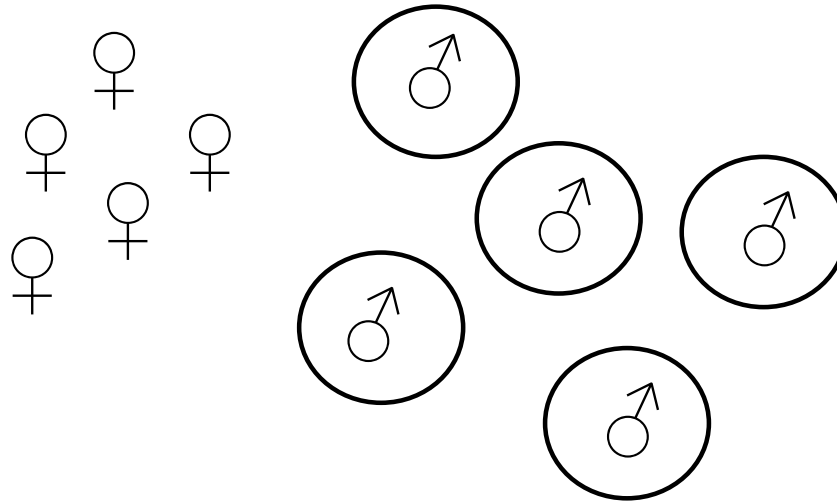
| Patches w/ males | Intervals w/ females-> 1 | 2 | 3 | 4 | 5 | $N_{i.}$ |
|---|---|---|---|---|---|---|
| 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| 2 | 1 | 0 | 0 | 0 | 0 | 1 |
| 3 | 1 | 0 | 0 | 0 | 0 | 1 |
| 4 | 1 | 0 | 0 | 0 | 0 | 1 |
| 5 | 1 | 0 | 0 | 0 | 0 | 1 |
| | | | | | $\Sigma$ | 5 |
| | | | | | | 5 |
| $N_{.j}$ | 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 | | | | | |

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

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

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

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

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

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

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

$\Sigma R_O(t) =$ the sum of the individual instantaneous OSRs

$\Sigma R(t) =$ the sum of the individual instantaneous Rs

$1/N_{females}(t) = 1/N_{i.}$

# Scenario 1:

**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 |
| | | | | | $\Sigma$ | 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 | | | | | |

# Scenario 2:

**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 |
| | | | | | $\Sigma$ | 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 3:

**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 |
| | | | | | $\Sigma$ | 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 | 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 |
| | | | | | | 5 |
| $N_{.j}$ | 1 | 1 | 1 | 1 | 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 |
| $1/N_{females}(t)$ | 1 | 1 | 1 | 1 | 1 | |

## Scenario 3:

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 |
| | | | | | 5 | 1 |
| $N_{.j}$ | 1 | 1 | 1 | 1 | 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 |
| $1/N_{females}(t)$ | 1 | 1 | 1 | 1 | 1 | |

# But there is a Problem…

Scenarios 2 and 3 are *clearly distinct* in the number of males that mate.

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

Also, while $\Sigma R(t) = R = R_O = 1$, $\Sigma R_O(t) = 25$.

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

## Scenario 2:

**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 |
| | | | | | | | $\Sigma$ | 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 3:

**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 |
| | | | | | | | $\Sigma$ | 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 | |
| $1/N_{females}$(t) | | 1 | 1 | 1 | 1 | 1 | | |

# Why?

Because $\Sigma R_O(t) = 25$ equals

$$(N_{males}/H_{females})T$$

Where **T** = the number of intervals containing females (=5),

and $1/H_{females}$ is the **harmonic mean** number of females per interval,

$$= (1/T)(\Sigma\ 1/N_{females}) = 1$$

# The Harmonic Mean

$$1/\mathbf{H}_{females} = (1/\mathbf{T})(\Sigma\ 1/\mathbf{N}_{females})$$

Allows small values to contribute *disproportionately* to the value of $1/\mathbf{H}_{females}$.

Because $\mathbf{R}_O(t) = \mathbf{N}_{males}/\mathbf{N}_{.jfemales}$,

***apparently*** *high* levels of male competition will *disproportionately contribute* to the overall value of $\Sigma\mathbf{R}_O(t)$.

# Summary 2

Current methods for measuring OSR/PRR tend to *cause errors* in estimates of the selection intensity.

Estimates can be too high, too low, or simply not representative of how selection *actually operates*.

Presumed evolutionary consequences of biased OSRs are likely also *erroneous*.
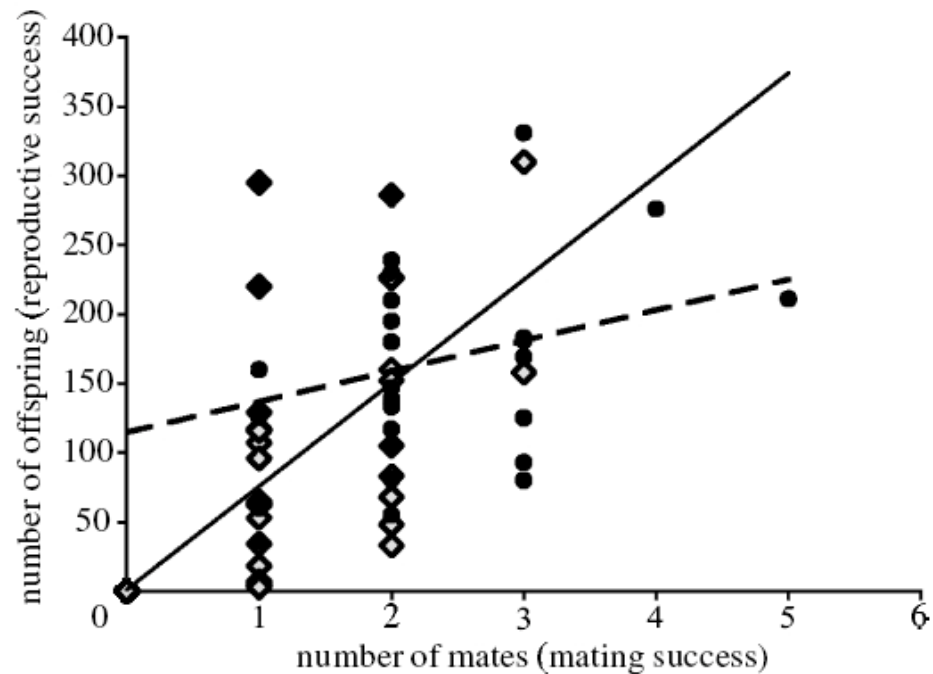
# **Objectives**

1. Definitions of OSR/PRR.

2. What do they *really* measure?

3. Do better measures exist?

# The Best 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.*

# The Opportunity for Selection

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

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.

$$I_\male = V_{O\male}/(O_\male)^2 \qquad I_\female = V_{O\female}/(O_\female)^2$$

# The Sex Difference in the Opportunity for Selection, $I_{mates}$

Wade 1979; Arnold & Wade 1983; Shuster & Wade 2003

$$\{ I_{\male} - I_{\female} \} = I_{mates}$$

The relative magnitudes of $I_{\male}$ and $I_{\female}$ determine whether sexual selection modifies males or females

**What If You Can't Assign Parentage Easily?**

**Intervals w/ females->**

| Patches w/males | 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 | | | | | |

**Shuster & Wade 2003**

pp. 94-100

$$V_{Nij} = \overline{V}_{mates(t)} + V_{(R[t])}$$

$$V_{Nij} = \overline{V}_{t(k)} + (V_{mates})/(T)^2$$

$$I_{mates} = (T/R)^2 \{ V_{(R[t])} + (\overline{V}_{mates(t)} - \overline{V}_{t(k)}) \}$$

**Intervals w/ females->**

| Patches w/males | 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 | | | | | |

**Shuster & Wade 2003**

pp. 94-100

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

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

$$I_{mates} = (T/R)^2\{V_{(R[t])} + (\overline{V}_{mates(t)} - \overline{V}_{t(k)})\}$$

**Intervals w/ females->**

| Patches w/males | 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 | | | | | |

**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?

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

**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

# Mating Systems and Sexual Selection

**(Emlen & Oring 1977)**



• Male reproduction is limited by the *spatial distribution* of resources and by the *temporal distribution* of sexually receptive females.

• **By partitioning the total variance in $N_{females}$, the *intensity of sexual selection* can be directly measured.**

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

# Summary 3

*Better* parameters than OSR, for estimating temporal variation in the intensity of sexual selection, *do exist*.

They require more *precise* estimates of who mates and who does not.

Evolutionary predictions from observed biases in OSR/PRR *must be reconsidered*.