# The Invasion of Alternative Mating Strategies 

Stephen M. Shuster

BIO 666: Animal Behavior
Fall 2009
Northern Arizona University

## Mating Strategies (Alternative)

Polymorphisms in reproductive behavior, morphology or life history associated with competition for mates.

Genetic/Life History Example


Orange, blue and yellow males in the lizard, Uta stansburiana

Developmental Example


Developmental strategies in male Onthophagus beetles.

## Behavioral Example



Extra-pair copulations (EPCs) in songbirds.

## In Each of These Cases,

Novel phenotypes appear to have invaded, become modified and persist in natural populations.

## Proximate Causes

Hormonal and neurological factors that regulate the timing and degree to which phenotypic differences appear.

## Ultimate Causes

The genetic architectures underlying phenotypic expression.
These depend on the circumstances in which mating opportunities arise.

## That is,

On the intensity of selection favoring distinct reproductive morphologies.

On the predictability of mating opportunities relative to individual life span.

## 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.
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

## Population Sex Ratio

The population sex ratio, $\boldsymbol{R}$, is the ratio of the total number of females to the total $\qquad$ number of males, or,

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

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

## Two Classes of Males

$\qquad$
Mating males $\left(\boldsymbol{p}_{\boldsymbol{m}}\right)=$
 males with one or more mates.
Non-mating males
$\left(\boldsymbol{p}_{0}\right)=$ males with no mates.
Since $\left(\boldsymbol{p}_{\boldsymbol{m}}+\boldsymbol{p}_{\boldsymbol{0}}\right)=1$, $\boldsymbol{p}_{\boldsymbol{m}}=\left(1-\boldsymbol{p}_{\boldsymbol{0}}\right)$.
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

## The Average Number of Mates

 per Male, $m$Equals the number of mates per male, $\boldsymbol{i}$, times the frequency of each male class, $\boldsymbol{p}_{\boldsymbol{i}}$, summed over all males.

Thus, $\boldsymbol{m}=\Sigma i p_{i}$


## Other Relationships

$\qquad$
$\qquad$
If $\boldsymbol{m}=\Sigma i p_{i}$
and if $\boldsymbol{R}=\boldsymbol{m}$,
then
$\boldsymbol{R}=\Sigma i p_{i}$.

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

The Average Harem Size, $\boldsymbol{H}$
Can be expressed as
 the total number of females, divided by the fraction of males who secure mates, thus,

$$
\begin{gathered}
\boldsymbol{H}=\sum i p_{i} /\left(1-p_{0}\right) \\
=\boldsymbol{R} /\left(1-p_{0}\right) \\
\boldsymbol{H}=\boldsymbol{R} /\left(p_{\mathrm{s}}\right)
\end{gathered}
$$



## Sexual Selection is a Powerful Evolutionary Force Because:

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

## Strong Sexual Selection

 Creates a "Mating Niche"Unconventional males need only achieve mating success greater than the reciprocal of harem size to invade.

$$
\boldsymbol{s}>1 / \boldsymbol{H}
$$

Orchestia darwinii: $\alpha$ - and $\beta$-males $\qquad$

$\alpha$-males: robust with an enlarged chela; they displace other $\alpha$-males from breeding territories.


## Orchestia darwinii: $\alpha$ - and $\beta$-males

$\qquad$

$\beta$-males: mature early, lack enlarged chelae, avoid fights, but are $\qquad$ attracted to female aggregations. $\qquad$
$\qquad$

## The Mating Success of $\beta$-males

$\beta$-males are successful in mating with some of the females in the harems of $\alpha$-males.

Their success equals a fraction of that achieved by haremholding $\alpha$-males.

$\qquad$
$\qquad$
$\qquad$
$\qquad$

## The Fitness of $\beta$-males

$\qquad$

That fraction, $\boldsymbol{S}$, equals the success rate of $\beta$ males invading harems.

Thus, the fitness of $\beta$ males, $\boldsymbol{W}_{\beta}$, equals,

$$
W_{\beta}=\boldsymbol{s} H_{\alpha}
$$

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$ class of males is difficult to identify.

## Thus,

The apparent relationship between the mating success of $\alpha$ - and $\beta$-males is,

$$
\boldsymbol{H}_{\alpha}>\boldsymbol{s} \boldsymbol{H}_{\alpha}
$$

and therefore,

$$
\boldsymbol{W}_{\alpha}>\boldsymbol{W}_{\beta}
$$

Giving the appearance that $\beta$-males "make the best of a bad job."

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
This approach considers only the average
$\qquad$ fitness of $\alpha$-males that actually mate.

## In Fact,

The average fitness of all $\alpha$-males, $\boldsymbol{W}_{\alpha(\text { all })}$, is equal to R.
$\boldsymbol{R}$ includes the average mate numbers of mating and non-mating $\alpha$ -
 males.

## To Invade a Population,

-The average fitness of a mutant strategy must exceed the average fitness of the conventional strategy.
-That is, the average fitness of $\beta$-males must exceed the
 average fitness of $\alpha$ males.

## We Can Express This Condition As,

$\qquad$

$$
\boldsymbol{W}_{\beta}>\boldsymbol{W}_{\alpha(\mathrm{all})}
$$

Or by substitution,

$$
s H_{\alpha}>R
$$

## By Rearrangement This

$\qquad$ Becomes,

$$
s>R / H_{\alpha}
$$

And if $\boldsymbol{R}=1$, $s>1 / H_{\alpha}$

## Remember that,

$$
p_{0}=1-(1 / H)
$$

Or by rearrangement,

$$
\left(1-p_{0}\right)=1 / H
$$

So if,

$$
s>1 / H_{\alpha}
$$

Then by substitution,

$$
\boldsymbol{s}>\left(1-\boldsymbol{p}_{\boldsymbol{0}}\right)
$$

## Differently Put,

The more females are clumped within the harems of a few $\alpha$-males (i.e., more $\alpha$-males are excluded from mating),
the easier invasion by $\beta$-males becomes.

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

## A Worked Example

Let $\boldsymbol{H}=4$.
If $s>1 / H$
then $s$ need only be $>0.25$ !

That is, satellite males need only mate $25 \%$ as successfully as the average polygynous male!


# Strong Sexual Selection <br> Favors Alternative Mating Strategies 

$\qquad$
$\qquad$
$\qquad$
Unconventional males need only achieve mating success greater than the reciprocal of harem size to invade, and to PERSIST. Therefore...

## A Classic Study

Hyla cinerea by Gerhardt et al. (1987) who recorded the mating success of calling, satellite, and non-calling males over 3 years.


Of the 57 males who mated, 50 were callers and 7 males were satellites, suggesting that the average success of callers was greater than for satellites.


## Equal Fitnesses

$\qquad$
Gerhard et al. (1987) concluded $\qquad$ that the fitnesses of the two male phenotypes were equal because $\qquad$ nearly equal proportions of each population were successful in mating (11-12\%).

$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$
$\qquad$

## Stated Differently,

If $\boldsymbol{p}_{0 \text { calling }}$ equals
$p_{0}=1-(1 / H)$ 0.89 , then the average harem size of calling males, $\boldsymbol{H}_{\text {calling }}$ equals 9.32 (not reported by Gerhardt et al.).


## And If,

$s>1 / H$
Where $\boldsymbol{s}$ represents the success satellites must obtain by stealing mates from calling males, then $\mathrm{s}>1-\boldsymbol{p}_{\text {ocalling }}$ or 0.11 , which is approximately equal to the fraction of the total matings satellite males obtain (7/57 $=0.12$ ).

## "Making the Best of a

 Bad Job"Is a fallacy.
Individuals with fitness less than average, by definition, are selected against.
Persistence within a population is impossible without equality of fitnesses over time.

## Equal Fitness Over Time

The condition that is necessary and sufficient for the persistence of distinct genotypes.


