The evolutionary dynamics of sexual dimorphism

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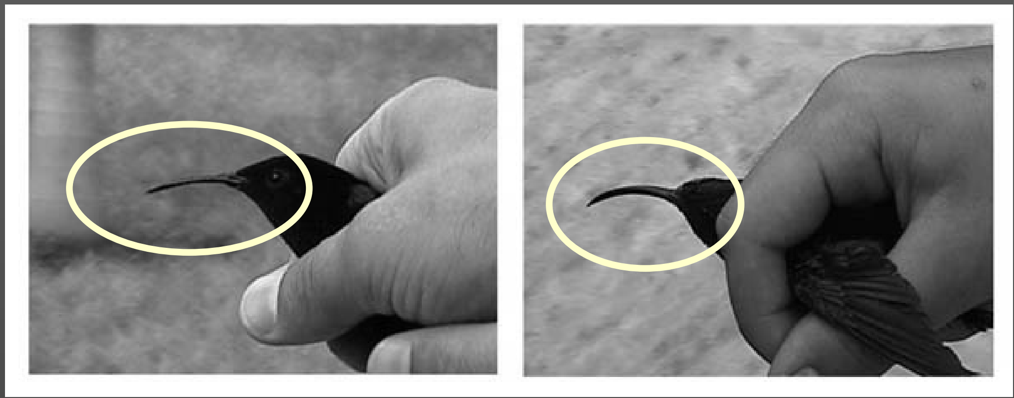
Which type of Ecological Polymorphism?



Purple-throated Carib (Eulampis jugularis)

Heliconia caribaea

Heliconia bihai

Species?

Sexes?

Within-sexes?

Dominance-Recessivity?

2000. Science 289:441-443

Overview

Sexual dimorphism or genetic polymorphism?

Sexual selection and sexual dimorphism

Fish

Character displacement

and

Sexual dimorphism/Speciation

Slatkin (1984)

Character displacement can make species or sexes diverge, and the models look almost the same

Doebeli and Dieckmann (1999, 2003)

The evolution of character displacement can lead to speciation

Speciation and sexual selection

Schluter (2000)

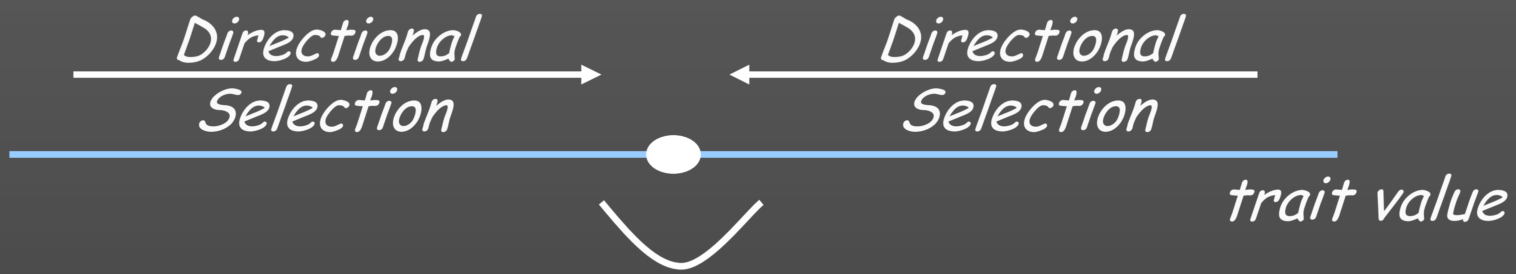
"The addition of sexual selection to theories of speciation represents perhaps the single greatest theoretical advance in the area of speciation in adaptive radiation."

Shine (1989)

Ecological differences between the sexes: cause or consequence of sexual dimorphism?

"Emergence" of Genetic Variation

Evolutionary Branching Point



Disruptive Selection

This can eventually lead to

-sympatric species
- reduced migration
- dominance-recessivity
-linkage groups

Sexual dimorphism and Mate Choice Evolution

If sexual dimorphism can evolve, can we still get evolutionary branching?

When mating is non-random, does this affect the evolution of sexual dimorphism?

When mating is non-random, do we still get evolutionary branching?

Not considered today:

Variation in female preference that acts as a resource distribution for males

Branching in "mating" loci

Male mate choice

Local mating pools

Two Sex Model

Autosomal genes for sex phenotypes
sex phenotypes are a reaction norm
with two states

$$\boldsymbol{N}_{t+1} = \boldsymbol{A}_t . \boldsymbol{N}_t$$

Resident population density

$\boldsymbol{N} = (N_{females}, N_{males})$

$$\boldsymbol{A}_t = \boldsymbol{E}_t . \boldsymbol{M}_t$$

Mating Matrix ***M***

Ecological Feedback ***E***

$\boldsymbol{N}_{t+1} = \boldsymbol{E}_t.\boldsymbol{M}_t.\boldsymbol{N}_t$

Two Sex Model

Mating Process

$$\boldsymbol{M}_t = \frac{r}{4}\begin{pmatrix} m_{1,t} & m_{2,t} \\ m_{1,t} & m_{2,t} \end{pmatrix}$$

Female dominant mating system

$m_1 = c_t$

$m_2 = c_t N_{f,t} / N_{m,t}$

Ecology

$$\boldsymbol{E}_t = \begin{pmatrix} E_{f,t} & 0 \\ 0 & E_{m,t} \end{pmatrix}$$

Two Sex Model

Mutant population dynamics

$$\boldsymbol{N}'_{t+1} = \boldsymbol{A}'(\mathbf{z}', \mathbf{z}).\boldsymbol{N}'_t$$

$$\boldsymbol{E}' = \begin{pmatrix} E(z'_f, \mathbf{z}) & 0 \\ 0 & E(z'_m, \mathbf{z}) \end{pmatrix}$$

$$\boldsymbol{M}' = \frac{r}{4} \begin{pmatrix} c(z'_f, z_m, z_m) & c(z_f, z'_m, z_m)\dfrac{\hat{N}_f(\mathbf{z})}{\hat{N}_m(\mathbf{z})} \\ c(z'_f, z_m, z_m) & c(z_f, z'_m, z_m)\dfrac{\hat{N}_f(\mathbf{z})}{\hat{N}_m(\mathbf{z})} \end{pmatrix}$$

female that chooses

chosen male

background males

Trait vector

$z = (z_f, z_m)$

- *Female traits*
- *Male traits*

- *prime denotes mutant*

Two Sex Model

Invasion Fitness

$$\lambda(\mathbf{z}',\mathbf{z}) = \frac{1}{2}\frac{c(z'_f, z_m, z_m)}{c(z_f, z_m, z_m)}\frac{E(z'_f, \mathbf{z})}{E(z_f, \mathbf{z})} + \frac{1}{2}\frac{c(z_f, z'_m, z_m)}{c(z_f, z_m, z_m)}\frac{E(z'_m, \mathbf{z})}{E(z_m, \mathbf{z})}$$

When mate choice has no cost for females,

one can set invasion fitness to

$$\lambda_{\text{nocost}}(\mathbf{z}',\mathbf{z}) = \frac{1}{2}\frac{E(z'_f, \mathbf{z})}{E(z_f, \mathbf{z})} + \frac{1}{2}\frac{c(z_f, z'_m, z_m)}{c(z_f, z_m, z_m)}\frac{E(z'_m, \mathbf{z})}{E(z_m, \mathbf{z})}$$

Without sexual selection:

$$\lambda_{\text{noss}}(\mathbf{z}',\mathbf{z}) = \frac{1}{2}\frac{E(z'_f, \mathbf{z})}{E(z_f, \mathbf{z})} + \frac{1}{2}\frac{E(z'_m, \mathbf{z})}{E(z_m, \mathbf{z})}$$

Two Sex Model

Canonical equation of evolutionary response

$$\frac{d}{dt}\mathbf{z} = \boldsymbol{M}\beta(\mathbf{z})$$

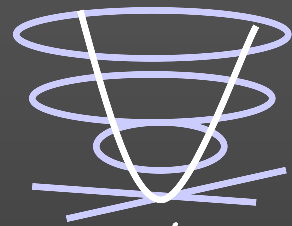
M is the mutational variance-covariance matrix scaled

Invasion Fitness Gradient β

$$\beta(\mathbf{z}) = \nabla'\lambda(\mathbf{z},\mathbf{z}) = \begin{pmatrix} \frac{\partial}{\partial z'_f}\lambda(\mathbf{z}',\mathbf{z})\Big|_{\mathbf{z}'=\mathbf{z}} \\ \frac{\partial}{\partial z'_m}\lambda(\mathbf{z}',\mathbf{z})\Big|_{\mathbf{z}'=\mathbf{z}} \end{pmatrix}$$

Sexes or Species?

- *Potential End Points of Evolution* $\mathbf{z^*}$: $\beta(\mathbf{z}^*) = 0$
- *Invasibility: Eigenvalues of Hessian* $\mathbf{H}(z^*)$
- *Convergence Stability or Reachability: Eigenvalues of Jacobian* $\mathbf{J}(z^*)$



$$\mathbf{J}(z^*) = \mathbf{H}(z^*) + \mathbf{Q}(z^*)$$

$$\mathbf{H}(\mathbf{z}^*) = D_{11}\lambda(\mathbf{z}^*, \mathbf{z}^*)$$

$$\mathbf{Q}(\mathbf{z}^*) = D_{12}\lambda(\mathbf{z}^*, \mathbf{z}^*)$$

Random Mating

evolutionary stops have

$$\frac{\partial}{\partial z'_f} E(z'_f, \mathbf{z})\Big|_{\mathbf{z}'=\mathbf{z}} = 0$$

$$\frac{\partial}{\partial z'_m} E(z'_f, \mathbf{z})\Big|_{\mathbf{z}'=\mathbf{z}} = 0$$

The ecological feedback is maximized

Male and female phenotypes can be equal or different

Random Mating

evolutionary stops with equal phenotypes in females and males have

$$D_1E(z^*,\boldsymbol{z}^*)=0$$

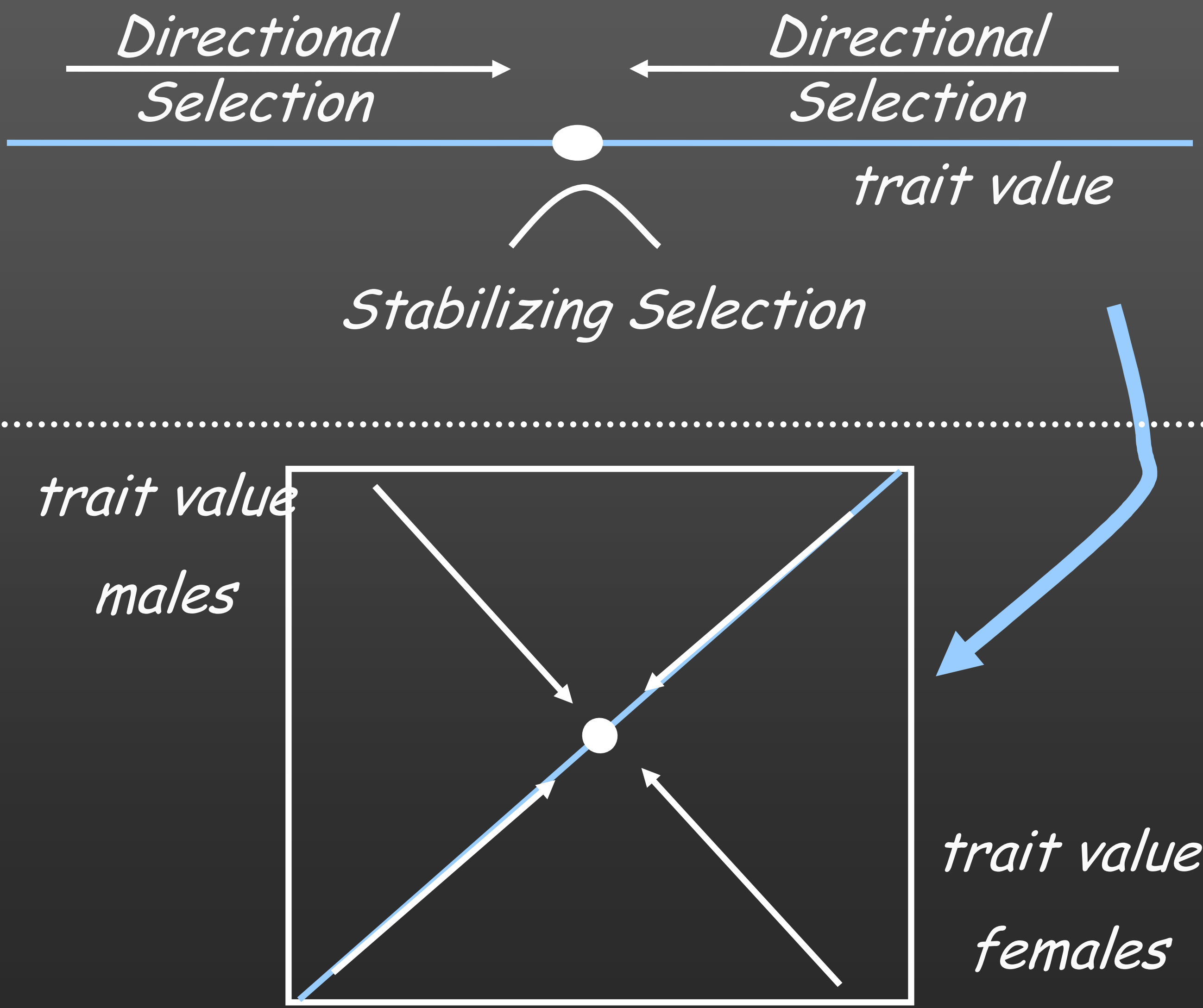
$$D_{11}E(z^*,\boldsymbol{z}^*)=h$$

$$D_{12}E(z^*,\boldsymbol{z}^*)=\begin{pmatrix} q_1 \\ q_2 \end{pmatrix}$$

$$\boldsymbol{H}(\boldsymbol{z}^*)=\frac{1}{2}\begin{pmatrix} h & 0 \\ 0 & h \end{pmatrix}$$

$$\boldsymbol{J}(\boldsymbol{z}^*)=\frac{1}{2}\begin{pmatrix} q_1+h & q_2 \\ q_1 & q_2+h \end{pmatrix}$$

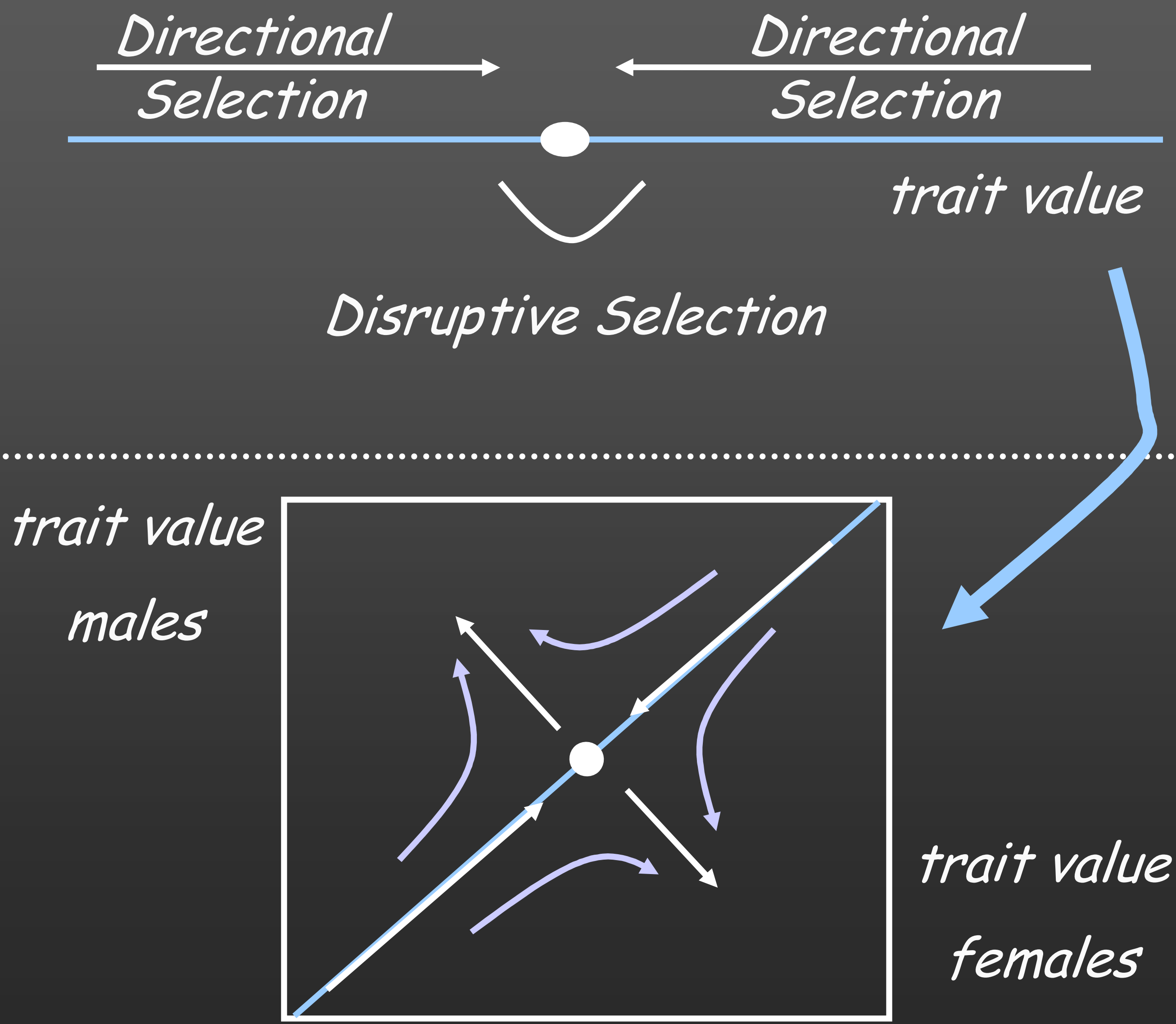
CSS, convergence stable, non-invadable

No sex differentiation	
Sexual dimorphism can evolve	

Evolutionary Branching Points

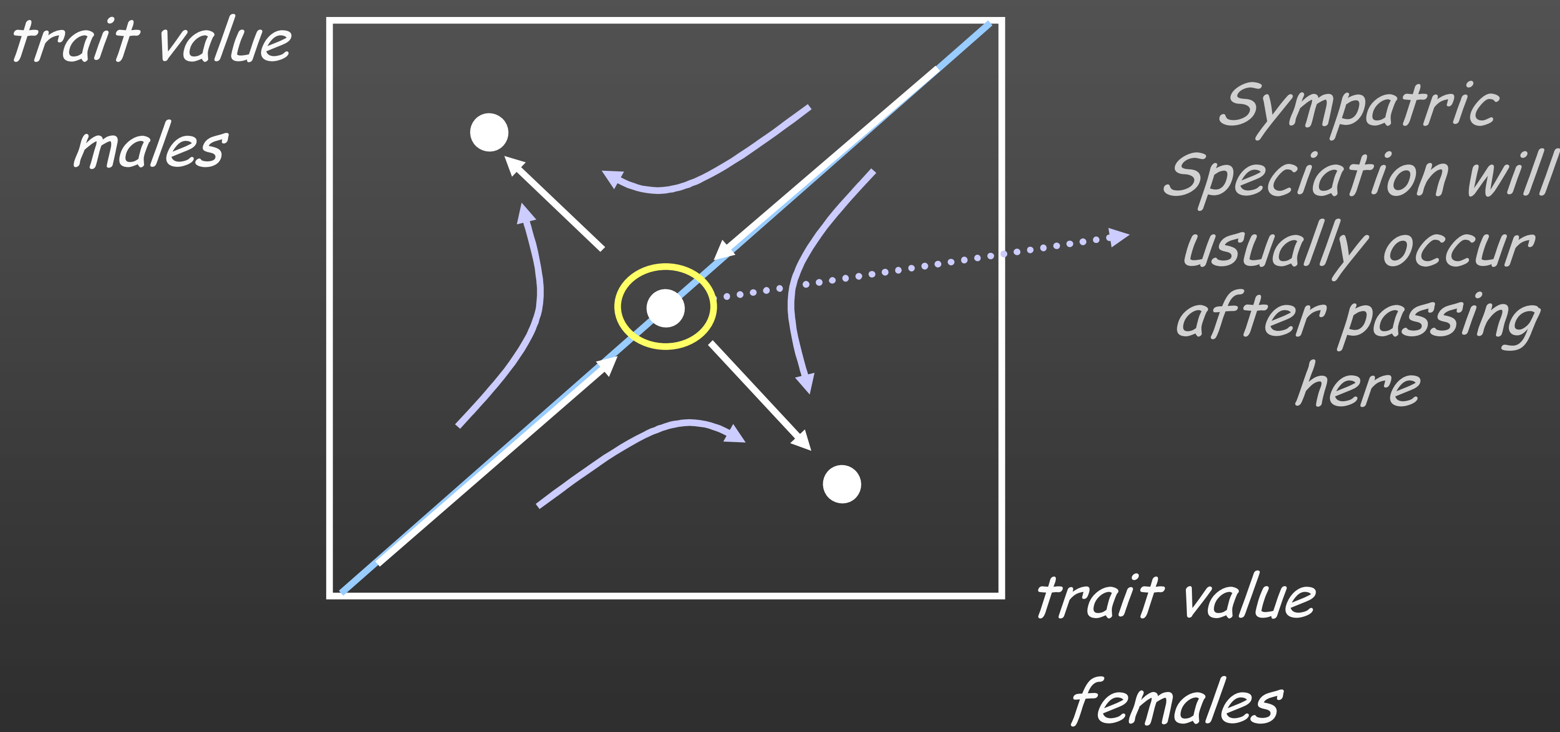
No sex differentiation

Sexual dimorphism can evolve



Dimorphic Sexes or Evolutionary Branching?

Branching Point -> Saddle Point



What can save branching?

" Secondary evolutionary branching"

Asymmetric competition example
Large has an advantage over small

$$E(z'_i, \mathbf{z}, \hat{\mathbf{N}}) = 1 - \sum_{j=f,m} \frac{\alpha(z_i - z_j) N_j}{k(z_i)}$$

$$\alpha(z_i - z_j) = c\left(1 - \frac{1}{1 + \nu e^{-\gamma(z_i - z_j)}}\right)$$

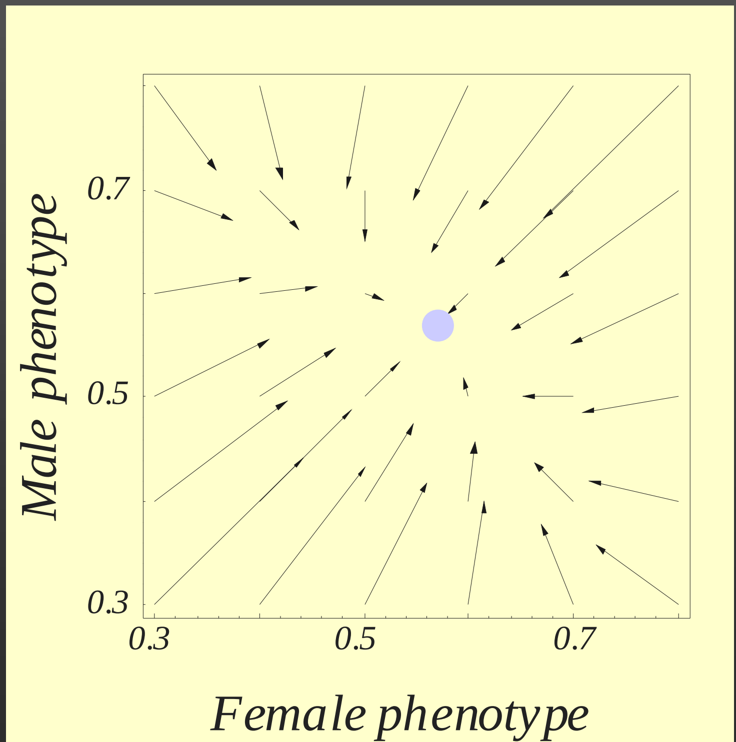
$$k(z_i) = \frac{m}{\sqrt{2\pi\sigma^2}} e^{-\frac{(z_i)^2}{2\sigma^2}}$$

Similar to Kisdi (1999)

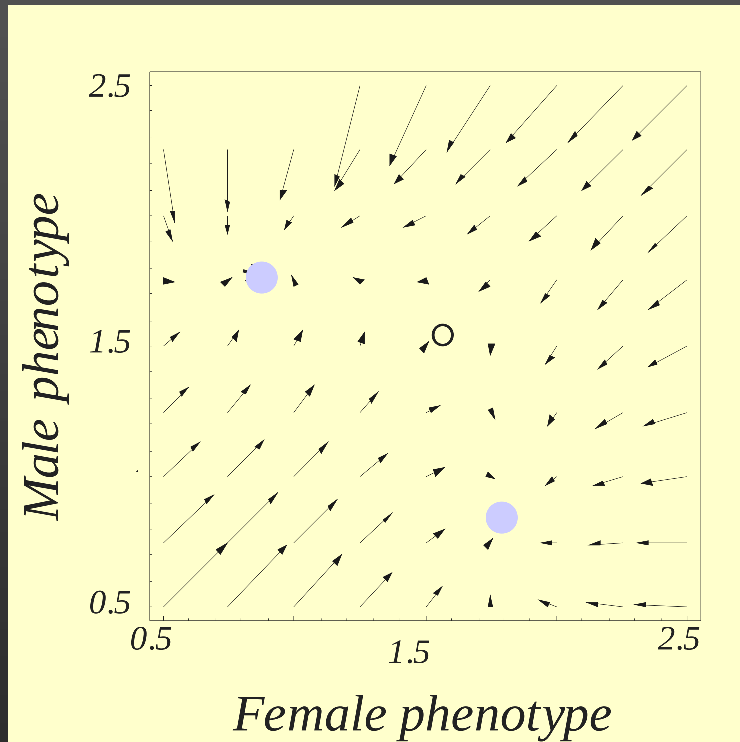
What can save speciation?

Asymmetric competition example

C = 1, *ν* = 1, *γ* = 1, *m* = 1, *r* = 3



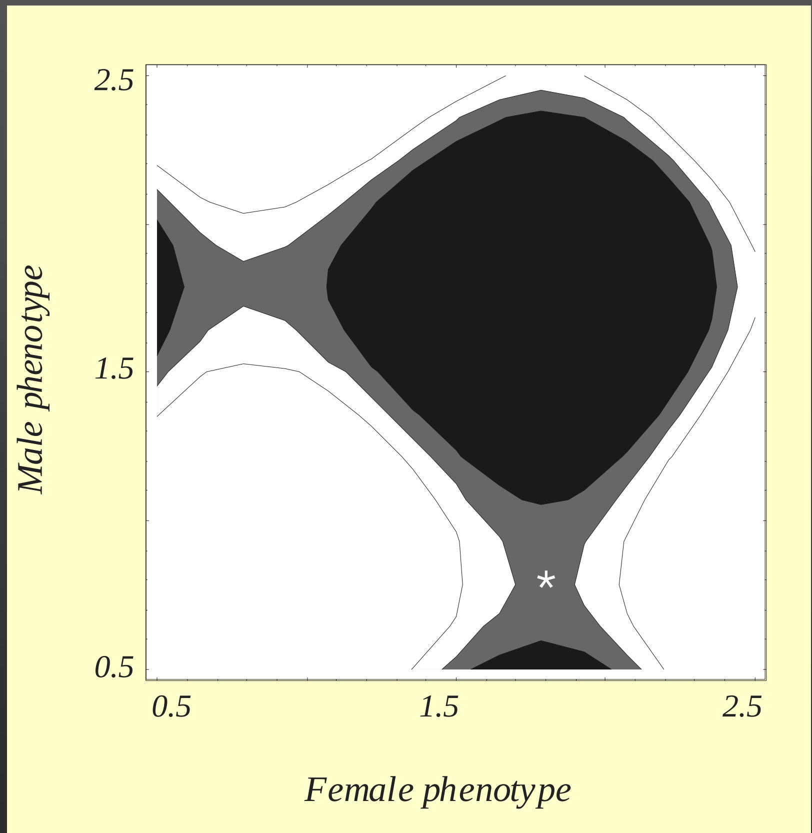
γ = 0.75

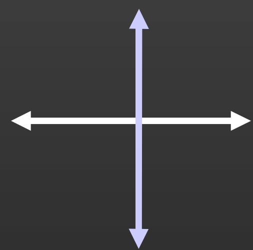


γ = 1.25

What can save branching?

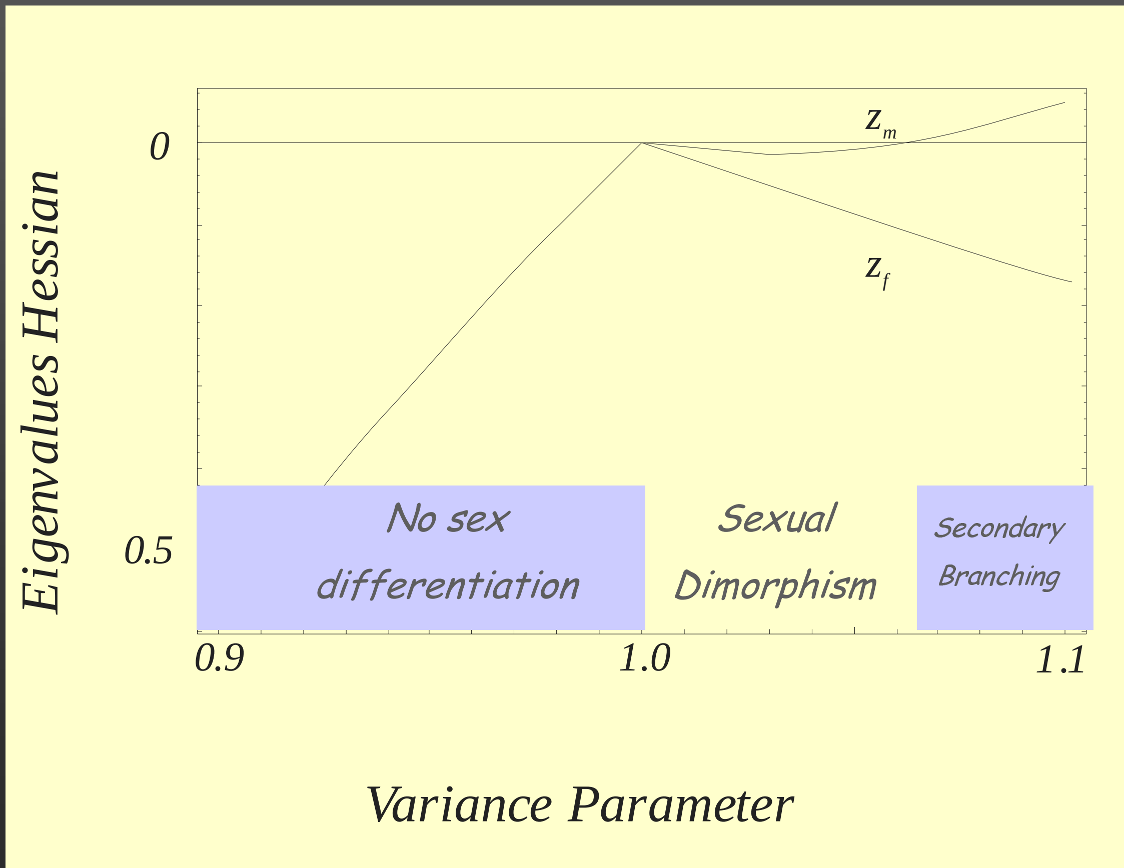
Asymmetric competition example





What can save speciation?

Asymmetric competition example



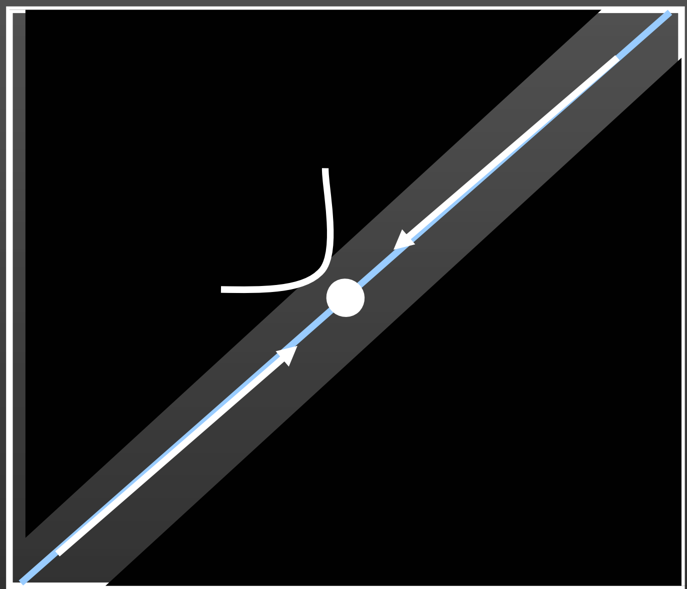
What can save branching?

A matching mechanism in mate choice

Assortative Mating

trait value

females



trait value

males

Branching restored !

Sexual Dimorphism or What?

When allowing for sex differentiation,

the emergence of genes with major effects and the possibility of sympatric speciation

will generally not occur

as in the model without sex differentiation

Speciation can be saved by:

- *Genetic constraints*
- *Secondary evolutionary branching*
- *Assortative mating*

Mate Choice in General?

Mate Choice

potential evolutionary stops z^* have

$$\left.\frac{\partial}{\partial z'_f}\frac{c(z'_f, z_m, z_m)}{c(z_f, z_m, z_m)}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*} + \left.\frac{\partial}{\partial z'_f}\frac{E(z'_f, \mathbf{z})}{E(z_f, \mathbf{z})}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*} = 0$$

$$\left.\frac{\partial}{\partial z'_m}\frac{c(z_f, z'_m, z_m)}{c(z_f, z_m, z_m)}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*} + \left.\frac{\partial}{\partial z'_m}\frac{E(z'_m, \mathbf{z})}{E(z_m, \mathbf{z})}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*} = 0$$

There is a balance between sexual and natural selection

Male and female phenotypes will more often be different at an evolutionary stop

When there is no mating cost for females, mating traits only expressed in females are neutral (Fisherian Runaway)

Mate Choice

Hessians have eigenvalues proportional to

$$\left.\frac{\partial^2}{\partial z'^2_f}\frac{c(z'_f, z_m, z_m)}{c(z_f, z_m, z_m)}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*} - 2\left(\left.\frac{\partial}{\partial z'_f}\frac{E(z'_f, \mathbf{z})}{E(z_f, \mathbf{z})}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*}\right)^2 + \left.\frac{\partial^2}{\partial z'^2_f}\frac{E(z'_f, \mathbf{z})}{E(z_f, \mathbf{z})}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*}$$

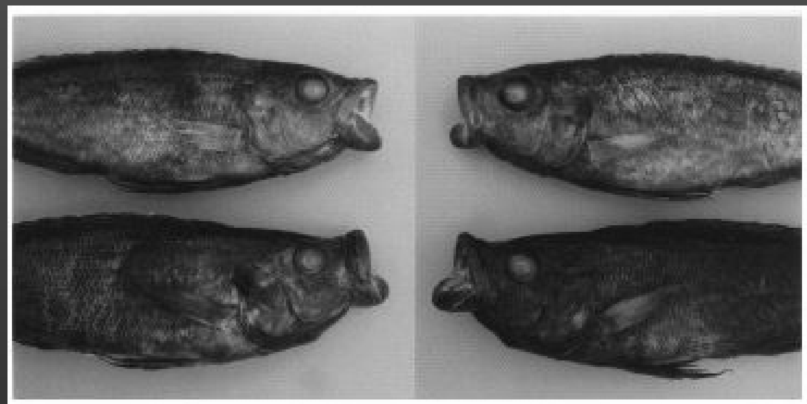
$$\left.\frac{\partial^2}{\partial z'^2_m}\frac{c(z_f, z'_m, z_m)}{c(z_f, z_m, z_m)}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*} - 2\left(\left.\frac{\partial}{\partial z'_m}\frac{E(z'_m, \mathbf{z})}{E(z_m, \mathbf{z})}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*}\right)^2 + \left.\frac{\partial^2}{\partial z'^2_m}\frac{E(z'_m, \mathbf{z})}{E(z_m, \mathbf{z})}\right|_{\mathbf{z}'=\mathbf{z}=\mathbf{z}^*}$$

If c is concave, the pattern of invasibility is expected to tend more towards non-invasibility

-> the likelihood of (secondary) branching should often be reduced

The Evolutionary Ecology of Dominance - Recessivity

- *Industrial melanism in the peppered moth (Haldane 1956)*
- *Batesian mimicry in butterflies (Clarke and Sheppard, 1960)*
- *wing dimorphism in insects (Roff and Fairbarn 1994)*
- *handedness in scale-eating cichlid fish (Hori 1993)*



R L

Perissodus & Handedness

Fitness Proxy: relative predation success

Predation succes =

P[attacking left]* ripping success left* Rarity advantage left

+

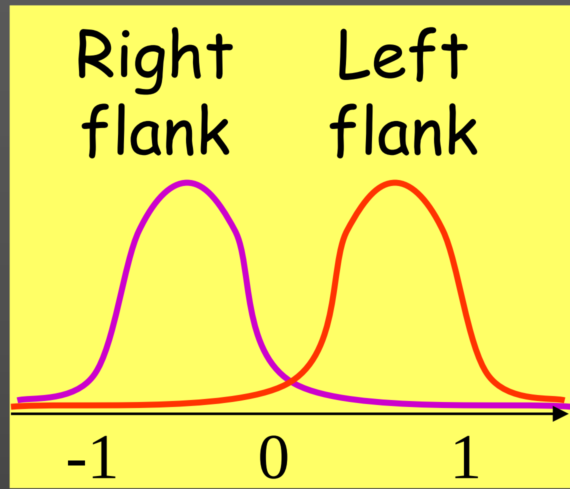
P[attacking right]* ripping success right * Rarity advantage right

Perissodus & Handedness

Ripping Success

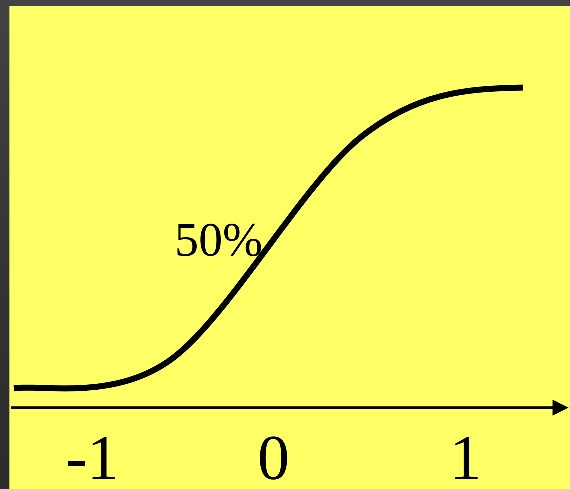
Gaussian with mean at

Orientation -0.5 (RF) or 0.5 (LF)



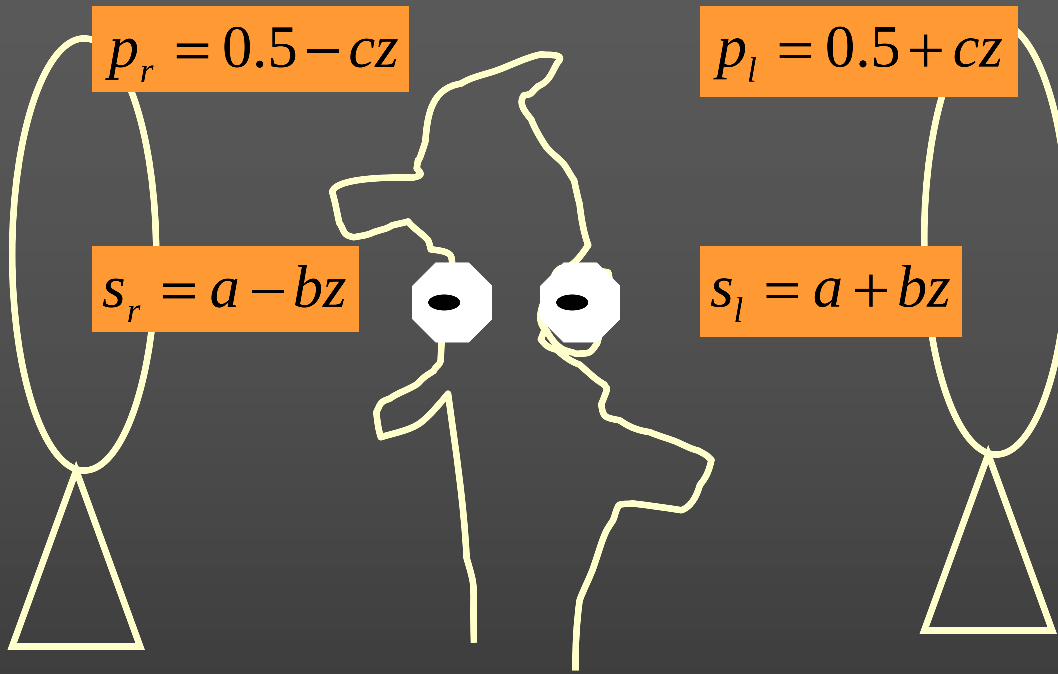
P[Attacking left]

$$\frac{\exp(orientation)}{1+\exp(orientation)}$$



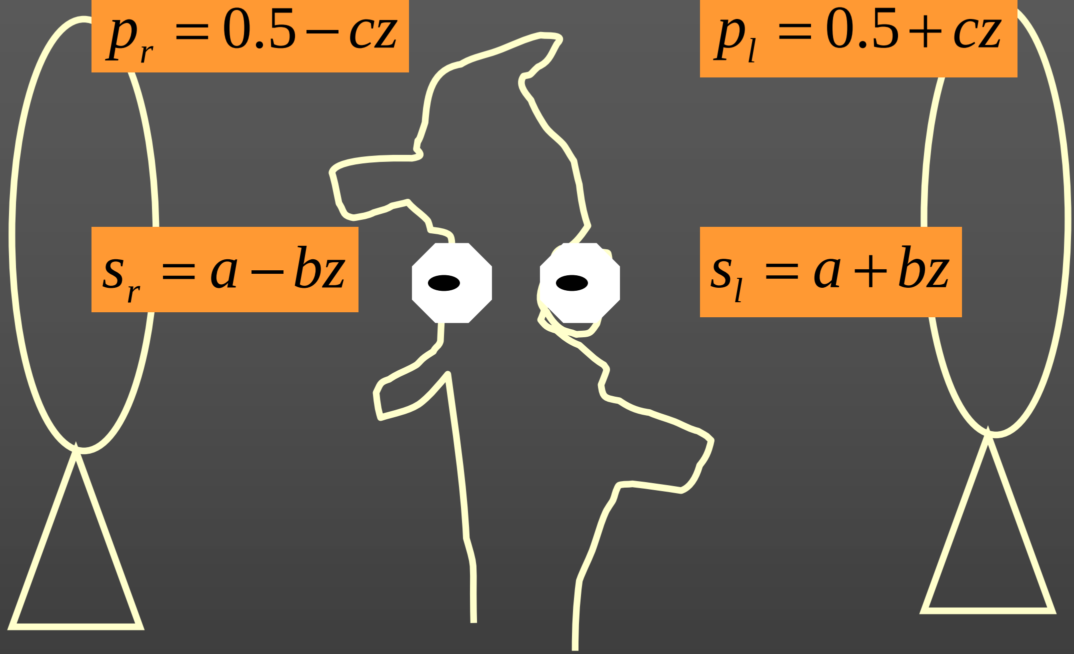
Left Beak Orientation Right

Perissodus & Handedness



z Beak Orientation $z \in [-1, 1]$,
>> is more towards right

Perissodus & Handedness



$$p_r = 0.5 - cz$$

$$p_l = 0.5 + cz$$

$$s_r = a - bz$$

$$s_l = a + bz$$

$$\lambda(z', z) = \frac{p_l(z')s_l(z')p_r(z) + p_r(z')s_r(z')p_l(z)}{p_l(z)s_l(z)p_r(z) + p_r(z)s_r(z)p_l(z)}$$

$$h = \frac{2bc}{a}$$

$$j = h + q = \frac{b}{a} - c$$