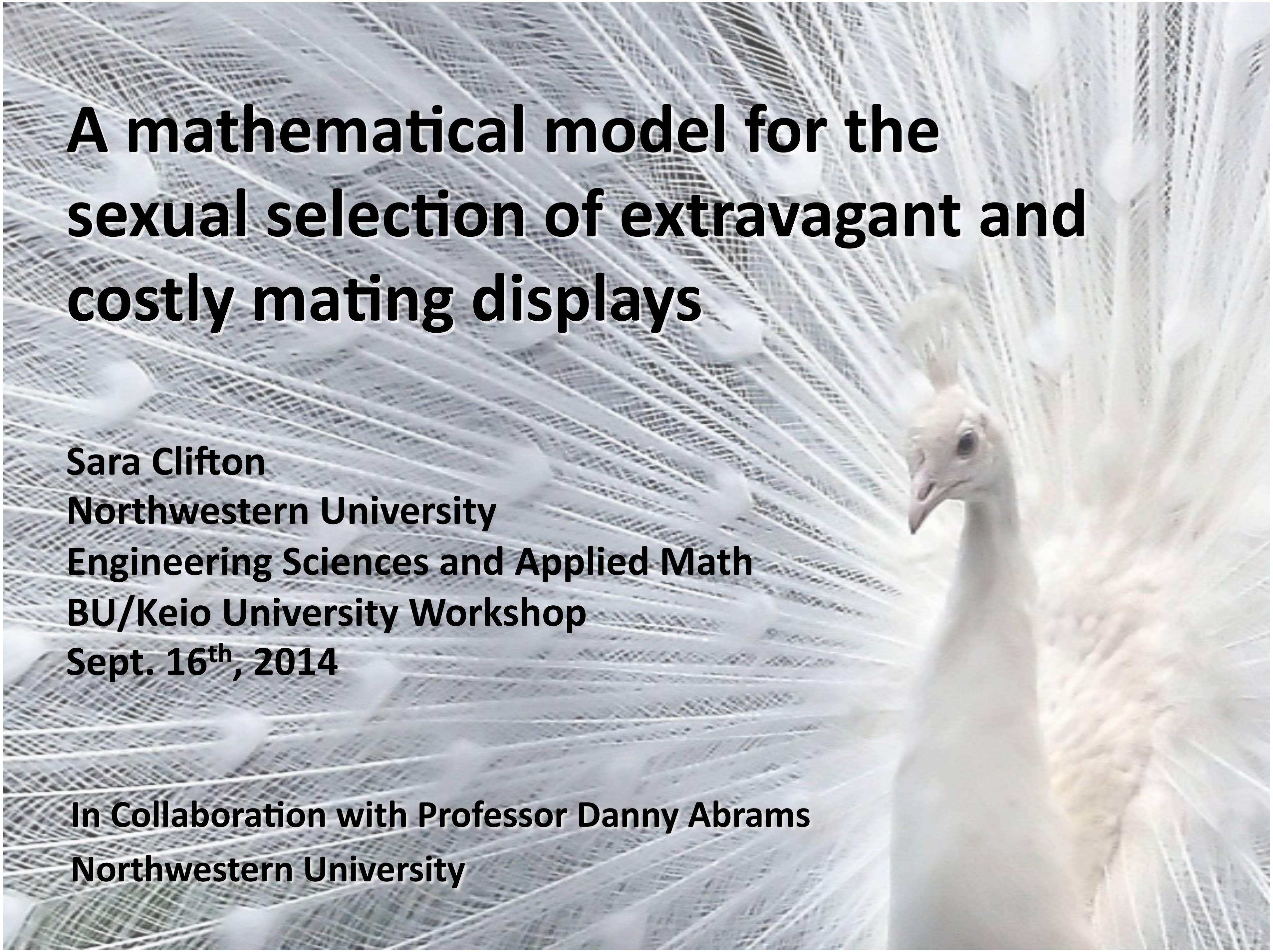


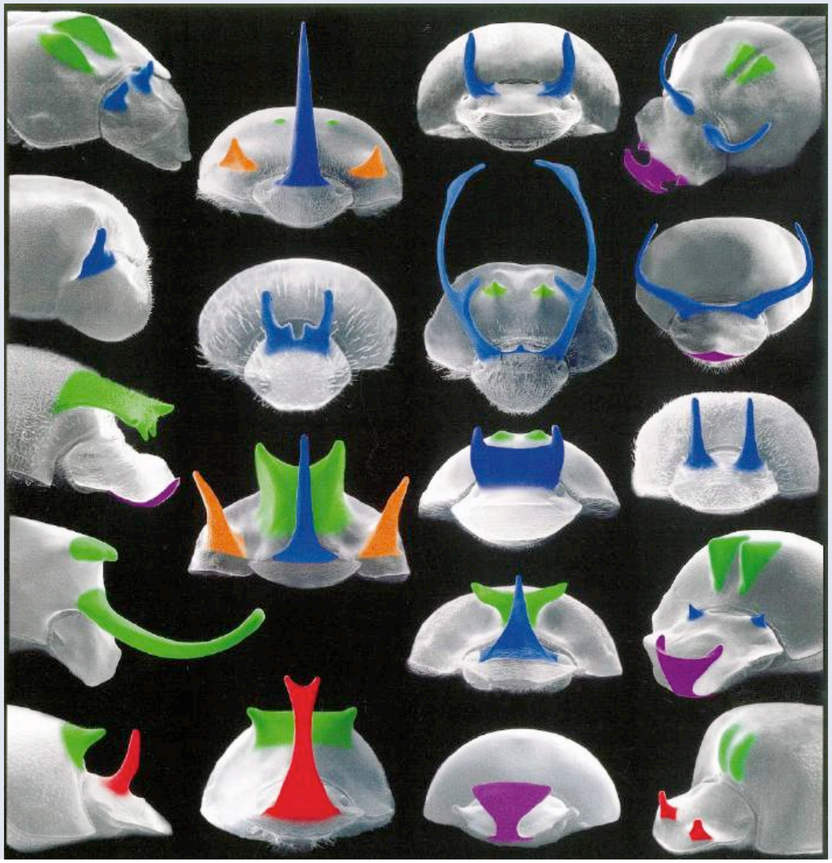
A mathematical model for the sexual selection of extravagant and costly mating displays

Sara Clifton
Northwestern University
Engineering Sciences and Applied Math
BU/Keio University Workshop
Sept. 16th, 2014

In Collaboration with Professor Danny Abrams
Northwestern University

High cost of sex appeal

- Requires extra resources (Emlen 1999)



High cost of sex appeal

- Cumbersome

High cost of sex appeal

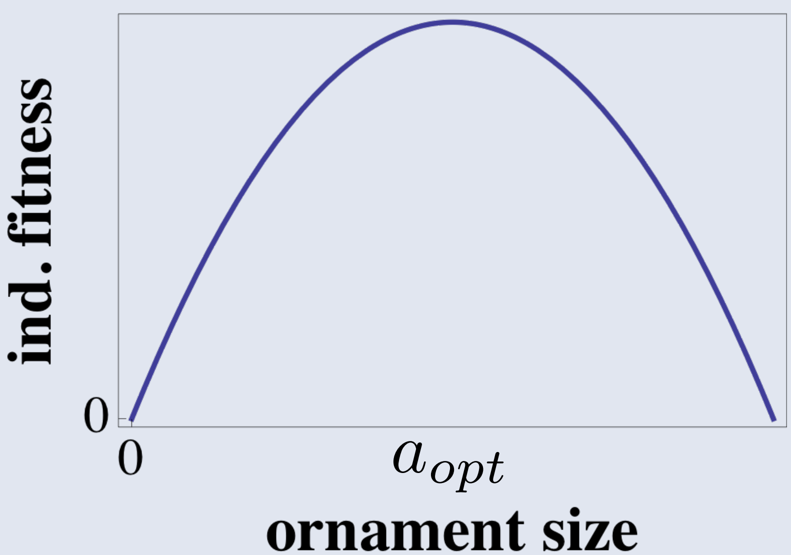
- Dangerous

Handicap Principle

- Handicapping ornaments an honest signal of high quality (Zahavi 1975)
  - Parasite resistance (Hamilton, Zuk 1982)
  - Testosterone levels (Ditchkoff et al. 2001)
  - Antioxidant production (Wenzel et al. 2012)

Model

- Assume each animal has an intrinsic health h_i
- Assume intrinsic cost/benefit of ornamentation changes individual fitness of animal:



$$\varphi_i^{(ind)} = a_i(2a_{opt} - a_i)$$

Advertising size

Optimal advertising size as a function of h_i

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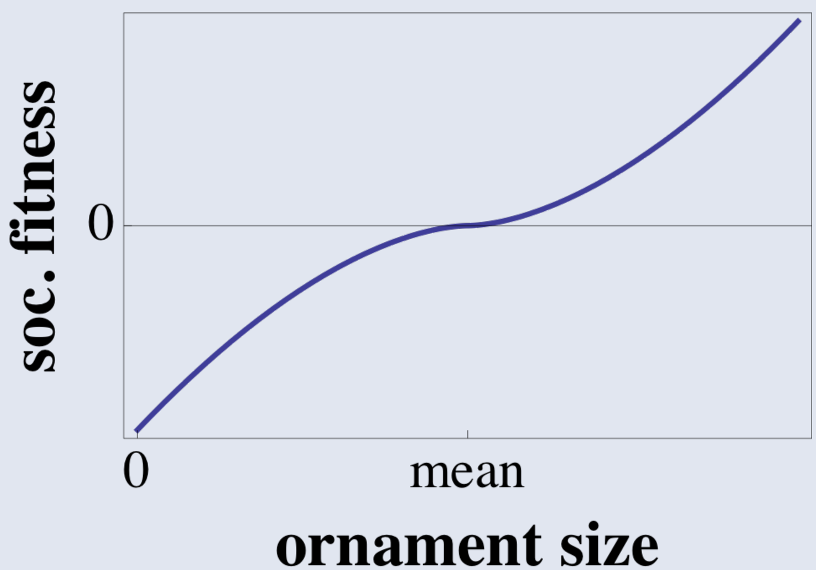
Model

- Assume a social benefit of larger-than-average ornaments:

$$\varphi_i^{(soc)} = \mathrm{sgn}\,(a_i - \bar{a})|a_i - \bar{a}|^{\gamma}$$



Ensures monotonicity

Sensitivity to deviations from the population mean

Model

- Incorporate social and individual effects into a total fitness:

$$\varphi_i = s\,\varphi_i^{(soc)} + (1-s)\,\varphi_i^{(ind)}, \quad 0 \le s \le 1$$

Tunes relative importance of social effects

Model

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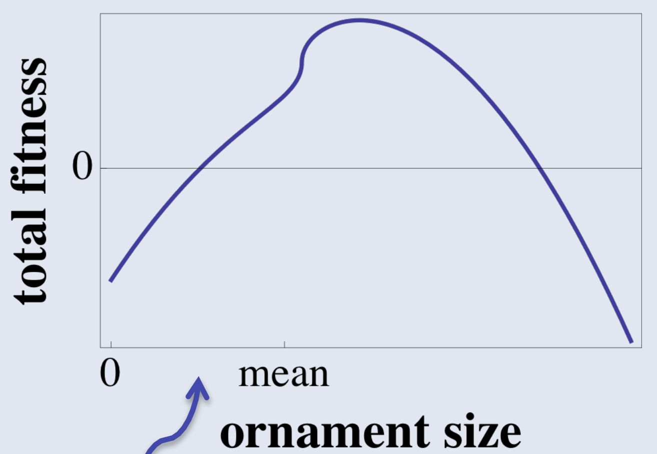
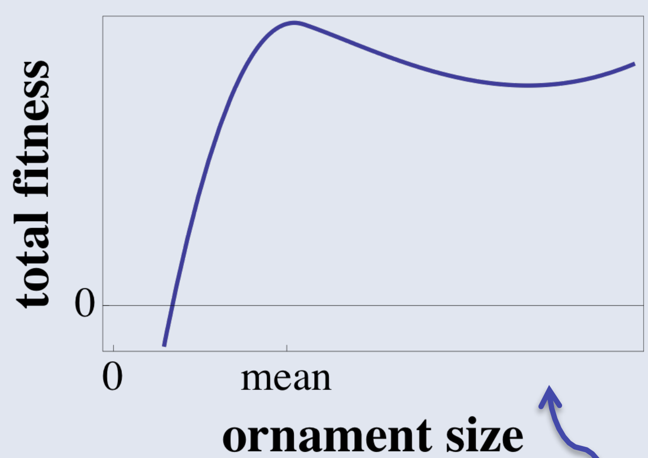
$$\varphi_i = s\,\varphi_i^{(soc)} + (1-s)\,\varphi_i^{(ind)}, \quad 0 \le s \le 1$$

Tunes relative importance of social effects



Small social sensitivity γ



Large social sensitivity γ

Model

- Create a dynamical system where equilibria correspond to fitness extrema:

$$\frac{\mathrm{d}a_i}{\mathrm{d}t} = c\frac{\partial \varphi_i}{\partial a_i}$$

Time scaling constant

Model

- Create a dynamical system where equilibria correspond to fitness extrema:

$$\frac{\mathrm{d}a_i}{\mathrm{d}t} = c\frac{\partial \varphi_i}{\partial a_i}$$

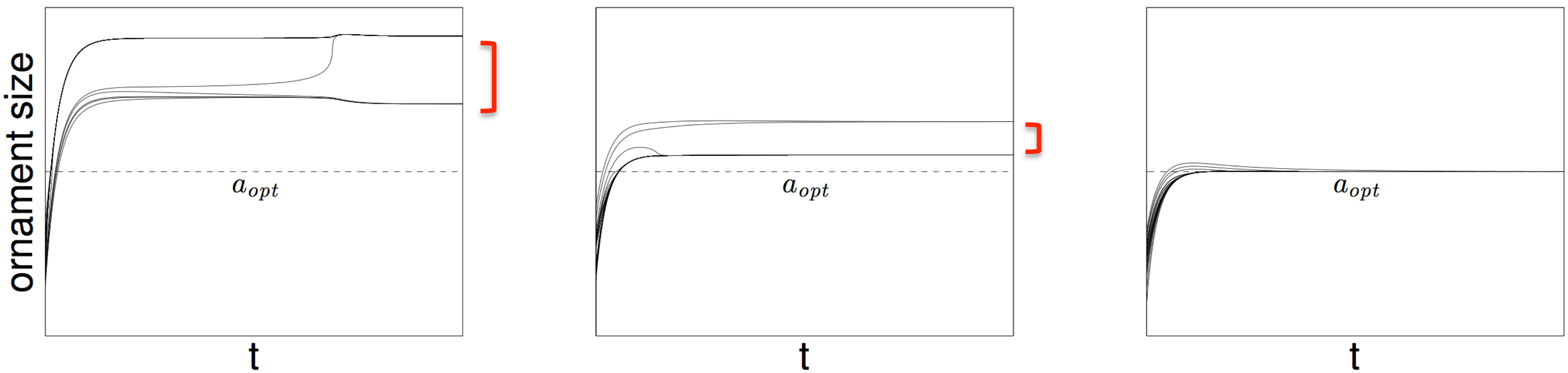
Time scaling constant

$$\frac{\mathrm{d}a_i}{\mathrm{d}t} = c\Big[s\,\gamma\Big(1-\frac{1}{N}\Big)|a_i-\bar{a}|^{\gamma-1} + 2\,(1-s)(a_{opt}-a_i)\Big]$$

Number of individuals

Preliminary Numerical Results

low social sensitivity ⟷ high social sensitivity



(a) $\gamma = 1/2$ (b) $\gamma = 3/2$ (c) $\gamma = 2$

Investigate uniform fixed point

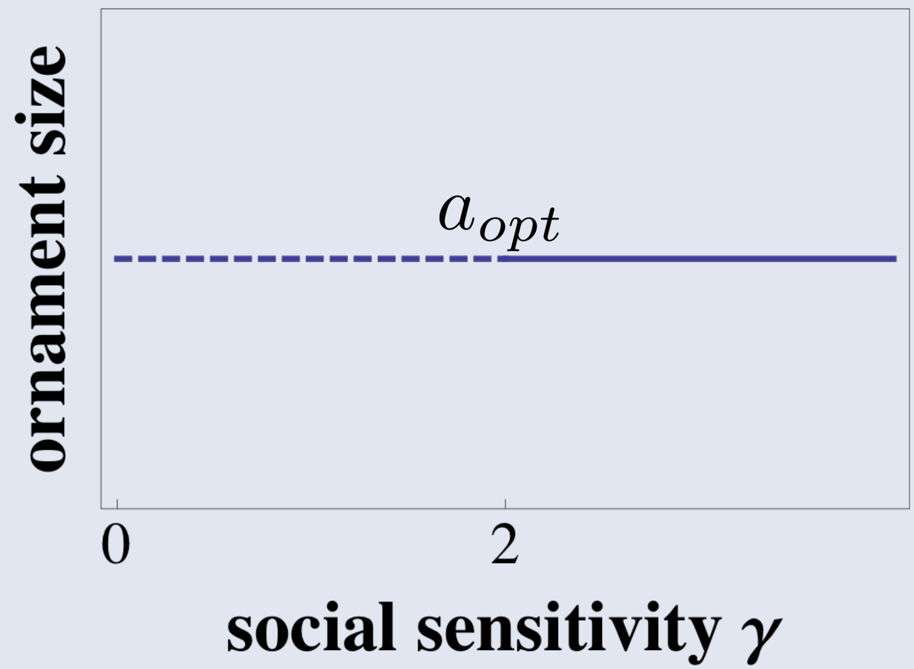
- Reduce system to one equation (taking $a_i = a$)

$$\frac{\mathrm{d}a}{\mathrm{d}t} = c\Big[2\,(1-s)(a_{opt}-a)\Big]$$

- Fixed point is $a = a_{opt}$
- Look at linear stability of fixed point within $a_i = a$ manifold

Uniform fixed point

- Unstable for $\gamma < 2$; stable for $\gamma > 2$
- Bifurcation at $\gamma = 2$ due to quadratic individual fitness



Investigate two niche fixed point

- Consider two groups, with ornament sizes a_1, a_2 and fraction x in group 1

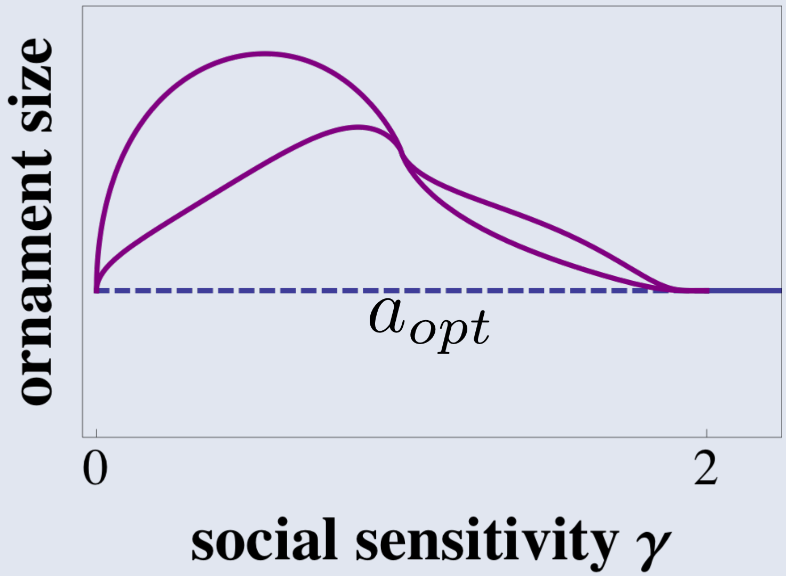
- Reduce to two niche system

$$\frac{\mathrm{d}a_1}{\mathrm{d}t} = \cdots, \quad \frac{\mathrm{d}a_2}{\mathrm{d}t} = \cdots$$

- System has one fixed point, a function of x and model parameters

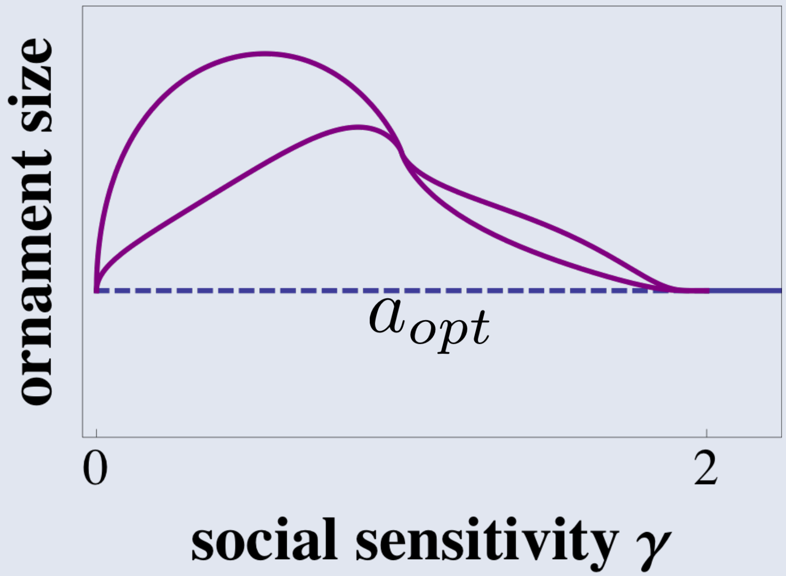
Two niche fixed point

- Within two niche manifold, fixed point is linearly stable for $\gamma < 2$ *for all* fractions x



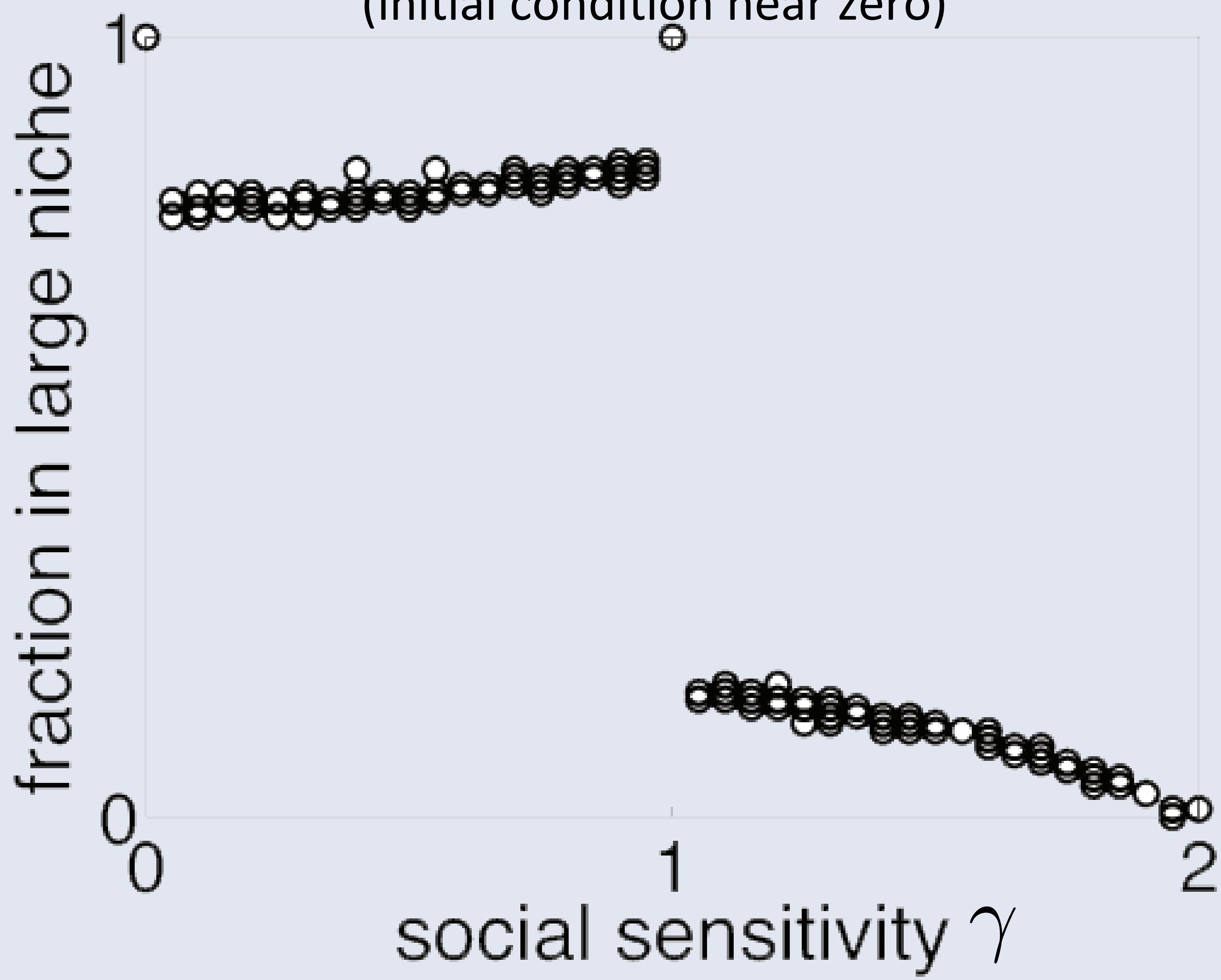
Two niche fixed point

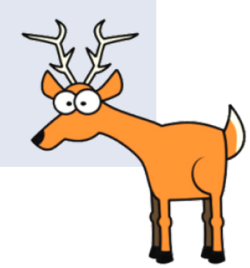
- Within two niche manifold, fixed point is linearly stable for $\gamma < 2$ *for all* fractions x
- Problem: Numerics show only *certain ranges* of x are stable



Numerical steady states

(initial condition near zero)





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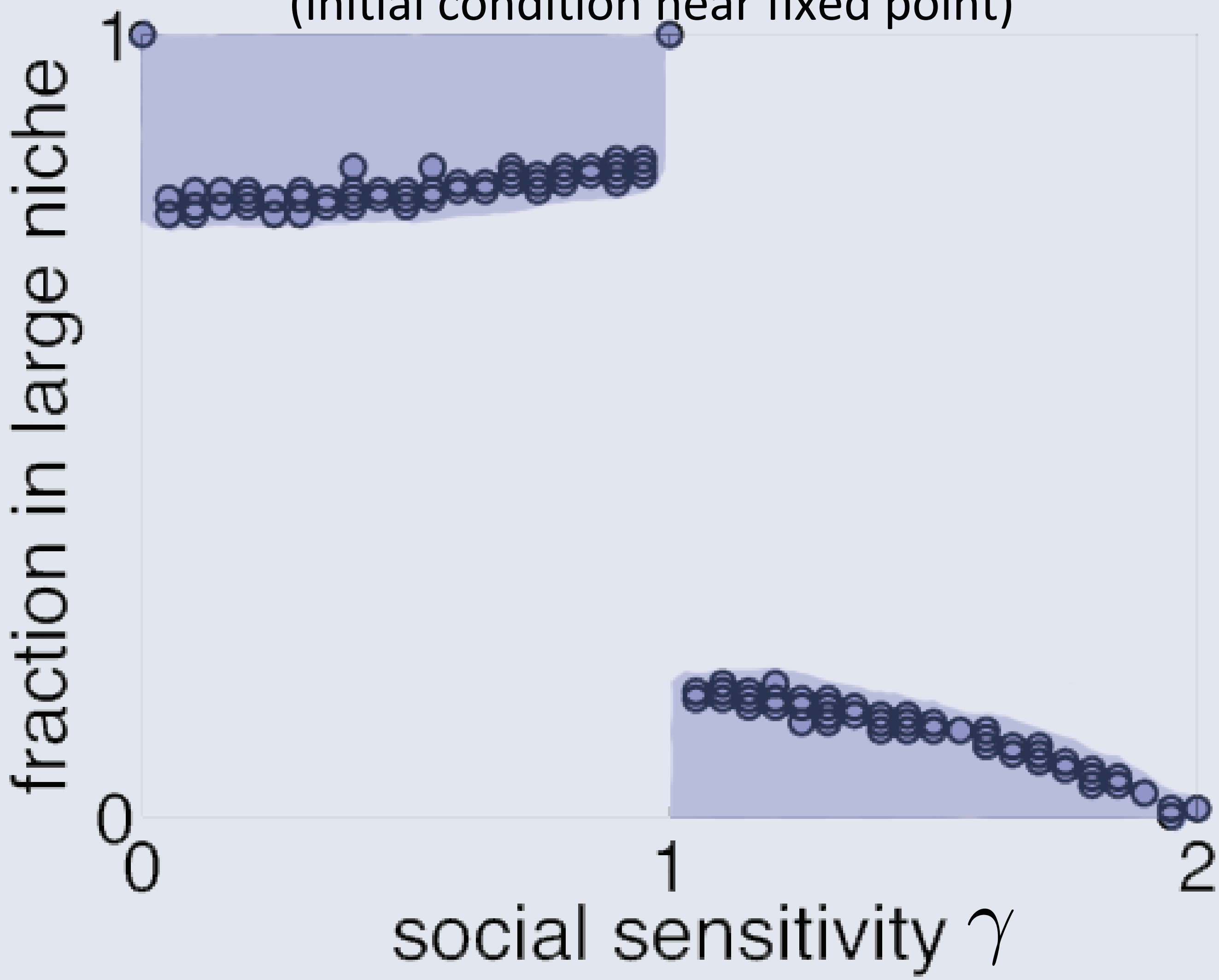
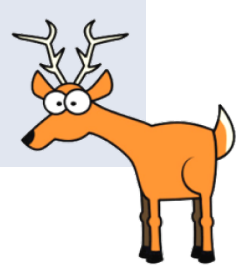
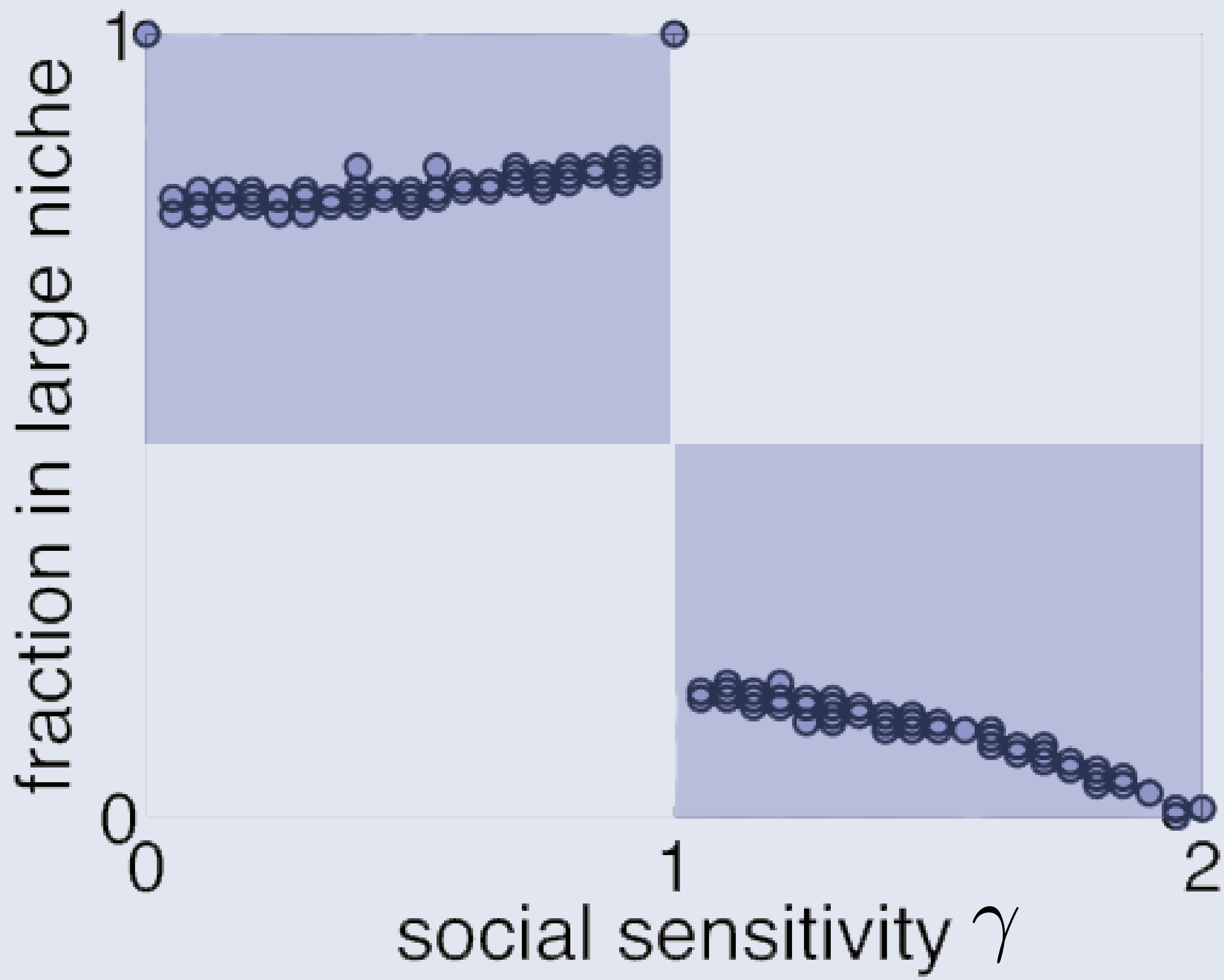
Numerical steady states

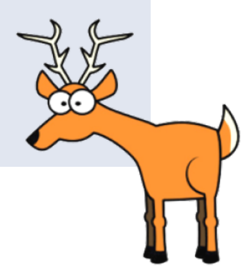
(initial condition near fixed point)





Expected stable steady states





Form continuum model

- Go from microscopic to macroscopic view:

$$\left.\begin{aligned} \frac{\mathrm{d}a_1}{\mathrm{d}t} &= \cdots \\ \frac{\mathrm{d}a_2}{\mathrm{d}t} &= \cdots \\ &\vdots \\ \frac{\mathrm{d}a_N}{\mathrm{d}t} &= \cdots \end{aligned}\right\} N \to \infty \qquad \frac{\partial p}{\partial t} = \cdots$$

System of N ordinary DEs becomes one partial DE for a *distribution* of ornament sizes $p(a,t)$

Continuum model

- Distribution satisfies continuity equation:

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial a}\left(p\,\frac{\mathrm{d}a}{\mathrm{d}t}\right)$$

Continuum model

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Continuum model

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$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial a}\left(p\,\frac{\mathrm{d}a}{\mathrm{d}t}\right)$$

where

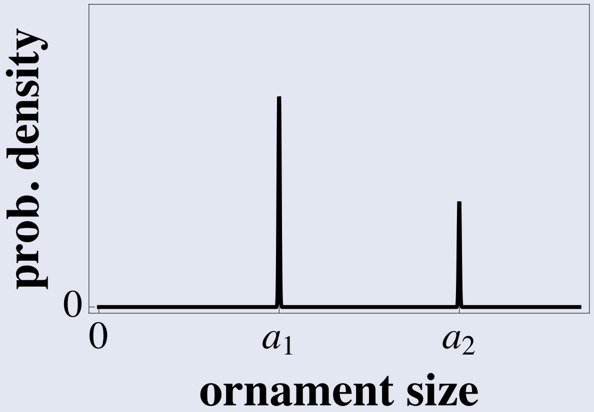
$$\frac{\mathrm{d}a}{\mathrm{d}t} = c\left[s\gamma|a-\bar{a}|^{\gamma-1} + 2(1-s)(a_{opt}-a)\right]$$

$$\bar{a}(t) = \int_{-\infty}^{\infty} a(t)\,p(a,t)\,\mathrm{d}a$$

Investigate two niche steady state

- Two niche steady state is

$$p = x\,\delta(a-a_1) + (1-x)\,\delta(a-a_2)$$



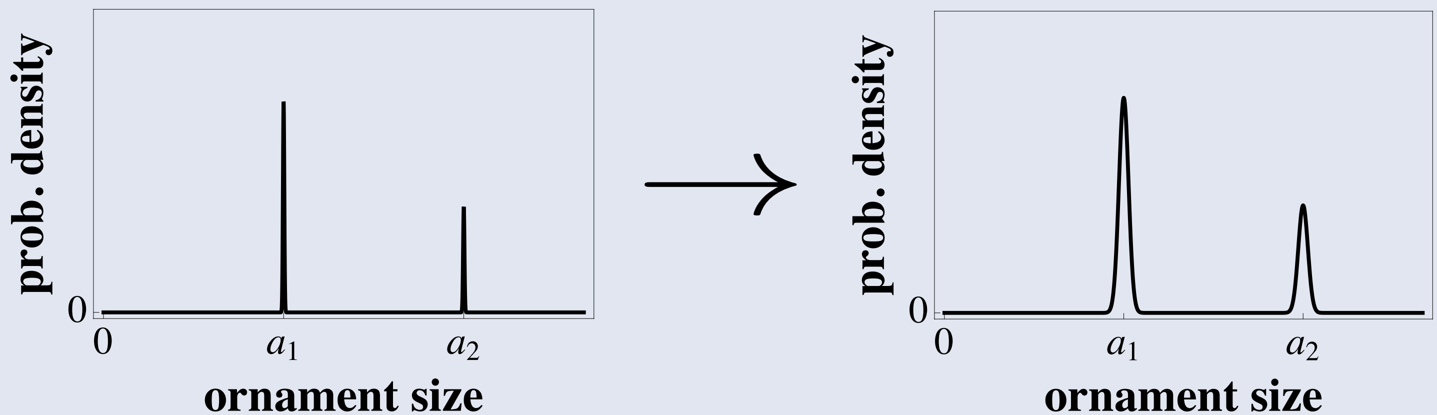
Investigate two niche steady state

- Two niche steady state is

$$p = x\,\delta(a - a_1) + (1-x)\,\delta(a - a_2)$$

- "Perturb" delta functions into Gaussians $(\sigma(t) << 1)$

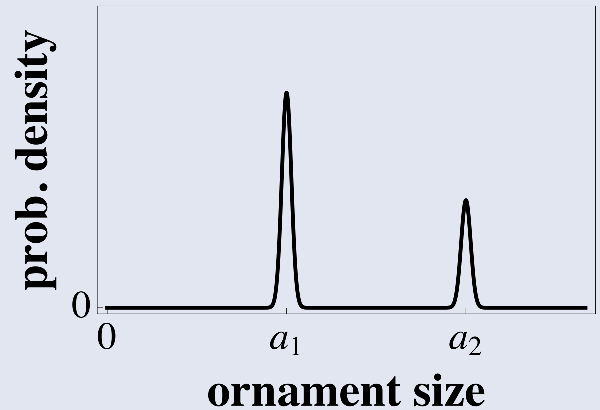
$$p = x\,\mathcal{N}\left[a_1, \sigma_1(t)^2\right] + (1-x)\,\mathcal{N}\left[a_2, \sigma_2(t)^2\right]$$



Investigate two niche steady state

- Plug this into continuity equation, solve for dynamics of σ_1, σ_2 near the fixed points a_1, a_2

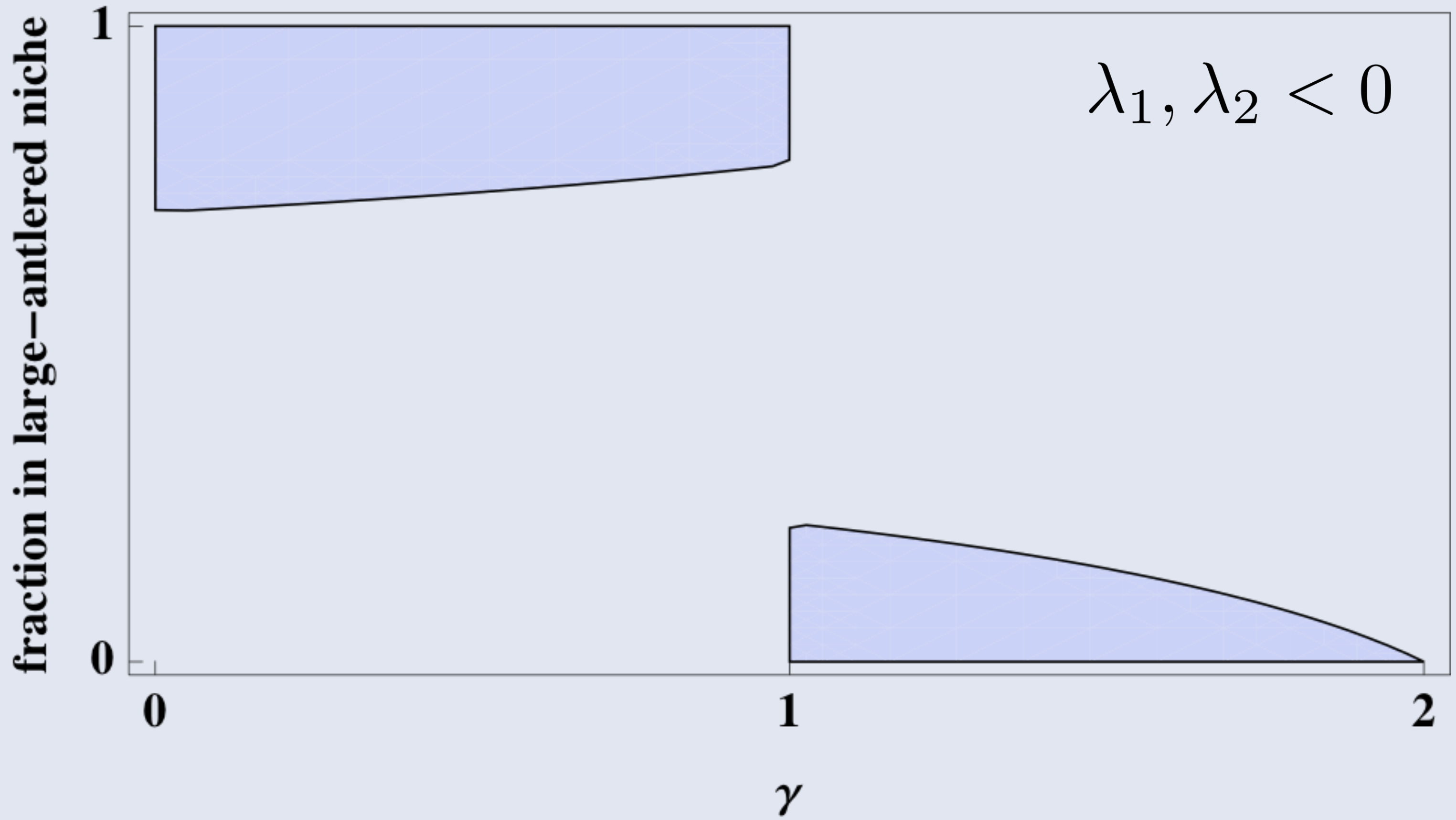
$$\frac{\mathrm{d}\sigma_1}{\mathrm{d}t} = \lambda_1\sigma_1 + \mathcal{O}(\sigma_1^3)$$
$$\frac{\mathrm{d}\sigma_2}{\mathrm{d}t} = \lambda_2\sigma_2 + \mathcal{O}(\sigma_2^3)$$



- Two niche fixed point is linearly stable when

$$\lambda_1, \lambda_2 < 0$$

Two niche steady state stable region



(social sensitivity)

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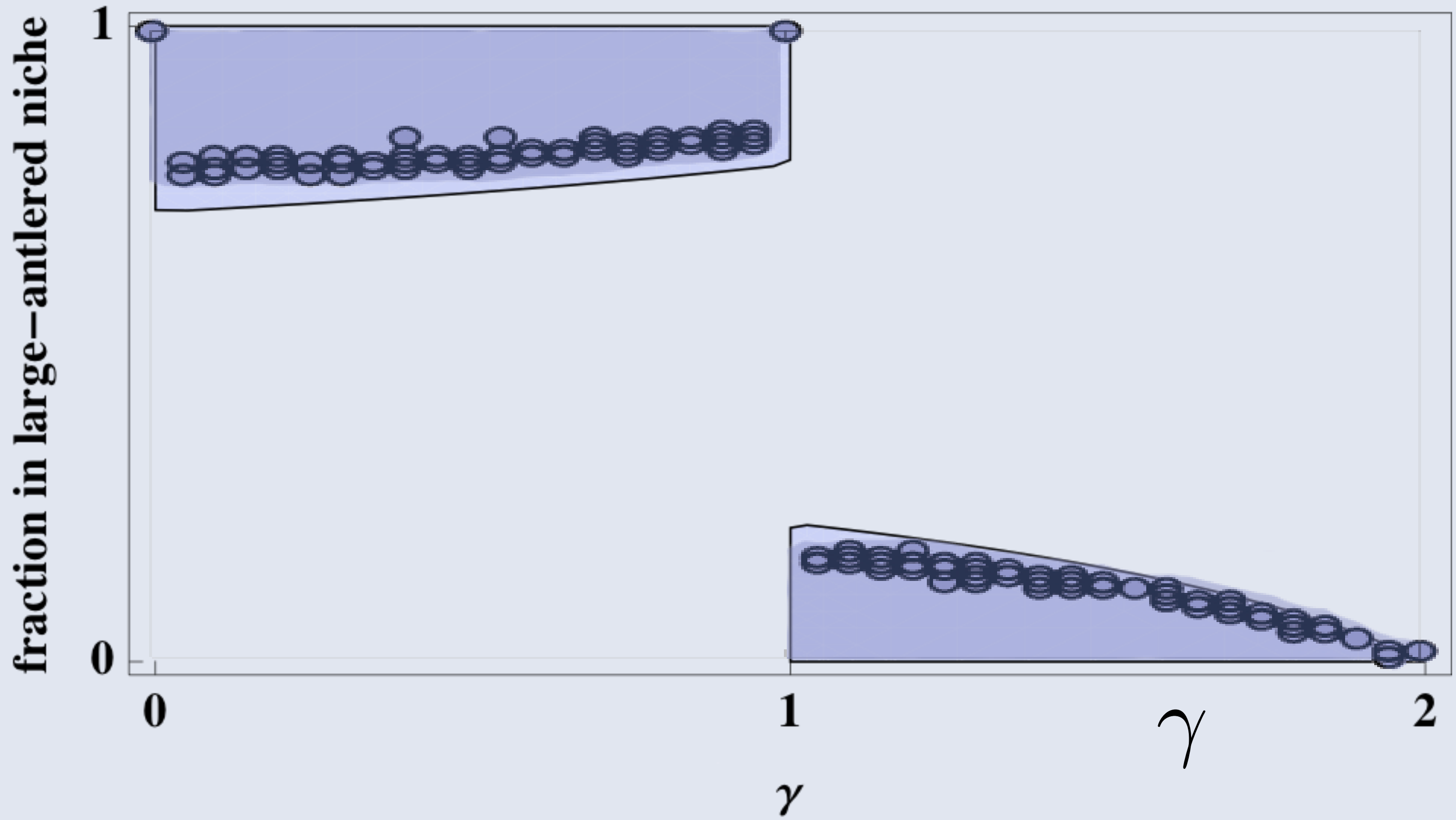
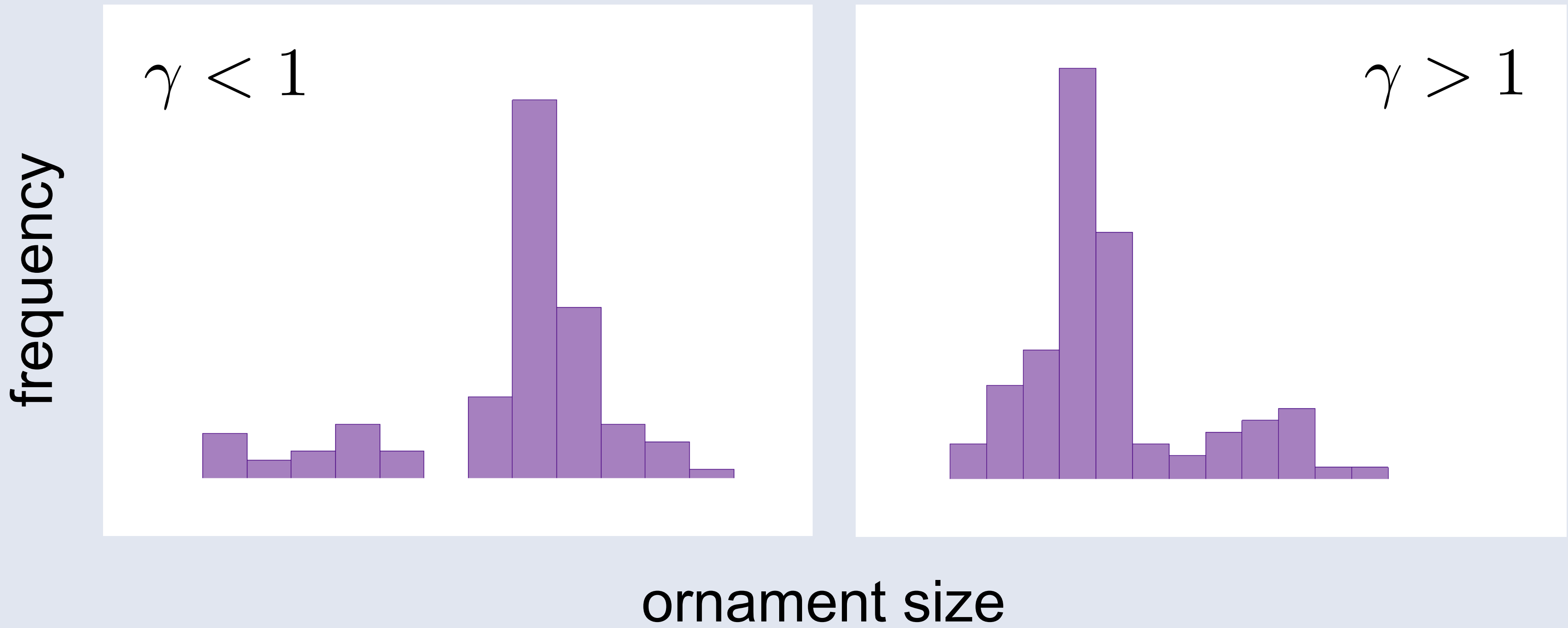
Recall numerical stable region



(social sensitivity)

Non-uniform health

- Add variation in animal health (affects optimal ornament size)
- Sample numerical results:



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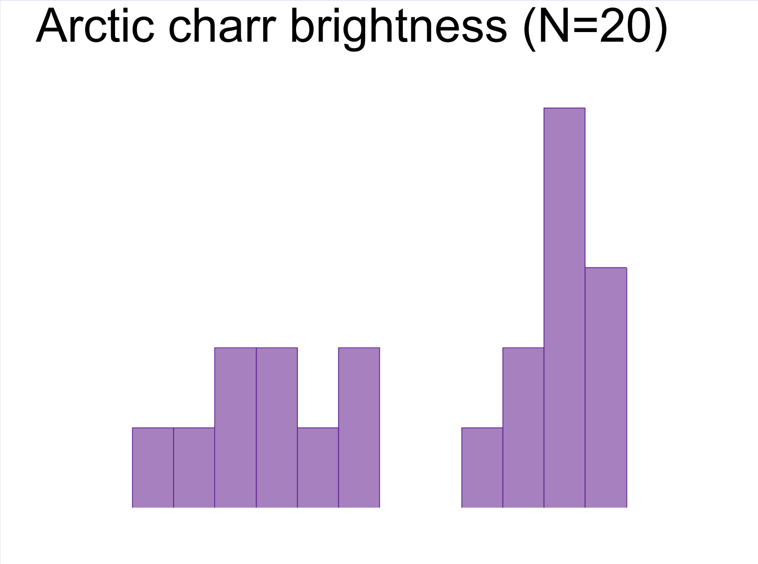
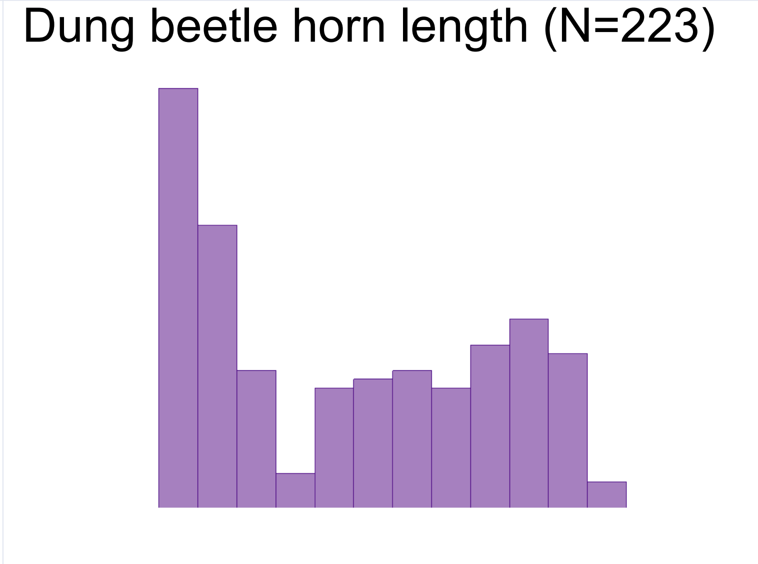
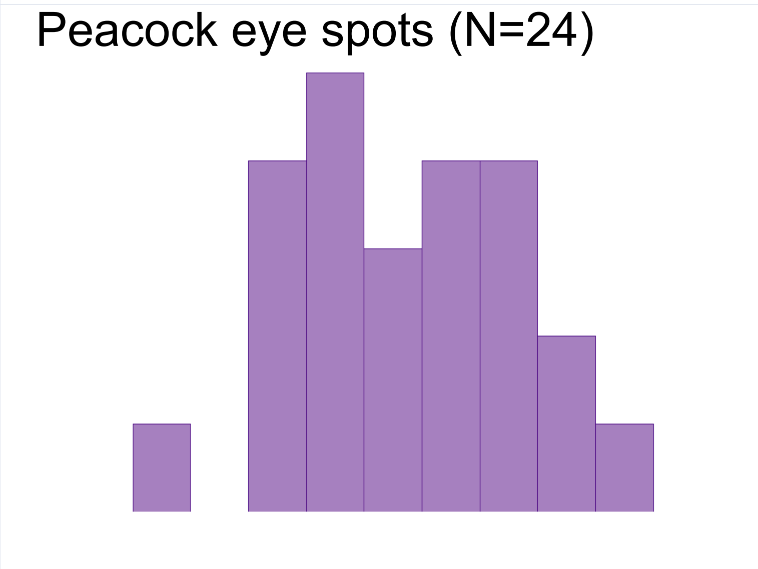
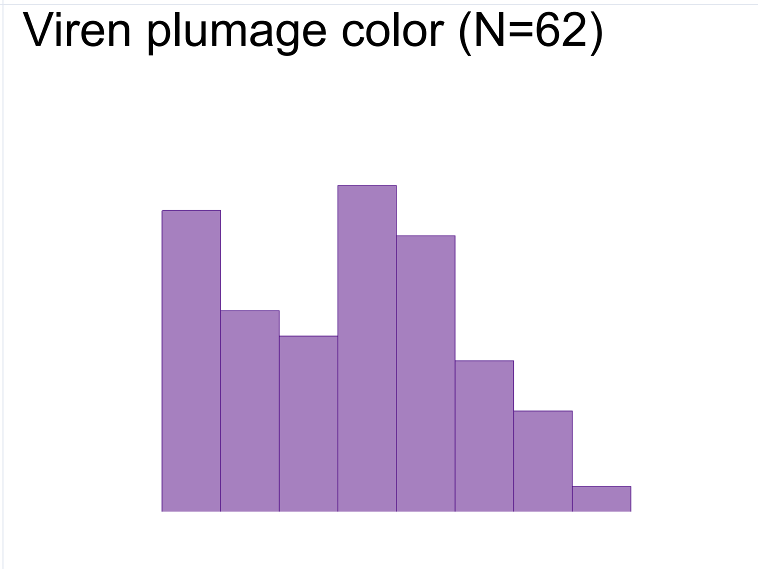


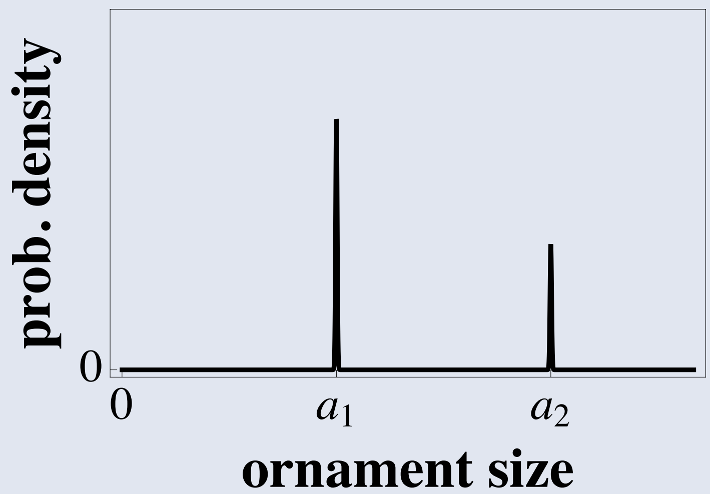


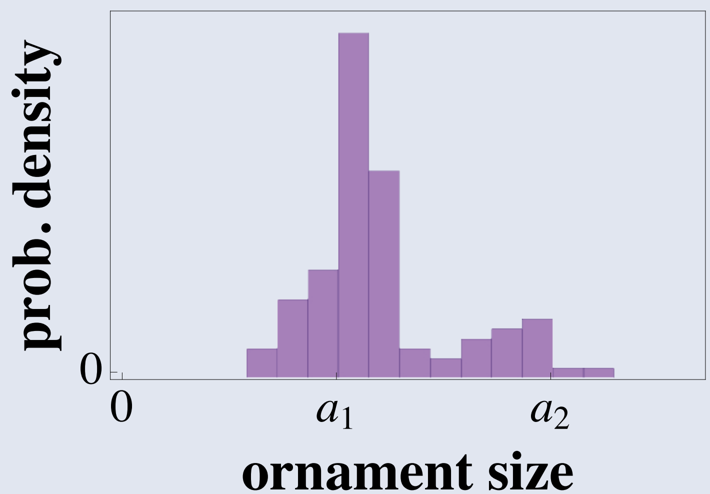




Recap

- Minimal model has only one- and two-niche steady states
- For small social sensitivity, stable fixed point is two niche

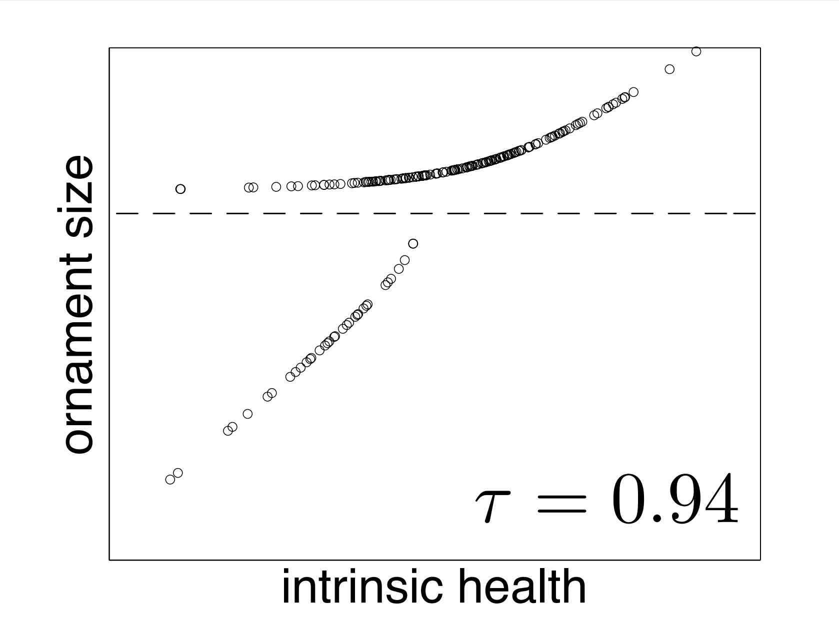




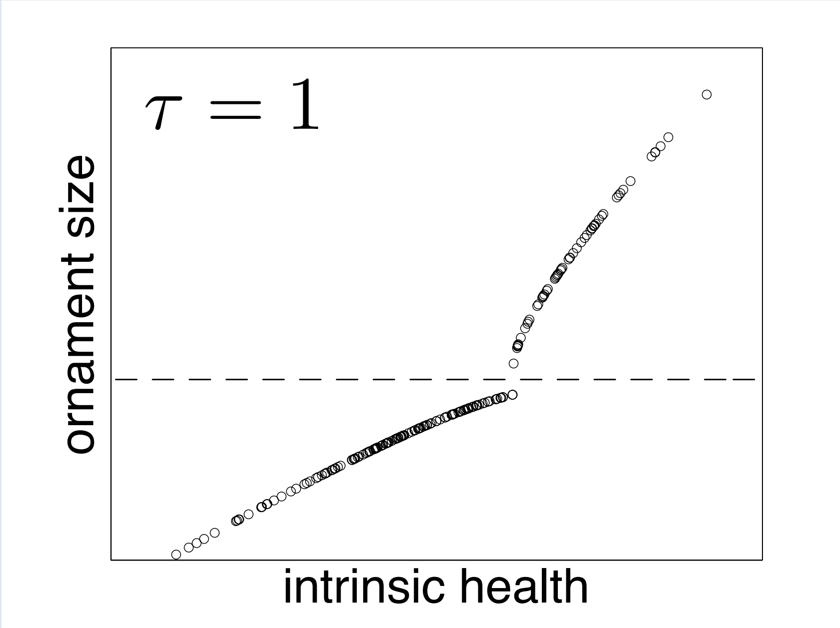
Advertising is honest (mostly)

- Rank correlation τ between intrinsic health and ornament size is close to 1

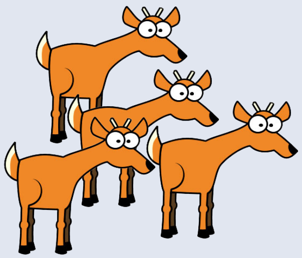
$\gamma < 1$



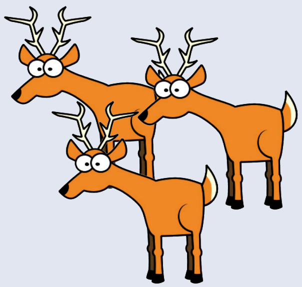
$\gamma > 1$



Summary of model predictions



Model predicts two niche stratification of advertising



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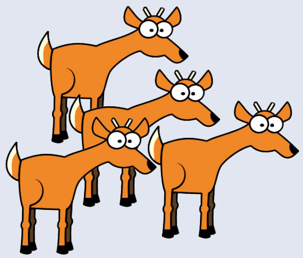

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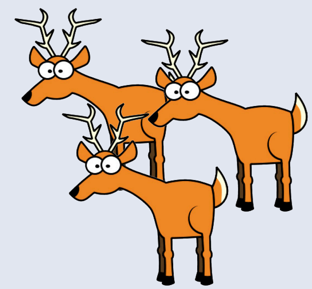
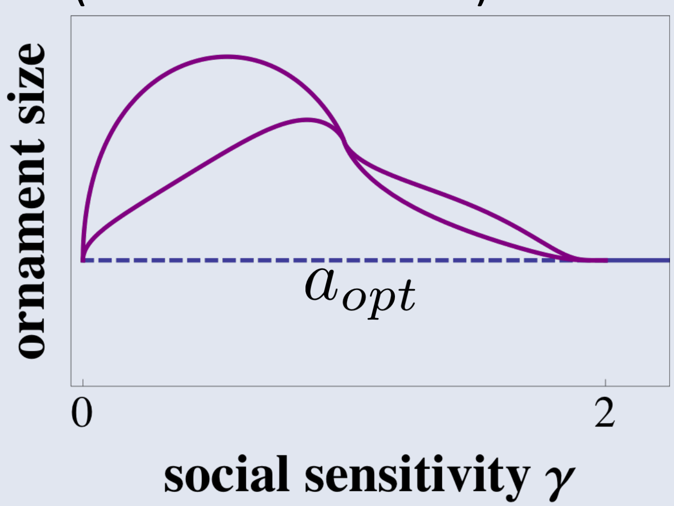


Social effects lead to larger-than-optimal ornaments (lower herd fitness)



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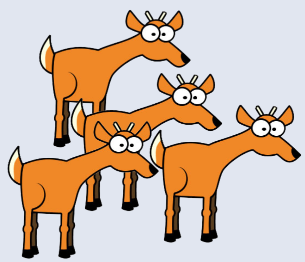

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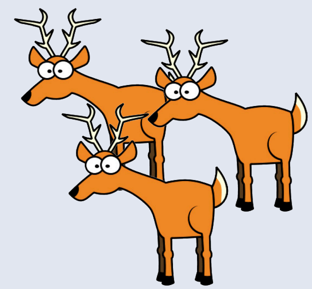

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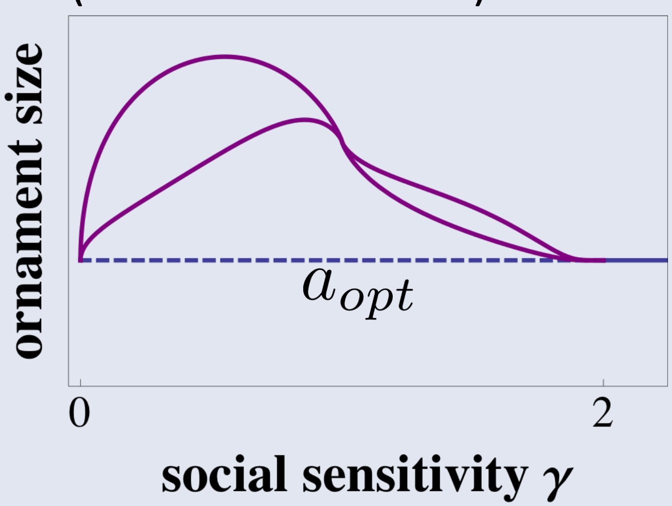
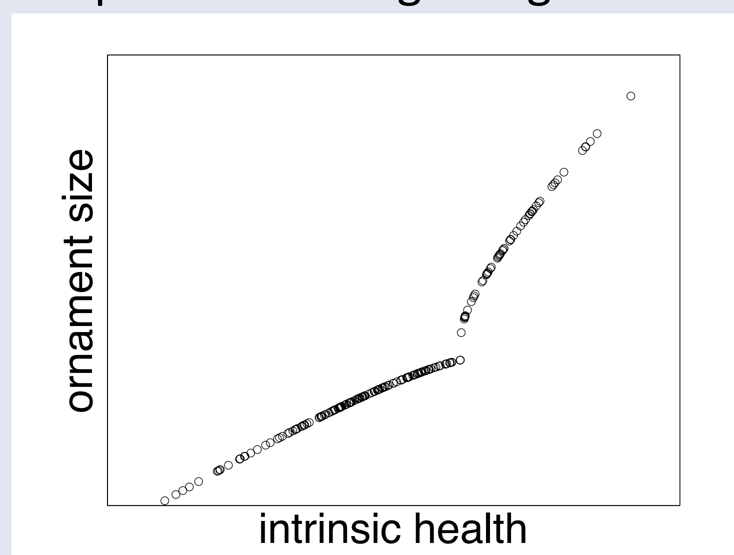
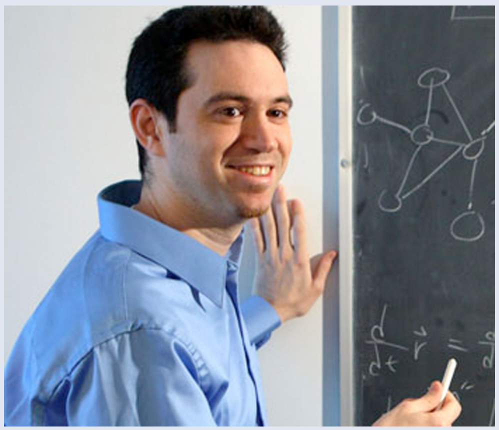


Handicap principle implies honest signaling



Thanks



Professor Danny Abrams

NSF Graduate Research Fellowship Program

Grant No. DGE-1324585

James S. McDonnell Foundation

Supplemental

- Two-niche system for large N:

$$\frac{\mathrm{d}a_1}{\mathrm{d}t} = c\left[s\gamma\Big((1-x)\,|a_1-a_2|\Big)^{\gamma-1} + 2(1-s)(a_{opt}-a_1)\right]$$

$$\frac{\mathrm{d}a_2}{\mathrm{d}t} = c\left[s\gamma\Big(x\,|a_1-a_2|\Big)^{\gamma-1} + 2(1-s)(a_{opt}-a_2)\right]$$

- Two-niche fixed point for large N:

$$a_1 = a_{opt} + \left(\frac{s\gamma}{2(1-s)}\right)^{\frac{\gamma-3}{\gamma-2}} \left((1-x)\left|x^{\gamma-1}-(1-x)^{\gamma-1}\right|^{\frac{1}{2-\gamma}}\right)^{\gamma-1}$$

$$a_2 = a_{opt} + \left(\frac{s\gamma}{2(1-s)}\right)^{\frac{\gamma-3}{\gamma-2}} \left(x\left|x^{\gamma-1}-(1-x)^{\gamma-1}\right|^{\frac{1}{2-\gamma}}\right)^{\gamma-1}$$

Supplemental

- More general model: Assume only

$$\varphi_i = s\,\varphi_i^{(soc)} + (1-s)\,\varphi_i^{(ind)}, \quad 0 \le s \le 1$$

Monotonic increasing (for $\varphi_i^{(soc)}$)

Singly-peaked at a_{opt} (for $\varphi_i^{(ind)}$)

- Then fixed point of $\frac{\mathrm{d}a_i}{\mathrm{d}t} = c\frac{\partial \varphi_i}{\partial a_i}$ can only exist for $a_i \ge a_{opt}$

Supplemental

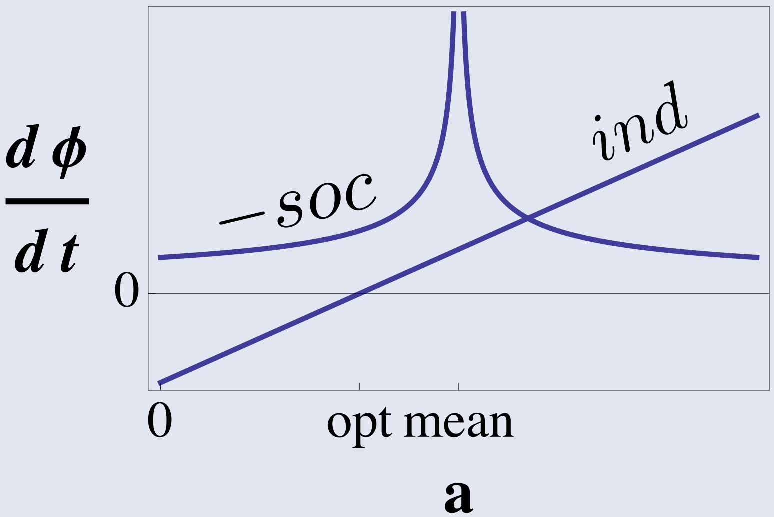
- Further assume

$$\frac{\mathrm{d}^3}{\mathrm{d}a_i^3}\varphi_i^{(soc)} > 0 \quad \text{or} \quad \frac{\mathrm{d}^3}{\mathrm{d}a_i^3}\varphi_i^{(soc)} < 0$$

except possibly at $a = \bar{a}$

- Additionally, assume

$$\frac{\mathrm{d}^3}{\mathrm{d}a_i^3}\varphi_i^{(ind)} \equiv 0$$



Supplemental

- Only possible phase planes are