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 $h_i$
Model

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

$$ \varphi_i^{(soc)} = \text{sgn} \left( a_i - \bar{a} \right) |a_i - \bar{a}|^\gamma $$

Ensures monotonicity

Sensitivity to deviations from the population mean
Model

- Incorporate social and individual effects into a total fitness:

\[ \varphi_i = s \varphi_i^{soc} + (1 - s) \varphi_i^{ind}, \quad 0 \leq s \leq 1 \]

Tunes relative importance of social effects
Model

- Incorporate social and individual effects into a total fitness:

\[ \varphi_i = s \varphi_i^{(soc)} + (1 - s) \varphi_i^{(ind)}, \quad 0 \leq s \leq 1 \]

Tunes relative importance of social effects
Model

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

\[
\frac{da_i}{dt} = c \frac{\partial \varphi_i}{\partial a_i}
\]

Time scaling constant
Model

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

\[
\frac{da_i}{dt} = c \frac{\partial \varphi_i}{\partial a_i}
\]

Time scaling constant

\[
\frac{da_i}{dt} = c \left[ s \gamma \left(1 - \frac{1}{N}\right) |a_i - \bar{a}|^{\gamma - 1} + 2 (1 - s)(a_{opt} - a_i) \right]
\]

Number of individuals
Preliminary Numerical Results

low social sensitivity  \rightarrow  high social sensitivity

(a) $\gamma = 1/2$

(b) $\gamma = 3/2$

(c) $\gamma = 2$
Investigate uniform fixed point

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

$$\frac{da}{dt} = c \left[ 2 \left( 1 - s \right) (a_{opt} - a) \right]$$

- 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
  \[
  \frac{da_1}{dt} = \ldots , \quad \frac{da_2}{dt} = \ldots
  \]
- 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)
Numerical steady states
(initial condition near fixed point)
Expected stable steady states

fraction in large niche

social sensitivity $\gamma$
Form continuum model

- Go from microscopic to macroscopic view:

\[
\begin{align*}
\frac{da_1}{dt} &= \ldots \\
\frac{da_2}{dt} &= \ldots \\
&\vdots \\
\frac{da_N}{dt} &= \ldots \\
\end{align*}
\]

\( N \to \infty \quad \frac{\partial p}{\partial t} = \ldots \)

System of N ordinary DEs becomes one partial DE for a distribution of ornament sizes \( p(a, t) \)
Continuum model

- Distribution satisfies continuity equation:

\[ \frac{\partial p}{\partial t} = - \frac{\partial}{\partial a} \left( p \frac{da}{dt} \right) \]
Continuum model

- Distribution satisfies continuity equation:

\[
\frac{\partial p}{\partial t} = - \frac{\partial}{\partial a} \left( p \frac{da}{dt} \right)
\]

where

\[
\frac{da}{dt} = c \left[ s \gamma |a - \bar{a}|^{-1} + 2(1 - s)(a_{opt} - a) \right]
\]
Continuum model

- Distribution satisfies continuity equation:

\[ \frac{\partial p}{\partial t} = -\frac{\partial}{\partial a} \left( p \frac{da}{dt} \right) \]

where

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

\[ \bar{a}(t) = \int_{-\infty}^{\infty} a(t) p(a, t) \, da \]
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 $\sigma_1, \sigma_2$ near the fixed points $a_1, a_2$

\[
\frac{d\sigma_1}{dt} = \lambda_1 \sigma_1 + O(\sigma_1^3)
\]
\[
\frac{d\sigma_2}{dt} = \lambda_2 \sigma_2 + O(\sigma_2^3)
\]

- Two niche fixed point is linearly stable when $\lambda_1, \lambda_2 < 0$
Two niche steady state stable region

\[ \lambda_1, \lambda_2 < 0 \]
Recall numerical stable region
Non-uniform health

- Add variation in animal health (affects optimal ornament size)
- Sample numerical results:
  
  \[
  \gamma < 1 \quad \gamma > 1
  \]

  [Histograms showing frequency distribution of ornament size for different values of \( \gamma \).]
Arctic charr brightness (N=20)  
Dung beetle horn length (N=223)  
Peacock eye spots (N=24)  
Viren plumage color (N=62)
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 $\tau$ between intrinsic health and ornament size is close to 1

\[
\begin{align*}
\gamma &< 1 \\
\gamma &> 1
\end{align*}
\]

\[
\tau = 0.94
\]

\[
\tau = 1
\]
Summary of model predictions

Model predicts two niche stratification of advertising
Summary of model predictions

Model predicts two niche stratification of advertising

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

![Diagram showing ornament size vs social sensitivity $\gamma$ with $\alpha_{opt}$ as a threshold]
Summary of model predictions

Model predicts two niche stratification of advertising

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

Handicap principle implies honest signaling

\[ a_{opt} \]

\[ \text{social sensitivity } \gamma \]

\[ \text{ornament size} \]

\[ \text{intrinsic health} \]
Thanks

Professor Danny Abrams

Grant No. DGE-1324585

James S. McDonnell Foundation
Supplemental

- Two-niche system for large $N$:
\[
\frac{da_1}{dt} = c \left[ s\gamma \left( (1 - x) |a_1 - a_2| \right)^{\gamma^{-1}} + 2(1 - s)(a_{opt} - a_1) \right]
\]
\[
\frac{da_2}{dt} = c \left[ s\gamma \left( x |a_1 - a_2| \right)^{\gamma^{-1}} + 2(1 - s)(a_{opt} - a_2) \right]
\]

- Two-niche fixed point for large $N$:
\[
a_1 = a_{opt} + \left( \frac{s\gamma}{2(1 - s)} \right)^{\frac{\gamma-3}{\gamma-2}} \left( (1 - x) \left| x^{\gamma-1} - (1 - x)^{\gamma-1} \right| \right)^{\frac{1}{2-\gamma}}
\]
\[
a_2 = a_{opt} + \left( \frac{s\gamma}{2(1 - s)} \right)^{\frac{\gamma-3}{\gamma-2}} \left( x \left| x^{\gamma-1} - (1 - x)^{\gamma-1} \right| \right)^{\frac{1}{2-\gamma}}
\]
Supplemental

- More general model: Assume only

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

Monotonic increasing

Singly-peaked at $a_{opt}$

- Then fixed point of $\frac{da_i}{dt} = c \frac{\partial \varphi_i}{\partial a_i}$ can only exist for $a_i \geq a_{opt}$
Supplemental

- Further assume

\[ \frac{d^3}{da_i^3} \varphi_i^{(soc)} > 0 \quad \text{or} \quad \frac{d^3}{da_i^3} \varphi_i^{(soc)} < 0 \]

except possibly at \( a = \bar{a} \)

- Additionally, assume

\[ \frac{d^3}{da_i^3} \varphi_i^{(ind)} \equiv 0 \]
Supplemental

• Only possible phase planes are