Course Overview - 2009

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Seminars - 2009

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<td>3 December</td>
<td>Sexual size dimorphism</td>
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Please read both papers and bring them along!

Sexual Size Dimorphism

Sexual differences in body size and morphology are widespread

Why do males and females have different body sizes in many animals?

Male-biased sexual size dimorphism

Female-biased sexual size dimorphism

Southern elephant seal: 7x
Cichlid fish Lamprologus callipterus: 12x
Blanket octopus Tremoctopus violaceus: 10,000-40,000x

Sexual Size Dimorphism (SSD)

- Why are many animals sexually dimorphic?
  - Sexual selection
  - Natural selection
  - Fertility selection
- How does size dimorphism develop?
- What keeps the sizes of males and females together?
Sexual selection for large size

- Large male size is advantageous in
  - male-male competition: in contests or fights over females or in endurance rivalry, eg elephant seals, dragonflies

Female-biased     Male-biased
0.00     0.02     0.04     0.06     0.08     0.10     0.12
r = 0.453, P = 0.023, n = 24 contrasts
Raihani et al. 2006, Animal Behaviour 71: 833-838

Sexual selection for large size, cont...

- Females may prefer large males
  - because large males provide better resources e.g. territory, or viable genes, e.g. in frogs, elephants
  - BUT size often increases with age and experience, so it is not clear whether sexual selection prefers size per se, or some other traits of the male

- Body size is difficult to manipulate experimentally, so it is hard to separate these explanations

Sexual selection for large size, cont...

- In sex-role reversed species the females compete for males, and males raise the young
- In many sex-role reversed species females >> males
- In moorhens, a sex-role reversed species, large size is advantageous for females, because large females have access to small & fat males


Sexual selection for large size, cont...

Large body size may be particularly advantageous to males in polygynous species

- The intensity of sexual selection is greater due to increased competition for mates, eg in bustards

r = 0.453, P = 0.023, n = 24 contrasts

Sexual selection for large size

Books & reviews

Sexual selection for small size

- Many raptors: females >> males
- Small males are more agile than large ones
  - small males can outmanoeuvre large ones, and
  - small males are preferred by females
    as shown in common kestrel \( \text{Falco tinnunculus} \)


Agility of Male Displays & SSD in Seabirds

In seabirds, evolutionary increases in male display agility correlate with evolutionary changes toward female-biased SSD

\[ r = 0.233, P = 0.050, n = 70 \text{ independent contrasts} \]

Serrano-Meneses & Székely 2006, Oikos 113: 385-394

Mating competition and display agility: bustards

- Division of resources
  - males and females can reduce/avoid competition, if they feed on different resources
  - classic example: huia, an extinct New Zealand bird; female = nectarivorous (top); male = insectivorous (bottom)

Rahari et al. 2006, Animal Behaviour 71: 833-838

Natural selection

- Division of resources
  - males and females can reduce/avoid competition, if they feed on different resources
  - classic example: huia, an extinct New Zealand bird; female = nectarivorous (top); male = insectivorous (bottom)

Criticisms
- It predicts difference in either direction between sexes, whereas the direction of SSD is typically non-random
- It is not clear whether sexual selection induced SSD and niche-division was a secondary outcome, or vice versa

Raihani et al. 2006, Animal Behaviour 71: 833-838

Fertility selection

- Clutch size and egg size often increases with female body size
- The number of fertilised eggs increases steeper with body size of females than of males in ectotherm animals, i.e. in insects, fishes, amphibians and reptiles
- Offspring quality increases with female size, eg in red deer

Temeles et al. 2000, Science

There is a correlation between flower length and curvature, and culmen length in the Purple-throated Carib hummingbird

Males feed from flowers of \( \text{Heliconia caribaeensis} \) and females feed from flowers of \( \text{H. bihai} \)

Temeles et al. 2000, Science

Natural Selection, cont....

- Food competition between the sexes may maintain SSD
- Selection for the exploitation of different resources may reduce food competition between mates

Wood frog

http://www.arkive.org/lesser-florican/sypheotides-indicus/video-09.html
Fertility selection, cont...

- Similarly, fecundity increases with female body size in water striders (directional selection)
- BUT longevity decreases (directional selection)

Thus stabilizing selection on lifetime fecundity

Rensch’s rule

- Across species, many animals exhibit a relationship between the degree of SSD and body size:
  - The degree of SSD increases with body size when males are larger than females
  - The degree of SSD decreases when females are the larger sex

What may explain the Rensch’s rule?

Across species, many animals exhibit a relationship between the degree of SSD and body size. When \( \beta > 1 \) (red line):

- The degree of SSD increases with body size when males are larger than females
- The degree of SSD decreases when females are the larger sex

The Big Picture 1: American Rubyspot

- *Hetaerina americana* is one of 37 dimorphic damselflies in the genus *Hetaerina*: males > females
- This is a resource-defence polygynous species
- Territoriality might be affected by age, body condition and body size
- Males display to females using the pigmented patch in the wings

Is Large Size Beneficial for Males?

(i) Large males sustain longer fights than smaller males

\[ r = 0.461, P = 0.001 \]

(ii) Large males hold territories for longer periods

\[ r = 0.220, P = 0.047 \]
**Fat reserves and body size**

- **T males:** $r = 0.69, p = 0.001, n = 22$
- **NT males:** $r = 0.27, p = 0.215, n = 22$

Interaction term body length * fat load significant ($p = 0.001$)

**But being large may be costly....**

More ornamented males face an increased risk of predation & conspicuousness to prey reduce foraging success (Grether & Grey 1996, Behav. Ecol.; Grether 1997, Proc. R. Soc. Lond.)

**The Big Picture 2: Comparative tests of hypotheses**

<table>
<thead>
<tr>
<th>Morphometric trait</th>
<th>Functional hypothesis</th>
<th>Measurements</th>
<th>Sex of</th>
<th>Reproductivity</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>Yes</td>
<td>Display</td>
<td>Male</td>
<td>Yes</td>
<td>Payne (1986)</td>
</tr>
<tr>
<td>Body mass</td>
<td>Yes</td>
<td>Display</td>
<td>Male</td>
<td>Yes</td>
<td>Downes and Hardy (2006)</td>
</tr>
<tr>
<td>Body mass, tail length, wing length</td>
<td>Yes</td>
<td>NA</td>
<td>NA</td>
<td>No</td>
<td>103 (99) Doe et al. (2000)</td>
</tr>
<tr>
<td>Body mass, wing length, tarsus length, bill length, tail length</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>190 (127) This work</td>
</tr>
</tbody>
</table>

Testing predictions of major hypotheses across avian families


**Sexual Size Dimorphism (SSD)**

- Why are many animals sexually dimorphic?
  - Sexual selection
  - Natural selection
  - Fertility selection

- How does size dimorphism develop?
  - What keeps the sizes of males and females together?

**How does SSD emerge in a population?**

1. Male and female offspring have different growth rates
2. One sex grows for longer than the other, although the growth rates are the same
3. Differential mortality of small and large animals

All 3 may occur, e.g. in house finch Carpodacus mexicanus arrows: growth termination for males (black) and females (white)


**The development of SSD in odonates**

What keeps together the sizes of males and females?

- Selecting for size in one sex influences the body size of the other e.g. in poultry
  → high genetic correlation between sexes
- Body size, as indicated by tarsus length, is highly heritable in collared flycatchers

<table>
<thead>
<tr>
<th>Offspring</th>
<th>Parent (A² ± SE)</th>
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<tr>
<td></td>
<td>Female</td>
</tr>
<tr>
<td>Female</td>
<td>0.61 ± 0.20***</td>
</tr>
<tr>
<td>Male</td>
<td>0.84 ± 0.19***</td>
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<tr>
<td>Average</td>
<td>0.72</td>
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* P < 0.05, ** P < 0.01, *** P < 0.001.

Summary

- Three major selection processes influence body size: sexual selection, natural selection and fertility selection
- Body size is difficult to manipulate experimentally, so evidences are often circumstantial and open to alternative explanations
- Different selective processes may interact & differentially influence the sizes of males and females
- High genetic correlation exists between males and females, that may negate the effects of selection