Amphibian Courtship and Mating

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Goal of the Lecture

To familiarize students with amphibian courtship and mating strategies, including the mechanics and costs of reproduction.

Reading Assignments:
1) Handout: call energetics
2) Duellman and Trueb: Chapter 3
3) Types of Calls: mp3 file on website

Lecture Structure

I. Breeding Site Cues
II. Anuran Vocalization
III. Secondary Sexual Characters
IV. Courtship
V. External vs. Internal Fertilization
VI. Comparative Costs of Reproduction
Finding a Mate

Cues Used to Find Conspecifics

1) Auditory Cues
- Used Exclusively by Anurans
- 10-100 m: Most Anurans
- >1000 m: Bullfrogs, Spadefoots

2) Olfactory Cues
- Breeding Site Odors (algae, blooming)
- Blinded and Olfactory Ablation Studies
- Green Frogs: 550 m
- Newts: 3-4 km

3) Visual Cues
- Celestial Bodies (sun, moon, stars)
- Nocturnal: stars and moon
- Fixed Visual Landmarks (forest edge)
- Blinded: Less Direct Routes

4) Magnetic Cues
- Diurnal: sun or skylight
- Nocturnal: stars and moon
- Blinded: Less Direct Routes
- Magneto-Perception (compass system)
- Masking Earth’s Magnetic Field
- Anurans: Migratory Experience
- Newts: Displaced 8 km; return to natal stream

5) Geotactic or Hygro tactic Cues
- Migrates downhill and toward moisture
- Non-random dispersal to and from wetlands

Vocalizations

Salamanders and Caecilians
- Some Plethodontids, Sirens, and Amphimias
- Family Caeciliidae (few)
- Barks, Squeaks, Whistles

Anurans
- All Anurans except Tailed Frogs (Ascaphidae) and Leiopelmatids
- Call: entire ensemble of acoustic signals in a sequence
- Note: single pulse (bird-voiced treefrog) or series of pulses (trill: gray treefrog)
- Loudness: measured in decibels (dB)
- Pitch: measured in frequency (Hz)

Body Size
- Large: Lower Frequencies, Higher Pulse Rates, Longer Duration
- Small: Higher Frequency, Lower Pulse Rates, Shorter Duration

Mechanics of the Typical Anuran Call

1) Inhale Lungs
2) Close Nares
3) Contract Trunk Muscles
   - Oblique Muscles
4) Larynx (vocal cords)
   - Muscular energy 
   - Acoustic energy
   - Single notes: inhale every time
   - Multiple Pulses: resonate & trunk muscles may periodically contract
5) Buccal Cavity
6) Vocal Slits
7) Vocal Sac
   - Resonates Sound
8) Nares Open

Sound Power
- 100-115 dB @ 0.5 m
- 90 dB: Songbirds

No correlation between body size and dB

Importance

- Short-distance (<500 m): #1 and #5
- Long-distance (>500 m): #2, #3, and #4

Maximum dispersal of most species is <3 km (Sinsch 1990)
### Types of Vocal Sacs

1) Median Subgular
   - **Single Sac in Throat**
   - **Most Common**
   - **Internal**
     - Skin not modified
     - Call from water (buoyancy)
     - Usually lower frequency

2) Paired Subgular
   - **Two Sacs in Throat**
   - Partially or Completely Separated
   - **External**
     - Skin modified: Thin and Folded

3) Paired Lateral
   - **Behind & Below Jaw**

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### Types of Anuran Calls

1) Advertisement Call
   - **A)** Courtship Call
     - Male vocalization used to attract female conspecifics for mating
   - **B)** Territorial Call
     - Male vocalization produced in response to an advertisement call from another male
     - Most common in tropical frogs
   - **C)** Encounter Call
     - Male vocalization produced in response to a close encounter with another male
     - Often: Quick Trill
   - **D)** Compound Advertisement
     - Combines both A and B

2) Reciprocation Call

3) Release Call
   - **Discoglossidae, Pelodytidae**
   - Female vocalization (some species) in response to a male advertisement call or amplexus

4) Distress Call
   - Loud vocalization (often a squeak) in response to a disturbance or capture by a predator
   - Usually higher frequency

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### Hybrid Calls

- **H. cinerea x H. gratiosa**
- Genetic Basis!!

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3
### Advertisement Call Strategies

1) **Simultaneous vs. Synchronous Callers**
   - Simultaneous: Explosive Breeders (BS <2 weeks)
   - Synchronous: Prolonged Breeders (BS >1 month)

2) **Change in Call Rate**
   - Increase call rate when female is detected
   - Increase # of pulses
   - 10-20 sec call once per minute
   - 5 second interval between calls

3) **Long Calls and Fast Rates**
   - Females prefer longer calls @ faster rates
   - Often correlated with body size

4) **Chorus Leaders**
   - Females attracted to speaker that initiated chorus
   - No evidence of dominance hierarchy

5) **Satellite Males**
   - Smaller Males
   - Intercept Females

### Advertising to Predators

**Frogs are not the only ones listening!!**

**Mammals**
- Raccoons
- Opossums

**Reptiles**
- Snakes
- Auditory Reception: 100-200 Hz

**Amphibians**
- Bufo marinus
- Rana catesbeiana
- Attracted to distress calls of other ranids

### Factors Influencing Advertisement Calls

1) **Temperature**
   - Linear relation with call and pulse rates
   - Relation degrades toward end of BS (t)
   - Temperature coupling: Females are attracted to calls produced at temperatures similar to their body temp

2) **Vegetation**
   - Grasslands: 500-1000 m
     - Longer, continuous calls @ lower freq
   - Forests: <500 m
     - Shorter calls @ higher frequency

3) **Soil**
   - Lower frequency (~1000 Hz, upperside)

4) **Rivers**
   - Short calls @ higher frequency
   - Streams: 275-4350 Hz (2530)
   - Forest Ponds: 272-3578 Hz (1726)

5) **Food Resources**
   - Some don’t call (e.g., Ascaphus)

- Unfed males 2X lipids as fed males
- Unfed males sustain 15 nights of calling on stored lipids alone
Chorus Effect
Conspecifics Influence Calling Behavior!

Illustrates the apparent selective advantage to call for longer durations!!

- Call duration increases with dense choruses of conspecifics
- However, call rate (calls/hr) decreases with dense choruses

Wells and Taigen (1986)

Energetics of Advertisement Calls
The MOST energetically demanding activity of a male frog!

Oxygen Rate:
- Linear Relation
- "Food Effect"

Energy Expended:

<table>
<thead>
<tr>
<th>Species</th>
<th>J/hr</th>
<th>J/hr/g</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. gracios</td>
<td>280</td>
<td>80</td>
</tr>
<tr>
<td>H. versicolor</td>
<td>200</td>
<td>22</td>
</tr>
<tr>
<td>H. cinctus</td>
<td>15</td>
<td>37</td>
</tr>
<tr>
<td>P. crucifer</td>
<td>25</td>
<td>21</td>
</tr>
</tbody>
</table>

2-3 hrs per night
3300 notes per hour

Energy Comparison:

<table>
<thead>
<tr>
<th>Activities</th>
<th>Calling</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>0.5X</td>
<td>1X</td>
</tr>
<tr>
<td>Burrowing</td>
<td>1X</td>
<td>3X</td>
</tr>
<tr>
<td>Foraging</td>
<td>1X</td>
<td>4X</td>
</tr>
<tr>
<td>Resting</td>
<td>1X</td>
<td>10X</td>
</tr>
</tbody>
</table>

Carbohydrate vs. Lipid Oxidation
- Dietary carbohydrates used preferentially
- 60-80% of E derived from lipid oxidation
- Seasonal effects (spring vs. summer)
- Prolonged breeders rely more on lipids (callers)
- Chorus Tenure: 20% BS (2 weeks)

Secondary Sexual Characteristics

Caecilians: The anal region of males forms a circular depression.

Salamanders:

1) Sexual Dimorphism:
   - Females larger in some families (e.g., Aneides)
2) Enlarged Cloaca:
   - Males appear swollen
   - Enlarged cloacal gland
3) Caudal and Dorsal Fin:
   - Aquatic Salamanders
   - Aneides
   - Strobomimesis
   - Salamandrids
4) Head Glands:
   - Male Plethodontids
   - Males larger
5) Nuptial Excrescences:
   - Aneides
6) Nasalid Grooves & Premaxillary Teeth:
   - Male Plethodontids
   - Elongated & Monocuspid (some)
### Secondary Sexual Characteristics

**Anurans**

<table>
<thead>
<tr>
<th>1) Sexual Dimorphism:</th>
<th>4) Nuptial Excrescences:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females larger (most)</td>
<td>Keratinized Epithelium</td>
</tr>
<tr>
<td>Converge: Aggressive Species</td>
<td>Stimulate ovulation</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>2) Vocal Sac: (external spp)</th>
<th>5) Tympanum:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species with clear ventral skin</td>
<td>Most Anurans: same size or larger in female</td>
</tr>
<tr>
<td></td>
<td>Females: male larger (R. catesbeiana &amp; clamitans)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>3) Eggs:</th>
<th>6) Others:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glands (several families)</td>
<td>Tusks or spines (some families)</td>
</tr>
<tr>
<td>Keratinized Epidermis</td>
<td>Hair-like projections (Trichobatrachus robustus)</td>
</tr>
<tr>
<td>Clear ventral skin</td>
<td></td>
</tr>
</tbody>
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### Amphibian Courtship

**Caecilians:** Very little known

**Salamanders:**
- Urodèles, cryptobrachids, and sirens (likely): none
- All others: elaborate

**General Steps:**
1. Male detects female, approaches and nudges with snout
2. Male blocks path and continues nudging or tail movements
3. Male moves away from female (she follows if enticed)
4. Male deposits spermatophore
5. Female picks up spermatophore with lips of cloaca

**Energetic Costs:**
- **Terrestrial**
  - 1 hour: 10膳% C > resting
  - 75% F > resting
- **Aquatic**
  - 2.7J (1%)
  - >1 courtship seq. (often)
  - Water quality can affect courtship bouts
  - Paedomorphic

### Amphibian Courtship

**Salamanders:**
- Family Ambystomatidae
- Early Breeders (except xeric)
  - January-March, Summer
- Deposit on Submersed Structure (usually vegetation)
- Predator
- Paedomorphic
Anuran Courtship
In general, NOT elaborate!

1) Advertisement Calls
   - Primary Courtship Cue
   - Male generally calls until nudged
   - Preamplectic rituals exist
   - Female positions for amplexus
   - Some frogs (sub-tropical/tropical)

2) Conspecific Recognition
   - Tactile Cues
   - Explosive Breeders & Satellite Males

Types of Amplexus

Anurans

- Abdominal contractions signal male
- Female releases sperm as eggs are deposited
- Male releases sperm as eggs are deposited
- Female arches ventrally: continuous contact
- Eggs are usually hydrated & defended
- Various development strategies

External Fertilization

Salamanders:
- Asian Salamanders, Hellbenders, & Sirens

Anurans:
- Abrupt Oviposition
- Abdominal contractions signal male
- Female deposits eggs, male moves over eggs and deposits sperm
- Pair of egg sacs or string

Aquatic Oviposition
- Abdominal contractions signal male
- Female deposits eggs, male moves over eggs and deposits sperm
- Pair of egg sacs or string

Arboreal Oviposition
- Oviposition often occurs on a leaf
- Abdominal contractions signal male
- Male moves forward as eggs are deposited
- Eggs are usually hydrated & defended
- Various development strategies
**Internal Fertilization**

**Caecilians:**
- Phalloidium: intromittent organ made of connective tissue from the cloaca that is used to deliver sperm
  - Sperm delivered down longitudinal tracts
  - Copulation occurs for 2-3 hrs

**Amphibians:**
- Ascaphidae
  - Fast-flowing streams
  - Cloacal extension: "tail"
  - "Tail" at 90 degree angle
  - Male in "sitting" position
  - Copulation occurs for 24-30 hrs
  - Cloacal Apposition
  - *E. coqui and jasperi

**Salamanders:**
- Spermatophore stores in spermatheca
- Sperm can be stored for >2 yrs (some)
- Ovulation stimulates sperm

**Cost of Reproduction**

**Tungara frog (Engystomops pustulosus)**

- **Males**
  - Sperm
  - Calling
  - Territorial Defense
  - Amplexus
  - 3.25 kJ = Calling Males
  - 1.02 kJ = Satellite Males
  - (Ryan 1985)

- **Females**
  - Eggs
  - Locate Suitable Male
  - 40.96 kJ
  - 45.99 kJ *Eleutherodactylus coqui* (Woolbright 1985)

**Some Species Multiple Clutches per Year**

**Explosive Breeders** (favorable years)

**Age of 1st Reproduction**
- 1 yr = most anurans
- 2+ yr = most caudates

**Female Investment: 20X Greater**

**Predation Risk: Greatest for Calling Males**