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) **See Website:** Wells (2007)
2) **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

Two cues are needed to orienteer (Sinsch 1990)

Cues Used to Find Conspecifics

Maximum dispersal of most species is <3 km

1) Auditory Cues

- Used Exclusively by Anurans
- 10-100 m: Most Anurans
- 500-1000 m: Bufonids, Spadefoots

2) Olfactory Cues

- Breeding Site Odors (algal blooms)
- Blinded and Olfactory Ablation Studies
  - Green Frogs: 550 m
  - R-B Newts: 3-4 km

Remove olfactory nerve

3) Visual Cues

- Celestial Bodies (circadian clock)
  - Diurnal: sun or skylight
  - Nocturnal: stars and moon
- Fixed Visual Landmarks (forest edge)
  - Blindfolded: Less Direct Route

4) Magnetic Cues

- Magneto-Perception (compass system)
- Masking Earth's Magnetic Field
- Anurans: Migratory Experience
- Newts: Displaced 8 km; return to natal stream

5) Geotactic or Hygrotactic Cues

- Migrate downhill and toward moisture
- Non-random dispersal to and from wetlands

Importance

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

Vocalizations

Salamanders and Caecilians

- Some Plethodontids, Sirens, and Amphiumas
- Family Caeciliidae (few)
- Barks, Squeaks, Whistles

➡ Predatory Defense

Anurans

- All Anurans: except Tailed Frogs (Ascaphidae) and Leiopelmatids
- Call: entire assemblage 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)
  - Mass and tension of vocal cords (and size/type of vocal sac)

Transmission:
- Anurans: <5000 Hz
- Humans: 800-2500 Hz

Lower Frequencies Travel Farther

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

Mechanics of the Typical Anuran Call

100 dB

Pipidae Exception

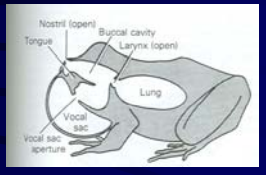
Rapid Contraction of Laryngeal Muscles

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

Types of Vocal Sacs

1) Median Subgular
- Single Sac in Throat
- Most Common

2) Paired Subgular
- Two Sacs in Throat
- Partially or Completely Separated

3) Paired Lateral
- Behind & Below Jaw

Internal
- Skin not modified
- Call from water (buoyancy)
- Usually lower frequency

#2 and #3

External #1 and #2
- Skin modified: Thin and Folded

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

Hybrid Calls
Both Characteristics
- H. cinerea x H. gratiosa

Genetic Basis!!

D) Compound Advertisement

Combines both A and B

"Co": B
"qui": A

Eleutherodactylus coqui

Types of Anuran Calls

2) Reciprocation Call Discoglossidae, Pelodytidae

Female vocalization (some species) in response to a male advertisement call or amplexus

3) Release Call

Acoustic signal (corporal vibrations) in response to an un-welcomed amplexus
- Stimulate by gently applying pressure with thumb and forefingers to axillary region

4) Distress Call

Loud vocalization (often a squeak) in response to a disturbance or capture by a predator
- Mouth Open

Advertisement Call Strategies

1) Simultaneous vs. Synchronous Callers

- •Simultaneous: Explosive Breeders (BS <2 weeks)
- •Synchronous: Prolonged Breeders (BS >1 month)

Males alternate calls to minimize overlap

2) Change in Call Rate — Unison Bout Calling

Increase call rate when female is detected

- •10-20 sec call once per minute
- •5 second interval between calls

5) Satellite Males

- •Smaller Males
- •Intercept Females

3) Long Calls and Fast Rates

Females prefer longer calls @ faster rates

- •Often correlated with body size

Long, Slow over Fast, Short

4) Chorus Leaders

- •Females attracted to speaker that initiated chorus
- •No evidence of dominance hierarchy

Advertising to Predators

Frogs are not the only ones listening!!

Mammals

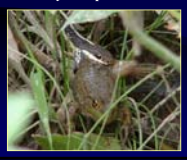
- •Raccoons
- •Opossums

- •Tropical Bats
- *Trachops cirrhosus*

Can distinguish calls (avoid toxic species)

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 decouples toward end of BS (ɐ)

•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: <100 m
  - Shorter calls @ higher frequency
  - Similar tone w/ gradual modulation

3) Soil

Lower frequency (<1000 Hz, opercular)

4) Rivers

Short calls @ higher frequency

- Streams: 1275-4300 Hz (2530)
- Forest Ponds: 272-3578 Hz (1726)

Centrolenids and Dentrobatids

Some don't call (e.g., Ascaphus)

5) Food Resources (Grafe 1996)

Call rates of unfed males are lower

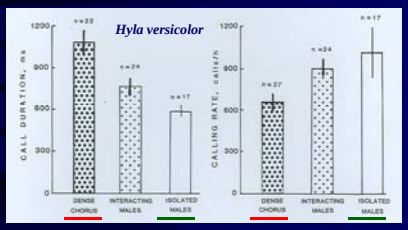
Unfed males 2X lipids as fed males

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!!



Wells and Taigen (1986)

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

Energetics of Advertisement Calls

The MOST energetically demanding activity of a male frog!

Oxygen Rate:

2-3 hrs per night

3300 notes per hour

Pough et al. (1992)

Energy Comparison:

Activities	Calling > Activity
Foam nest	1.5X
Burrowing	3X
Foraging	4X
Resting	10X

Energy Expended:

Species	J/hr	J/hr/g
H. gratiosa	280	22
H. versicolor	280	33
H. cinerea	80	16
P. crucifer	25	21

≈40 cal/hr or ≈100 cal/night

Carbohydrate vs. Lipid Oxidation

Dietary carbohydrates used preferentially

- 60% of ♀ derived from lipid oxidation

Prolonged breeders: rely more on lipids (callers)

- Chorus Tenure: 20% BS (2 weeks)

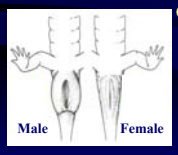
Secondary Sexual Characteristics

Caecilians: The anal region of males forms a circular depression.
Suction or clasping mechanism when the phallodeum is inserted.

Salamanders:

1) Sexual Dimorphism:
Females larger in some families
(e.g., Ambystomatids)

2) Enlarged Cloaca: Males appear swollen
(enlarged cloacal glands)



3) Caudal and Dorsal Fin:

Triturus vulgaris

- Aquatic Salamanders
  - Salamandridae
  - Ambystomatidae
- Males larger

4) Head Glands:

5) Nuptial Excrescences:
Keratinized Epidermis

6) Nasolabial Grooves & Premaxillary Teeth: Male Plethodontids → Elongated & Monocuspid (some)

Secondary Sexual Characteristics

Anurans

1) Sexual Dimorphism:
- Females larger (most)
- Converge: Aggressive Species

2) Vocal Sac: (external spp)

3) Eggs:

Species with clear ventral skin

4) Nuptial Excrescences:
- Keratinized Epidermis
- Stimulate ovulation

5) Tympanum:
- Most Anurans: same size or larger in female
- Ranids: male larger (esp. *R. catesbeiana* & *clamitans*)

6) Others:
- Glands (several families)
- Elongated 3rd finger (*Colostethus*)
- Tusks or spines (some families)
- Hair-like projections (*Trichobatrachus robustus*)

Amphibian Courtship

Olfactory and visual cues

Caecilians: •Very little known

Salamanders: •Hynobiids, cryptobrachids, and sirens (likely): none → External Fertilization

•All others: elaborate → Internal Fertilization

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
- •38% C > resting
- •75% F > resting

Lunglessness

Aquatic
- •>2 hrs (often)
- •>1 courtship seq. (often)
- •Water quality can affect courtship bouts
- •Ė limited (likely)!

Amphibian Courtship

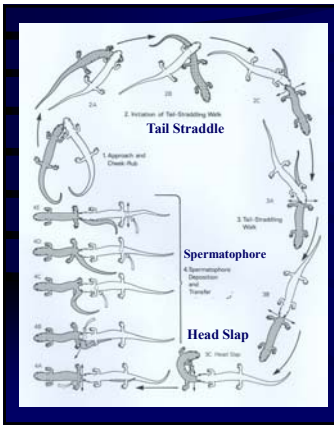
Salamanders: Family Ambystomatidae

- •Males arrive first
- •Early Breeders (except xeric) (January-March, Summer)
- •Deposit on Submersed Structure (usually vegetation)

- •Predators
- •Paedogenetic

Amphibian Courtship

Salamanders: *Plethodon jordani*



Photos: S. Arnold

Anuran Courtship

In general, NOT elaborate!

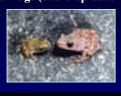
1) Advertisement Calls

- Primary Courtship Cue
- Male Generally Calls until Nudged

G. Krupa

- Female positions for amplexus
- Preamplectic rituals exist

Some frogs (sub-tropical/tropical)



2) Conspecific Recognition

Tactile Cues

- Size: *B. americanus* vs. *B. woodhousii*

Former: females smaller

G. carolinensis vs. *G. olivacea*

Former: females larger

- Skin Texture

Explosive Breeders & Satellite Males

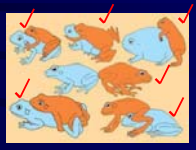
"No release call!"

Types of Amplexus

Anurans

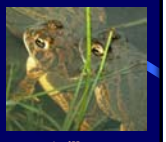
Duration: 1-2 hrs

Vents not Juxtaposed



Inguinal

Cephalic



Axillary

Others: glued (*Breviceps*), straddle (*Mantidactylus*), independent (*Dendrobates granuliferus*)

External Fertilization

Salamanders:
Asian Salamanders, Hellbenders, and Sirens

- Very similar to fish
- Female deposits eggs, male moves over eggs and deposits sperm
- Pair of Egg Sacs or String

Anurans:

Aquatic Oviposition (Clutch >100)

- Abdominal contractions signal male
- Female arches ventrally, male dorsally
- Male releases sperm as eggs are deposited
- Male may use hind feet to organize eggs
- Female *Bufo* frequently walk in water leaving eggs in 2 strings

Arboreal Oviposition (Clutch <50)

- Oviposition often occurs on a leaf
- Abdominal contractions signal male
- Male arches dorsally: continuous contact
- Male releases sperm as eggs are deposited
- Pair moves forward as eggs are deposited
- Eggs are usually hydrated & defended
- Various development strategies

Internal Fertilization

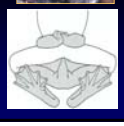
Caecilians (all):

- Phallodeum: 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

2-10 mm hgt

Anurans:

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



Salamanders (90%):

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

Lentic:	Twigs, Leaves (O_2) Newts wrap eggs!
Lotic:	Under stones (single) Stream banks
Terrestrial:	Under stones, logs or within logs Female protects

Cost of Reproduction

Túngara 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

→ ≈10,000 calories
→ 40.96 kJ
→ 45.99 kJ *Eleutherodactylus coqui*
(Woolbright 1985)

- Female Investment: 20X Greater

Some Species Multiple Clutches per Year → Explosive Breeders (favorable years)

- Predation Risk: Greatest for Calling Males

Age of 1st Reproduction
1 yr = most anurans
≥2 yr = most caudates