Amphibian Estivation and Hibernation

Lecture Outline

I. Introduction
II. Estivation
III. Hibernation
IV. Future Research

Amphibians range widely over globe

Why?
• Ability to withstand harsh conditions
• Life history needs met in short periods when conditions favorable
• Main challenges:
  1) Starvation
  2) Cold Hibernation
  3) Drought Estivation

• Solution: conserve resources as much as possible until next active period

Estivation

Allows survival in extreme desert conditions:
- Some species can survive for several years without rain

Metabolic reduction – conserve energy

Many reduce H$_2$O loss by:
- Burrowing into moist soil
- Forming cocoon

Characteristics of Estivators

• Inhabit desert-like environments
  – Seasonal / variable rainfall
• Most highly terrestrial
  – Return to water to breed (some exceptions)
• Many nocturnal

Boutilier et al 1979: Bufo marinus (non estivator in nature)
- Estivation induced in lab
Suggests: All fossorial amphibians may have metabolic reduction capability
Estivators – Life History

- Opportunistic Breeders
  - Triggered by rain
  - Lay eggs in ephemeral pools
  - Larvae develop quickly
  - After rains, subadults burrow into loose soil

- May spend most of life estivating

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Estivators – Life History Example

- Some Myobatrachidae:
  - Lay eggs in dry depressions
  - Don’t hatch until flood occurs
    - Arrested development of embryos
    - Slow rate of \(O_2\) consumption
    - Withstand up to 90% \(H_2O\) loss from egg
    - Can last several weeks if air is humid
  - Larvae also can reduce metabolic rate
    - Survive several days without rain

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Aquatic Estivators

(small group)

- Includes:
  - Ambystoma
  - Siren
  - Amphiuma

- Burrow into mud after water dries up
- Remain encased in hardened mud until rainy season
- Some shelter under loose debris or in other animals’ burrows
Estivation: Cues for Emergence

• **Rain**
  – May extend active season if rain continues

• **Photoperiod**
  – Semour (1973): Toads kept in constant light will come to surface

• **Temperature**
  – May not emerge during rains if temp too high or low

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Burrow Microenvironment

• **Important variables**
  – **Temperature**
  – **Soil water tension** (Affinity of soil for H₂O)
  – **Conc. of respiratory gases**

  Determined by depth, soil type, climate

Temperature:
  - Determines Metabolic rate (fuel usage)
  - Adjust by digging deeper – loose soils only

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Constraints to Estivation Time

• **Starvation**
  – Accumulate resources during feeding period

• **Water loss**
  – Adapted to function when dehydrated
  – Conserve / Store water
    • Absorb H₂O from soil
    • Waterproof cocoons
Cocoons

- Prevent evaporation
- 2 Types:
  1) Single / multiple layers of shed skin (stratum corneum)
  2) Layer of secreted mucous
    - *Siren intermedia*

Estivation – Withstanding Water Loss

- Water storage
  - Amphibian body: 77 – 83% water (mammals 70%)
  - Desert anurans: Store water in bladder to absorb later
- Take up H2O from soil – permeable skin
  - Some species accumulate urea
    - Increases osmolarity of body fluids
    - Also assists in metabolic reduction
      - *Muir et al 2007*

Estivation - Electrolyte Balance

- Problem: Buildup of urea is dangerous
  - Product of metabolism
  - Denatures proteins, disturbs enzyme function
- How do amphibians deal with this?
  - Elasmobranch fishes produce solutes such as methylamines to counteract
    - Has not been found in anurans
  - Possible modifications to protein structure
**Estivation - Metabolism Reduction**
- Allows prolonged estivation without food
- Regulated by changes in
  1) Enzyme / protein activity
  2) Subcellular location of enzymes
  3) Anabolic uses of carbohydrates

  Within 3 hrs, O2 uptake decreases to 30% of resting

**Estivation - Triggers for metabolism reduction**
- Poorly understood
- Possible physiological triggers
  - pH change: acidosis common but more likely a result than a cause
  - Hormonal control
  - Opiates
    - May maintain dormancy in *Bufo marinus*

**Estivation - Fuel Reserves**
- Lipids: from body fat and organs
  - Primary energy source during estivation
    - *Scaphiopus*: 72% (Jones, 1980)

- Carbohydrates
  - *Scaphiopus*: 5%

- Protein
  - Last resort (only when other sources used)
  - *Scaphiopus*: 23%
Estivation - Gas Exchange

- Respiration necessary to use fuel efficiently
- Difficult in mud or cocoons

1) Cutaneous (Scaphiopus)

2) Pulmonary (Pyxicephalus adspersus – cocoon forming)

Hibernation – adaptation to extreme cold

- Frogs are northernmost ectothermic tetrapods

- Salamanders also reach high latitudes

Distribution limits – hypotheses

- Ability of larvae to overwinter
  - Limits salamanders
  - Frogs more tolerant of low oxygen than salamanders
  - Generally, only larvae of aquatic adults can overwinter
    - Frogs: Ranids only

- Other factors:
  - Food availability
  - Cold tolerance of adults
  - Length of breeding season
Hibernation - Responses to cold and starvation

- Reduce metabolism
  - Result of temp decrease
  - Not always dormant: some move and feed

- Accumulate lipid reserves before winter
  - Depend on lipid oxidation for fuel during hibernation

- Adjustments to enzymes and proteins produced by organs
  - Optimize low-temp function
  - More efficient metabolism

- Adjust cellular membrane function
  - Change physical properties of membranes for optimal function
  - Permeability, enzyme and transport activities, receptor and neural functions

Factors:
- Temperature
- Moisture
- O₂ level
- Protect from predators
- Supply cues for emergence

1) Submergence under water or ice
   - Prevents: freezing, desiccation
   - Risks: hypoxia, salt loss

2) Hibernate in burrow
   - Prevents: hypoxia, predation
   - Risks: freezing, desiccation

3) Stay on land (rare)
   - Tolerate freezing
   - Disadvantage: requires intracellular changes

Hibernation - Caudates

- Aquatic species
  - Usually overwinter in water
  - Many remain active

- Terrestrial species
  - Hibernate on land
  - Plethodontids:
    - Intolerant of freezing
    - Many burrow to avoid low temps
    - Remain active, feed underground

Hibernation - Site Choice
**Hibernation - Anurans**

- **Bufonidae, Pelobatidae**
  - Hibernate underground
  - Not freeze tolerant

- **Hylidae**
  - Not good at digging
  - Use pre-existing burrows, crevices or debris

- **Ranidae**
  - Hibernate underwater (R. Sylvatica exception)

**Terrestrial Hibernation**

1) **Avoid subzero temp (most)**
   - Find moist, aerated hibernaculum
   - Use stored fat reserves

2) **Tolerate Freezing**
   - *Rana sylvatica, Hyla versicolor, H. crucifer, Pseudacris triceriata*
   - Adaptations:
     - Permit extracellular ice formation
     - Regulate cell volume
     - Protect subcellular organization

**Hibernation - Cryoprotectants**

- Important in amphibians that tolerate freezing
- Solutes that protect cellular structure

1) **Colligative**: Reduce osmolality of body fluid
   - Prevent too much extracellular ice from forming
   - Prevent intracellular volume from becoming too low

2) **Membrane**: Protect subcellular organization
   - Trihalose and proline: stabilize membrane
   - Glucose or glycogen: stabilize protein structure
   - Costanzo and Lee (2005): Urea acts as a cryoprotectant

**Video**: [http://www.youtube.com/watch?v=FjrJkFspM](http://www.youtube.com/watch?v=FjrJkFspM)
Aquatic Hibernation

Anaerobic conditions
- Cutaneous O₂ exchange impaired by boundary layers
  - Immobile layer of water next to skin
  - Amphibians can break with body movement
- Affects cardiovascular function
  - Decrease in heart rate, plasma volume
- Changes osmotic concentration
  - Increases body water
- Instructor 2001: Low O₂ causes reduced cell membrane permeability in *Rana temporaria*
  - Reduces energy requirements

Hibernation – Emergence Cues

- Temperature
  - Most important
  - Evidence: re-emerge on warm days in winter
- Rain
  - Especially important for terrestrial caudates
  - Necessary for migration without desiccation
  - Increases hibernaculum temperatures, melts frost

Future Research

- Microenvironments of estivators and hibernators
- Control systems
  - Mechanism for metabolic reduction
  - Estivators: alteration of ventilation and effect of CO₂
  - Aquatic hibernators: control of fluid and ion balance, cardiovascular control in hypoxic conditions
- Formation of urea
- Formation of cryoprotectants
- Internal signals for emergence
- Reestablishing body function after thawing