Evolutionary Physiology

- Physiology—the study of how organisms work
  - Function
  - empirical studies

Aquatic - Terrestrial Transition

- Gravitational Forces
- Greater thermal fluctuations
- Desiccation
- Loss of gills
  - Gas exchange
  - Acid-base regulation

First amphibian fossils found in the Devonian, 350 mya

Amniote radiation in the Carboniferous, 300 mya
Amphibian heart

Piscine hearts also contain a conus arteriosus

Conus Arteriosis
Cardiac ventricle

LAo= left aorta, RAo=right aorta, CCA=common carotid, V=ventricle

Cog-teeth valve

Autonomic control:
Sympathetic input → open
Parasympathetic input → closed

Cog-teeth-like valves

Hypotheses for functional significance of shunt

1) Extends dive time White (1969)
2) Reduces pulmonary edema Burggren (1982)
3) Facilitates digestion Jones (1993)
Gastric Acid Secretion

<table>
<thead>
<tr>
<th></th>
<th>Human</th>
<th>Croc</th>
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</thead>
<tbody>
<tr>
<td>Arterial PCO₂ (mm Hg)</td>
<td>40</td>
<td>27-30</td>
</tr>
<tr>
<td>Venous PCO₂ (mm Hg)</td>
<td>45</td>
<td>29-80+</td>
</tr>
</tbody>
</table>

Blood (gastric artery)

CO₂ → CO₂ + H₂O → HCO₃⁻ + H⁺

Carbonic anhydrase

H⁺

Cl⁻

HCO₃⁻

Cl⁻

Predictions of the hypothesis:

3) Facilitates digestion
   A) Shunt will occur after feeding
   B) Obstruction of the shunt will impair digestion

Methods

Ultrasonic flow probe placed around the left aorta (LAo) to measure shunt

S=stomach, RAo=right aorta, LAo=left aorta, RS=right subclavian, CC=common carotid

Sample of signal

TJ Uriona
ASSAY OF SURGERY

No Shunt: Radio-opaque material injected into right ventricle

Shunt: Radio-opaque material and acetylcholine injected into right ventricle

RAo = right aorta, LAo = left aorta, RS = right subclavian, CC = common carotid, RPA = right pulmonary artery, LPA = left pulmonary artery, PA = pulmonary artery, RA = right atrium, LA = left atrium, RV = right ventricle

Method to Measure Gastric Acid Secretion

No Shunt: Radio-opaque material injected into right ventricle

Shunt: Radio-opaque material and acetylcholine injected into right ventricle

Method Used to Block Shunt

Left aorta (LAo) surgically occluded, RV catheterized

Blood Flow through the LAo During Digestion

Mean flow (ml/min)

- 12 hr of fasting flow
- 12 hr of post-prandial flow

Observations made on 5 animals
**Results of Postprandial Gastric Acid Measurements**

Measurements made at 26°C 24 hours after consuming a meal of chopped steak weighing 5% of the alligators’ mass.

These data indicate the shunt serves digestion.

Postprandial humans with ulcer 0.9 mEq kg⁻¹ hr⁻¹.


**Methods**

Alligators ate a meal of hamburger weighing 5% of body mass and a bovine caudal vertebra. Radiography was used to study digestion of bone.

**Overcoming Buffer Capacity of Meal**

Alligators ate a meal of chopped steak of known buffer capacity weighing 5% of body mass. pH electrode used to measure the ability of the stomach to decrease the pH of the stomach contents.

30 observations made over 5.5 hrs postprandial

Mean + SEM, *p<0.001
Why is this important in ectothermic amniotes?

Aquatic - Terrestrial Transition

- Gravitational Forces
- Greater thermal fluctuations
- Desiccation
- Loss of gills
  - Gas exchange
  - Acid-base regulation

Competition for basking sites: make hay while the sun shines?

Increased risk of predation while basking

Competition for basking sites
Fasting and Postprandial Body Temperature of Alligators

- Temperature data logger implanted in stomach
- Thermal gradient available ranging from 40 to 15 °C

Effect of Body Temperature on Gastric Acid Secretion

- Control (sham surgery)
- Experiment (LAo occluded)

* * Significant difference between fasting and fed state P<0.05

Aquatic - Terrestrial Transition

- Gravitational Forces
- Greater thermal fluctuations
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Anaerobic Exercise

During activity 95% of carbohydrate is used by anaerobic pathways

- Blood pH 7.8 to 6.6 [H+] = 2 X 10^-7 mol l^-1
- Blood pH 7.4 to 7.2 [H+] = 5 X 10^-8 mol l^-1

Bennett, 1982
Baldwin et al 1995
Johnson et al. 1992
**Bicarbonate buffer system**

- Muscle → Capillary
- H+ (capillary) → Muscle

**Chemical Reactions:**

1. \( CO_2 + H_2O \rightleftharpoons HCO_3^- + H^+ \)
2. Depletion of \( HCO_3^- \)
3. Increase in \( PCO_2 \)
4. Excreted in the lungs
5. Excreted in the stomach? (Restore \( HCO_3^- \))

**Methods**

- Ultrasonic flow probe placed around the left aorta (LAo) to measure shunt

- \( S= \) stomach, \( RAo= \) right aorta, \( LAo= \) left aorta, \( RS= \) right subclavian, \( CC= \) common carotid

**Gas exchange of fasting American alligators during and after exercise**

\[ R = CO_2 \text{excretion} \times O_2 \text{consumption}^{-1} \]

**Gas exchange**

- No Shunt
- Shunt

**Sample of signal**

**Blood Flow Through the LAo of Fasting American Alligator after Exercise**

- One minute after exercise
- One hour after exercise

**Graph:**

- \( R \) (carbohydrates \( R = 1 \), fat \( R = 0.7 \))
- Mean ± s.e.m., \( N=5 \) (error bars contained within the symbols)
- Missing 1.4mEq/kg hr

*not significantly ( \( P>0.05 \)) different from pre-exercise*
Blood Flow through the LAo of Alligator

NH₄Cl infused intravenously into fasting American alligator, no effect of saline infusion

What potential contributions can the stomach make to acid clearance from the extracellular fluid?

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<td>mEq kg⁻¹ hr⁻¹</td>
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<td>Fordtran, J.S. and Walsh, J.H. 1973. J.</td>
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<tr>
<td></td>
<td></td>
<td>Clinical Investigation 52:645-657</td>
</tr>
<tr>
<td>Voluntary meal</td>
<td>Up to 23%</td>
<td>1 ???</td>
</tr>
<tr>
<td>% body mass</td>
<td></td>
<td>Uran, T.J. and Farmer, CG. 2006. JEB in press</td>
</tr>
<tr>
<td>Max renal</td>
<td>???</td>
<td>0.35</td>
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Why is this important in ectothermic amniotes?

Other reasons?

- Prevention of putrefaction when eating a large meal
- Digestion of teeth, bone, hooves, antlers, etc.
Summary

• Crocodilians shunt acidic blood around the lungs and into the left aorta (LAo) after eating and after exercise.

Exertion Serves Digestion

• Obstruction of LAo flow impairs digestion of bone and digestion of meat

Summary

• Obstruction of LAo flow decreases rates of gastric acid secretion
• Decrease is more pronounced at warm body temperatures than at cool body temperatures
Part II. Archosaur pulmonary structure/function

“The past may be forgotten, but it never dies.”
…..Rolleston 1911

Synapsids dominate in the Permian, 250 mya

Amniote radiation in the Carboniferous, 300 mya

The great archosaur lineage

Dominated the mesosoic

Romer 1966
What made archosaurs so great?

Hypothesis: Archosaur Cardiopulmonary System was a Key Innovation
- structure/function of avian and crocodilian lung

Ewer 1965

Archosauria

- Development
- Function
- Phylogeny

Inspiration

Modified from Brackenbury 1987

Cranial facial air sinuses
Four chambered heart

Lateral View

MRI image of Zebra Finch, courtesy of the Goller Lab (Thanks Coen)
Avian respiration

“Expiation

expiration

- cervical air sac
- mesobronchus
- ventrobronchi
- parabronchi
- dorsobronchi
- abdominal air sac
- caudal thoracic air sac
- cranial thoracic air sac
- clavicular air sac

normoxic

hypoxic

Pergamon Press

Enigma

Only during exposure to hypoxia/hypercapnia do avian lungs outperform mammalian lungs

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<td>Arctic fox</td>
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When breathing “normal” air (21% O₂, 0.03% CO₂), bird lungs are not more efficient than mammalian lungs

“‘A satisfactory answer has not been found to the benefit of unidirectional flow in the avian lungs.’


Enigma

- Only during exposure to hypoxia/hypercapnia do avian lungs outperform mammalian lungs
Only during exposure to hypoxia/hypercapnia do avian lungs outperform mammalian lungs but crocs outperform birds.

Why are bird and croc lungs so similar?

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<tr>
<td>American alligator</td>
<td>65%</td>
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<tr>
<td>(long apnea, Lung PO₂ = 45 mmHg)</td>
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* PO₂ (summit of Mt Everest) = 43 mmHg
In animals with a lung volume of 109 ml kg\(^{-1}\), only 4 ml kg\(^{-1}\) consists of lung tissue, the remaining 105 ml kg\(^{-1}\) is gas. Perry 1988

Hypotheses

A) APNEA (BREATH HOLD)
- 1) The heart pumps air
- 2) Cardiogenic flow is unidirectional during apnea
- 3) Cardiogenic flow contributes to high extraction

B) VENTILATION
- Unidirectional flow occurs during normal ventilation
How to measure air flow

- Flow in lungs
  - Thermistor flowmeters

- Ventilation
  - Pneumotachography

Results (Ventilation)

Flow in mesobronchus

Probe placement

medial view
Cardiogenic Unidirectional Flow

Flow in lungs

ECG

1 2 3 4 5 6 7 8
seconds

Flow in dorsobronchus

Novel Findings and Implications

• The heart pumps air in American alligators
  – Airflow is unidirectional

Novel Findings and Implications

• Unidirectional flow is not unique to birds, may be plesiomorphic for Archosaurs


The great archosaur lineage

Dominated the mesosoric

Romer 1966

Novel Findings and Implications

Mass extinction, appearance of archosaurs

Decline of archosaurs

Rise of mammals

Huey & Ward 2005

Science 308:398-401
Enigma
• Only during exposure to hypoxia/hypercapnia do avian lungs outperform mammalian lungs

Novel Findings and Implications
What made archosaurs so great?
Archosaurs had unidirectional airflow during the Late Permian and the Mesozoic

Acknowledgments

<table>
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<tr>
<th>US Biological Survey</th>
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<tr>
<td>– Dennis Haney</td>
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<td>– Gary Hill</td>
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<td>– Bob Lewis</td>
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<td>– Louis Mantini</td>
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<td>– Jim Williams</td>
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<th>Florida Freshwater Fish and Game</th>
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<td>– Allen Woodward</td>
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<th>Rockefeller Wildlife Refuge; Louisiana Wildlife and Fisheries</th>
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<td>– Ruth Elsey</td>
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Models for gas exchange

Varanid Lizard
Chameleion Lizard

Cardiogenic mixing occurs in mammals

- Speeds up the diffusion coefficient by about 6 fold, reduces physiological dead space
  - in mammals dead space makes about 4% of the respiratory system
Cardiogenic Airflow Measured at the Mouth in a Man

Peak to peak 10 L min⁻¹

West and Hugh-Jones, 1961

Cardiogenic Flow in Birds?

Brackenbury, 1987

Birds have a low respiratory frequency compared to mammals (e.g., mute swan = 3 breaths min⁻¹) Scheid and Piiper 1972

Remarkable fact that after three centuries of research all the great questions of the functional anatomy of the avian respiratory system remain unanswered. King 1957
Amniote Synapomorphy*:
Direct aortic and pulmonary openings into the ventricle

*Synapomorphy = shared derived character
Amniote = mammals, turtles, snakes, lizards, sphenodon, archosaurs

Potential significance of the stomach

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<td>Voluntary meal % body mass</td>
<td>16</td>
<td>1 ???</td>
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<td>Max renal mEq kg⁻¹ hr⁻¹</td>
<td>???</td>
<td>0.35</td>
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<tr>
<td>pH gastric acid ([H⁺])</td>
<td>0.8 (160 mEq L⁻¹)</td>
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<tr>
<td>pH urine ([H⁺])</td>
<td>7.4 (4x10⁻⁵ mEq L⁻¹)</td>
<td>4.5 (3x10⁻² mEq L⁻¹)</td>
</tr>
<tr>
<td>pH blood after exercise ([H⁺])</td>
<td>6.8 (2x10⁻⁴ mEq L⁻¹)</td>
<td>7.2 (5x10⁻⁵ mEq L⁻¹)</td>
</tr>
</tbody>
</table>
Humans rate of acid secretion from kidney

500 mEq day⁻¹ = 0.35 mEq kg⁻¹ hr⁻¹

Highest measurement of gastric acid 0.6 mEq kg⁻¹ hr⁻¹

Voluntarily eat 16% of body mass. Humans hard pressed to eat a meal of 1% body mass.

22 mEq/kg hr at 16°C.