Public Service Announcements

• Colony Monitoring – This Week

  Who: Haley, Sarah B.
  When: Weds October 12
  Where: Meet at OI, 3.300

• Colony Monitoring – Next Week

  Who: Dani, Sarah D.
  When: Weds October 19
  Where: Meet at OI, 3.30
Adaptations to Life in the Ocean

➢ Five Challenges:

• Waterproofing of Feathers
• Maintain Water & Salt Balance
• Regulate Body Temperature
• Dive: Store and Use Oxygen
• Deliver Energy to Chicks: Stomach Oil

➢ Consider Multiple Approaches:

Behavioral & Physiological Adaptations
1. Adaptations Ocean Life - Waterproofing

Feather micro-structure contributes to waterproofing

**Uropygial (preen) gland** secretes diester waxes called uropygiols that seabirds use for preening.

The gland is found near the base of tail and the oil is secreted via a grease nub. Birds transfer the oil onto the feathers by rubbing their head and bill against the nub.

While all seabirds have a uropygial gland, in some species - cormorants - it does not produce a lot of oil. Thus, feathers get wet. Wing spreading behavior... for feather drying.
2. Adaptations to Ocean Life - Salt Glands

Seabirds balance critical ion concentration and water flux via six pathways:

- Some seabirds drink fresh and salt water
- Prey varies in content of water / salt / energy

**Composition of Some Foods Consumed by Marine Birds**

<table>
<thead>
<tr>
<th>Food</th>
<th>Water (ml/kg)</th>
<th>Sodium (mmol/kg)</th>
<th>Energy (MJ/kg)</th>
<th>mmol Na/MJ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish</td>
<td>697</td>
<td>110</td>
<td>8.6</td>
<td>12.8</td>
</tr>
<tr>
<td>Squid</td>
<td>788</td>
<td>122</td>
<td>4.6</td>
<td>26.5</td>
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<tr>
<td>Krill</td>
<td>791</td>
<td>124</td>
<td>4.3</td>
<td>28.7</td>
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</table>

*Note: Values are means taken from data compiled by Green and Gales (1990).*
Salt Glands

Like marine reptiles, 10 orders of birds have salt glands located above the eyes. They are largest on seabirds. They produce NaCl solution twice as concentrated as seawater, which is released through nostrils as brine.
Water Balance

➢ Influenced by water turn-over.

➢ Water turn-over influenced by:

- Activity
- Body mass
- Taxonomy
Salt Balance

- Influenced by sodium (Na) turn-over.

- Sodium turn-over influenced by:
  - Habitat
  - Body Size
In addition to feathers and fat, seabirds use physiological and behavioral adaptations to minimize heat loss to surrounding environment.

Counter-current heat exchange
Adaptations to Ocean Life - Morphological Thermoregulation

Foraging Trade-Offs:

In cold water, diving birds without air insulation use fat to stay warm.

But fat is heavier than feathers, and more costly to carry around in flight.

But remember: frequent divers have higher flight costs than infrequent divers.

(Wilson et al. 1992)

(Spear & Ainley 1998)

Fig. 2. Mean SMF score ± SE of tropical and polar petrels. Species are: JF, Juan Fernandez Petrel; WN, White-necked Petrel; TA, Tahiti Petrel; KE, Kermadec Petrel; PH, Phoenix Petrel; HE, Herald Petrel; WW, White-winged Petrel; BW, Black-winged Petrel; BU, Bulwer's Petrel; SF, Southern Fulmar; AP, Antarctic Petrel; CA, Cape Petrel; MO, Mottled Petrel; KG, Kerguelen Petrel; SN, Snow Petrel; and BL, Blue Petrel. See Appendix for sample sizes.
Adaptations to Ocean Life - Behavioral Thermoregulation

Cooling off: Exposing legs, panting, opening up wings
Adaptations to Ocean Life - Behavioral Thermoregulation

Cooling off: Shading of Nesting Sites
Thermoregulation - Diving Penguins

Two paradoxical observations:

- **normothermic** peripheral tissues while inactive
- lower temperature of deep tissues during activity

<table>
<thead>
<tr>
<th>Bird</th>
<th>Pectoral muscle</th>
<th>Brood patch</th>
<th>Pectoral muscle</th>
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<td>36.9±0.2⁠a†‡</td>
<td>38.0±0.2⁠b†</td>
<td>38.0±0.4⁠a†</td>
<td>38.0±0.4⁠a†</td>
<td>38.3±0.3⁠a†</td>
<td>38.3±0.2⁠a†</td>
<td>38.7±0.2⁠a†</td>
<td>38.9±0.3⁠b‡</td>
<td>37.7±0.7</td>
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<td>38.3±0.6⁠b†</td>
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<td>39.0±0.2⁠a§</td>
<td>37.6±0.4⁠b‡</td>
<td>38.0±0.3⁠a*</td>
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<td>38.3±0.6⁠b†</td>
<td>38.3±0.6⁠b†</td>
<td>38.5±0.2⁠a†</td>
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<td>33.1±2.6⁠b†</td>
<td>28.0±3.0⁠b*</td>
<td>28.8±2.6⁠b*</td>
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<td>38.6±0.3⁠a*</td>
<td>35.9±0.5⁠a†</td>
<td>35.9±0.5⁠a†</td>
<td>36.2±0.7⁠a†</td>
<td>32.9±2.9⁠b*</td>
<td>27.9±2.9⁠b*</td>
<td>29.6±2.5</td>
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<td>38.3±0.2⁠a*</td>
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<td>36.6±0.7⁠b‡</td>
<td>37.6±1.6</td>
<td>37.6±1.6</td>
<td>37.6±1.6</td>
<td>29.6±2.5</td>
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</table>

Values are means ± SD; n, no. of animals. a,bComparison between tissues (different letters indicate a significant difference, P < 0.05).

(Schmidt et al. 2006)
Thermoregulation - Diving Penguins

Figure A: visualization of one dive cycle with description of the 5 phases: predive, descent (desc), bottom (bot), ascent (asc), and postdive.

Figure B: Initial / final and minimum / maximum tissue temperatures ($T, \degree C$) during each dive phase.

(Schmidt et al. 2006)
Thermoregulation

Pectoral and brood patch tissue temperatures (time vs. temp.) superimposed on diving activity chart (dive profile, time vs. depth).

Dive bout is split according to speed of Body Temp change, $\frac{dBT}{dt}$ (°C/min).

Dashed line at interface between sequences 2 and 3 illustrates the peripheral perfusion adjustment.

(Schmidt et al. 2006)
Thermoregulation - Diving Penguins

During diving, mean pectoralis temp: 37.6 +/- 1.6°C.

During diving, mean brood patch temp: 29.6 +/- 2.5°C.

Temperature of pectoral muscle was significantly higher during diving than during inactivity, and underwent temperature drops of up to 5.5°C.

Brood patch temperature decreases of up to 21.6°C.

(Schmidt et al. 2006)
4. Physiology of Diving

ADL (Aerobic Dive Limit):
Amount of time where energy demands are met with aerobic metabolism (burning oxygen stores)

What happens when ADL is surpassed?
- Lactic acid build-up
- Recovery time to degas (remove CO2 from blood)

(Boyd 1997)
Observation:

Different air-breathing predators achieve different dive durations (and depths)… suggesting species-specific ADLs.

Species-specific ADLs:

Maximum Dive Duration (s) scaled by Body Mass (kg):

pinnipeds (black)
seabirds (white)

(Boyd 1997)
# Mechanisms for Extending Dive Duration

- **Anaerobism (operating beyond the ADL limit):**

<table>
<thead>
<tr>
<th>Advantages</th>
<th>Disadvantages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allows to reach “deep” prey</td>
<td>Inefficient: 18% energy of aerobic metabolism</td>
</tr>
<tr>
<td>Can work if prey resources are predictable (spatially)</td>
<td>Lactic acid build-up: Time Loss</td>
</tr>
</tbody>
</table>

- **Aerobism (operating within the ADL limit):**

<table>
<thead>
<tr>
<th>Advantages</th>
<th>Disadvantages</th>
</tr>
</thead>
<tbody>
<tr>
<td>High metabolic efficiency</td>
<td>Other costs of hypometabolism:</td>
</tr>
<tr>
<td>Short recovery times at surface</td>
<td>Halted digestion &amp; Re-warming</td>
</tr>
</tbody>
</table>

(Boyd 1997)
Mechanisms for Extending Dive Duration

- Many diving species straddle aerobic / anaerobic boundary:
  
  Emperor penguins dive to 500 m (1500 ft)

  During dives, heart rate drops by 15% from 72 bpm when resting at surface.

  During a deep 18-minute dive, the heart rate progressively slowed to 3 bpm.

  During surface intervals between very deep and long dives, heart rate can increase to a maximum of 256 bpm, which likely aids in eliminating carbon dioxide and replenishing and reloading penguin's oxygen stores in its tissues.

(Meir et al. 2008)
(Williams et al. 2011)
To Achieve Aerobism: Enhanced Storage

- Larger Body Mass:

  Metabolic Rate increases more slowly as body mass increases; becomes less expensive per gram

  Storage (volume of blood, muscle) increases non-linearly with increasing body mass

\[
\ln (\text{Std MR}) = \ln (\text{Body Mass})
\]

(Costa 1991)
To Achieve Aerobism: Hypometabolism

- Bradychardia: slowing down of heart rate (dive response)

- Hypothermia: cooling body during diving, slows down metabolic rate

- Restricting blood flow to essential organs:
  - brain / eyes
  - locomotion

(Meir et al. 2008, Ponganis et al. 2011)
To Achieve Aerobism: Enhanced Storage

• Larger Oxygen Storage: Larger Blood Volume

<table>
<thead>
<tr>
<th>Species</th>
<th>Total body O₂ store (ml O₂ kg⁻¹)</th>
<th>% Respiratory</th>
<th>% Blood</th>
<th>% Muscle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bottlenose dolphin</td>
<td>29</td>
<td>21</td>
<td>33</td>
<td>46</td>
</tr>
<tr>
<td>Sperm whale</td>
<td>74</td>
<td>6</td>
<td>61</td>
<td>33</td>
</tr>
<tr>
<td>California sea lion</td>
<td>55</td>
<td>13</td>
<td>39</td>
<td>48</td>
</tr>
<tr>
<td>Harbor seal</td>
<td>62</td>
<td>7</td>
<td>57</td>
<td>35</td>
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<tr>
<td>Weddell seal</td>
<td>89</td>
<td>4</td>
<td>65</td>
<td>31</td>
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<tr>
<td>Elephant seal</td>
<td>85</td>
<td>4</td>
<td>67</td>
<td>29</td>
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<tr>
<td>Elephant seal*</td>
<td>88</td>
<td>4</td>
<td>68</td>
<td>28</td>
</tr>
<tr>
<td>Adélie penguin</td>
<td>63</td>
<td>48</td>
<td>26</td>
<td>26</td>
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<tr>
<td>King penguin</td>
<td>55</td>
<td>34</td>
<td>32</td>
<td>34</td>
</tr>
<tr>
<td>Emperor penguin</td>
<td>63</td>
<td>31</td>
<td>30</td>
<td>39</td>
</tr>
</tbody>
</table>

Seabirds adapted to diving have larger blood volume and lower respiratory volume. Why?

The buoyancy of air far exceeds that of tissues or blood, whose buoyancy does not change appreciably with depth.

(Lovvorn & Jones 1994, Ponganis et al. 2011)
To Achieve Aerobism: Enhanced Storage

- **Oxygen Storage - Muscle**

Oxygen can also be loaded in the muscles (pectoralis).

Myoglobin concentrations higher in deep divers.

- **Oxygen Storage - Spleen?**

(Lovvorn & Jones 1994, Ponganis et al. 2011)
By-products of Larger Mass

During dives, increased inertia (mass * velocity) from greater blood and muscle volume lowers the costs of foraging at the bottom by resisting upward buoyant force.

... but higher mass raises swimming costs because of more work needed to accelerate the (heavier) body with each stroke.

Ultimately, balance between buoyancy and inertia is influenced by:

- dive depth: compression of air spaces
- stroke kinematics: inertial effects
- relative time descending / bottom foraging

(Lovvorn & Jones 1994)
Energetic balance between Diving / Flight within a species:

Average dive depth (compression of buoyant air spaces), stroke kinematics (inertial effects), and the relative time spent descending versus at the bottom foraging determine balance between buoyancy and inertia for diving.

(Lovvorn & Jones 1994)
The Big Picture: trade-Offs

Energetic balance between Diving / Flight within a species:

- Wing loading / shape
- Body Mass
- Bouyancy

(Lovvorn & Jones 1994)
Energetic Trade-Offs of Foraging

- Foraging Costs: Integrate all activities
  
  \[[\text{Time Flying} \times \text{Flying Cost}] + [\text{Time Diving} \times \text{Diving Cost}] + [\text{Time Resting} \times \text{Resting Cost}]\]

- Foraging Costs: Influenced by food distribution
  
  - horizontal (foraging distance)
  - vertical (diving depth)
  - predictability (distance, time)
  - aggregation (distance, time)
Energetic Trade-Offs of Foraging

Pinnipeds and seabirds feed at sea, but rear their young onshore. This life history constraint should lead to convergent adaptations in foraging / reproductive ecology.

However, intrinsic differences in mammalian and avian reproductive biology limit the potential for convergence.

This paper examines both reproductive and foraging energetics of pinnipeds and seabirds. The goal are to:

- identify traits that might be considered convergent adaptations to life in the marine environment
- show how divergent life history patterns are optimal for different reasons.

(Costa 1991)
Energetic Trade-Offs of Foraging

Larger predators (seabirds, pinipeds) use more energy (per unit time) when foraging, than smaller predators.

Is being a penguin more expensive than being an albatross:
- For a given mass?
- As mass changes?

(Costa 1991)
Energetic Trade-Offs of Foraging

Seabirds invest greater total amount of energy and protein into the offspring than pinnipeds, but this comes at cost of making more trips to sea.

If we examine a plot of energy delivery per trip as a function of body mass for seabirds, we find that body mass accounts for most variability in energy delivery per trip (linear regression $r^2 = 0.98$).

Energy delivery rate is independent of locomotory mode; since albatrosses and penguins fall on the same line.  

(Costa 1991)
Energetic Trade-Offs of Foraging

Pinnipeds forage in a manner more consistent with predictions of central place foraging theory (more energy delivered in longer trips).

Pinnipeds exhibit greater ability to compensate to the shortened breeding season typical of high latitude environments.

(Costa 1991)
Energetic Trade-Offs of Foraging

Why?

Mammalian lactation enables pinnipeds to process and concentrate the material fed to the young.

Independent of mechanical limitations of stomach,

Mechanism buffers against variability: differences in prey quality, variation in distance or time away from rookery

(Costa 1991)
Ecological Significance of Stomach Oil

- **Stomach oil** is composed of neutral dietary lipids found in the proventriculus of birds in order Procellariiformes.

- All albatrosses, procellarids, storm petrels use the oil.

- Only the diving petrels do not produce stomach oil.

- Chemical make up varies from species to species, but contains both wax esters and triglycerides.

(Warham 1977)
Ecological Significance of Stomach Oil

➢ Functions:

- light and dense energy reserve
- replenishes water reserves (1 ml / g)

... and a defensive weapon for surface-nesting species

(Warham 1977)
References


