Growth and Development

Embryonic development

- From fertilization to hatching, the embryo undergoes sequence of 42 distinct developmental stages
- The first 33 stages vary little among species
- The final stages species-specific

For example: stage # 39 is very short in Passerines, which hatch in helpless state (altricial), but it is prolonged in the Megapodes that hatch in an advanced physical state (superprecocial)

Hatching

- Chick shifts into the tucking position, punctures air cell membrane, and begins breathing in the air cell
- Egg shell is pecked as chick rotates counterclockwise by pivoting its legs
- Hatching muscle gives power
- Egg tooth helps crack shell 'pipping'

Timing of hatching

- Asynchronous in species that begin incubation before clutch complete (raptors, owls, kingfishers)
- Synchronous (most songbirds, waterfowl, galliformes)
- Communication among chicks (within the eggs) can facilitate synchronous hatching
- Parents brood recently hatched young to help the dry out and warm up
Early experience
- Many birds “imprint” on the first moving object they see
- In precocial species (geese, ducks and cranes) this often becomes ‘mother’ for chicks
- Recognition of predators and food involves both innate and learned behaviors
  - e.g., chicks innately peck at the red spot on a Herring Gull’s bill to stimulate adults to feed

Modes of development
• Altricial (helpless when hatched)
• Precocial (independent at hatching)

<table>
<thead>
<tr>
<th>Character</th>
<th>Altricial</th>
<th>Precocial</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eyes at hatching</td>
<td>Closed</td>
<td>Open</td>
</tr>
<tr>
<td>Down</td>
<td>Fluffy</td>
<td>Plain</td>
</tr>
<tr>
<td>Mobility</td>
<td>Immobile</td>
<td>Mobile</td>
</tr>
<tr>
<td>Parent care</td>
<td>Essential</td>
<td>Inessential</td>
</tr>
<tr>
<td>Nest structure</td>
<td>Parasitic</td>
<td>Self-founding</td>
</tr>
<tr>
<td>Egg size</td>
<td>Small (&lt;10g)</td>
<td>Large (&lt;20g)</td>
</tr>
<tr>
<td>Egg color</td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Beak size</td>
<td>Small (2mm)</td>
<td>Large (6+)&lt;50mm</td>
</tr>
<tr>
<td>Snail intestine</td>
<td>Large (13-14.5x)</td>
<td>Small (6.5-10x)</td>
</tr>
<tr>
<td>Growth rate</td>
<td>Fast (2-4 times precocial rate)</td>
<td>Slow</td>
</tr>
</tbody>
</table>

More detailed classification of hatchlings by Nice (1962)

<table>
<thead>
<tr>
<th>Condition</th>
<th>Down</th>
<th>Head</th>
<th>Beak</th>
<th>Nourishment</th>
<th>Parental care</th>
<th>Nest</th>
<th>Egg size</th>
<th>Egg color</th>
<th>Beak size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altricial</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Paraactic</td>
<td>Essential</td>
<td>Yes</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
</tr>
<tr>
<td>Precocial</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Self-feeding</td>
<td>Inessential</td>
<td>Yes</td>
<td>Large</td>
<td>Large</td>
<td>Large</td>
</tr>
</tbody>
</table>

Examples
- Superprecocial
  - Young are wholly independent at hatching
  - Examples: Moundbuilders, Black-headed Ducks

http://en.wikipedia.org/wiki/Margaret_Morse_Nice
### Precocial
- **Nidifugous** – leave the nest immediately
- **Independent** – parents defend chicks and help them to locate food

**Examples**
- ducks,
- shorebirds,
- quails, grouse,
- murrelets,
- ostrich, kiwis

### Semiprecocial
- **Nidicolous** - some mobility but stay in nest. Capable of body temperature regulation
- **Fed by parents**

**Examples**
- gulls, terns, auks,
- petrels, penguins

### Subprecocial
- **Nidifugous** – leave the nest immediately
- **Defended and fed** directly by parents

**Examples**
- grebes, loons,
- guans, pheasants,
- rails, cranes

### Semialtricial
- **Nidicolous**, but they can move around the nest on their first day
- **Fed and brooded extensively by parents**

**Examples**
- albatrosses, nightjars, herons, hawks, owls
Altricial
• Naked, blind, and helpless at hatching (Gill describes as “grublike”)
• Fed and cared for in the nest by their parents

Examples
- songbirds
- woodpeckers
- hummingbirds
- kingfishers
- pigeons
- parrots
- pelicans

Thermoregulation
• Homeothermy – the ability to maintain a stable body temperature and generate metabolic heat (endothermy) allows birds to maintain high, constant body temperature
• Precocial chicks (quail) maintain body temp upon hatching better than altricial chicks (starling)
• Ability to regulate temp improves with age and # of broodmates

Thermoregulation
• Skeletal muscle, particularly leg muscle, is the main source of heat production for growing birds
• Natal down and thickening of feather coat as chick grows is important for heat retention
• Staying cool is important for birds that nest in hot sun (recall adaptations from physiology lecture. Adults also wet chicks with regurgitated water and wet feathers, and provide shade.)

Energy and Nutrition
Growth constitutes 21-40% of the chick’s energy budget during developmental period

Essential Nutrients
• Protein early in development
• Calcium for bone growth, in particular sulfur containing amino acids (cysteine) needed for feather growth
Growth rates

- Sigmoidal growth curve describes the increase in body mass over the nestling period
- Variation within species due to differences in food supply, temperature, and % adult weight at fledging
- Mass increase levels off below adult size in some ground feeders and above adult size in some aerial feeders

Evolution of growth rates

- David Lack (1968) hypothesized that growth rate reflected a balance between selection for fast growth (to avoid predation) and slow growth (to reduce food requirements)
- Robert Ricklefs “tissue allocation hypothesis” provides more general model

Growth rates vary among species

- 30-fold variation among bird species
- Most variation explained by body size (small species grow faster than large species)
- Other patterns:
  - Open nesters grow faster than cavity nesters
  - Temperate land birds grow faster than tropical land birds
  - Altricial birds grow faster than precocial birds

Feeding nestlings

- Begging calls stimulate food delivery by parents
- Visual stimuli of gaping mouths can facilitate food delivery
- Food delivery rate varies according to age of young
- The transfer of food occurs in a variety of ways
- Esophageal fluids provide concentrated food to young

<table>
<thead>
<tr>
<th>Bird</th>
<th>Protein (%)</th>
<th>Lipid (%)</th>
<th>Carbohydrates (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pigeon</td>
<td>33</td>
<td>50</td>
<td>17</td>
</tr>
<tr>
<td>Robin</td>
<td>8</td>
<td>30</td>
<td>62</td>
</tr>
<tr>
<td>Pigeon</td>
<td>39</td>
<td>20</td>
<td>41</td>
</tr>
</tbody>
</table>

From Table 10A
Feeding rates vary greatly among species

- Hummers once a minute
- Average land bird 4-12 times/hr
- Great Tit up to 990 times daily!
- Procellariids every few days, sometimes weeks!

Other aspects of Parental care:

- Anti-predator defenses
  - Vigilance at nest
  - Distraction displays
  - Active defense
- Nest sanitation – removal of fecal sacs

Sibling competition and siblicide

- Sibling competition varies greatly among species
- Earlier hatched chicks are bigger, which gives them an advantage in competition for food brought by parents
- Siblicide is common in raptors, owls, skuas, herons, and gannets
- Rosella Parrot chicks share

Fledging

- Nestling period – the interval between hatching and departure from the nest
- Fledging period – the interval between hatching and flight
- First few days out of nest is period of peak mortality for most birds

Exercise develops strength prior to fledging
The road to independence...

- Fledglings of many altricial species associate with parents for days to months after fledging as they learn how, when, and where to feed
- Length of apprenticeship depends on difficulty of learning feeding skills