Avian Ecology:
Life History, Breeding Seasons, & Territories
Life History Theory –

Why do some birds lay 1-2 eggs whereas others 12+?

Why do some species begin reproducing at < 1 year whereas others not until 10+?
I. Introduction

Life History Theory — Framework for understanding how physiological traits and behaviors are under the control of evolution

Traits —
Survival
Clutch Size
Incubation period length
Nestling period length
Total Lifetime Energy Available

\[ TE = G + M + R_{c+f} \]
Key concept –
Trade-offs exist between life history traits

• Black-capped Chickadee
  • Reproduction – 15 fledglings/year
  • Survival - < 50% probability surviving to next year
• Royal Albatross
  • Reproduction – 1 young/2 years
  • Survival - > 95% probability surviving to next year
Several Generalities of Avian Survival Rates

• Larger bird species tend to have higher survival relative to smaller species
<table>
<thead>
<tr>
<th>Species</th>
<th>Annual Adult Survival (%)</th>
<th>Average Weight oz (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Tit</td>
<td>30</td>
<td>0.4 (11)*</td>
</tr>
<tr>
<td>Barn Swallow</td>
<td>37</td>
<td>0.7 (19)</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>30</td>
<td>0.8 (21)</td>
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<tr>
<td>European Starling</td>
<td>47</td>
<td>2.9 (80) female</td>
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<tr>
<td></td>
<td></td>
<td>3.0 (85) male</td>
</tr>
<tr>
<td>American Robin</td>
<td>52</td>
<td>2.8 (77)</td>
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<tr>
<td>Blue Jay</td>
<td>55</td>
<td>3.1 (87)</td>
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<tr>
<td>California Quail</td>
<td>50</td>
<td>6.1 (170) female</td>
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<td></td>
<td></td>
<td>6.3 (176) male</td>
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<tr>
<td>Sooty Shearwater</td>
<td>91</td>
<td>10.3 (287)</td>
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<tr>
<td>Northern Fulmar</td>
<td>94</td>
<td>17 (479) female</td>
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<tr>
<td></td>
<td></td>
<td>21.8 (609) male</td>
</tr>
<tr>
<td>American Coot</td>
<td>40</td>
<td>20 (560) female</td>
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<tr>
<td></td>
<td></td>
<td>26 (724) male</td>
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<tr>
<td>Black-crowned Night-Heron</td>
<td>70</td>
<td>31.5 (883)</td>
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<tr>
<td>Herring Gull</td>
<td>70</td>
<td>37.3 (1,044) female</td>
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<td></td>
<td></td>
<td>43.8 (1,226) male</td>
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<tr>
<td>Mallard</td>
<td>52</td>
<td>38.7 (1,082)</td>
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<tr>
<td>White Stork</td>
<td>79</td>
<td>107–125 (3,000–3,500)*</td>
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<tr>
<td>Canada Goose (canadensis race)</td>
<td>84</td>
<td>118 (3,314) female</td>
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<tr>
<td></td>
<td></td>
<td>136 (3,814) male</td>
</tr>
<tr>
<td>Yellow-eyed Penguin</td>
<td>90</td>
<td>185 (5,200)*</td>
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<tr>
<td>Tundra Swan</td>
<td>92**</td>
<td>221 (6,200) female</td>
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<tr>
<td></td>
<td></td>
<td>254 (7,100) male</td>
</tr>
<tr>
<td>Royal Albatross</td>
<td>97</td>
<td>296 (8,300)*</td>
</tr>
</tbody>
</table>

*Weight and survival data from Brooke and Birkhead (1991)
**Survival data from Limpert and Earnst (1994).
• Immature birds have lower rates than mature birds
  (1\textsuperscript{st} yr Gulls ~ 30\% vs. 2\textsuperscript{nd} + ~ 80\%)

• Birds in tropics tend to have higher rates than relatives at higher latitudes
  (~ 80\% vs. ~ 50\%)

• Birds have higher survival rates than mammals of similar size
Survivorship Curves – allows us to compare species

Birds experience a constant rate of mortality throughout adult life.
Variation in annual survival rates between different species helps us understand differences in reproductive strategies

• Species with low prospects for future reproduction (e.g. low annual survival rates) will expend more energy into current effort (larger clutches, more breeding attempts etc.).

• Species with high prospects will expend less energy into current effort.
Average Number of Young Fledged Per Year
(Adjusted for Probability of Parental Survival to That Age)

Eurasian Tree Sparrow

Yellow-eyed Penguin

Age (Years)
Reproductive strategies also depend on survival prospects of eggs & young.

If probability of producing a successful nest is low, what strategy would natural selection favor?

Don’t put all your eggs in one basket!
Survival of eggs and young

Most important source of egg mortality is nest predation.
Bear River Migratory Bird Refuge
O – Line Dike
June 9, 2007
3:19 am
Bear River Migratory Bird Refuge
O – Line Dike
June 24, 2007
4:09 am
Bear River Migratory Bird Refuge
Whistler Canal
May 24, 2007
9:34 am
<table>
<thead>
<tr>
<th>Species</th>
<th>% Nests Lost to Predation</th>
<th>Location</th>
<th>Reference</th>
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</thead>
<tbody>
<tr>
<td>Yellow-billed Cuckoo</td>
<td>39%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Eastern Phoebe</td>
<td>49%</td>
<td>Southern Indiana</td>
<td>(Weeks 1979)</td>
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<tr>
<td>Greater Pewee</td>
<td>71%</td>
<td>Central Appalachians</td>
<td>(Hill and Gates 1988)</td>
</tr>
<tr>
<td>Acadian Flycatcher</td>
<td>39%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Red-eyed Vireo</td>
<td>49%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Warbling Vireo</td>
<td>38%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Carolina Wren</td>
<td>64%</td>
<td>Northwestern Alabama</td>
<td>(Haggerty and Morton 1995)</td>
</tr>
<tr>
<td>American Robin</td>
<td>39%</td>
<td>Pacific NW of N. America</td>
<td>(Sallabanks and James 1999)</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>40%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Hermit Thrush</td>
<td>83%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>American Redstart</td>
<td>52%</td>
<td>New Hampshire</td>
<td>(Sherry and Holmes 1992)</td>
</tr>
<tr>
<td>Black-and-white Warbler</td>
<td>26%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Hooded Warbler</td>
<td>47%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
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<tr>
<td></td>
<td>44%</td>
<td>Pennsylvania</td>
<td>(Evans Ogden and Stutchbury 1975)</td>
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<tr>
<td></td>
<td>30%</td>
<td>Ohio</td>
<td>(Evans Ogden and Stutchbury 1975)</td>
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<tr>
<td></td>
<td>36%</td>
<td>Ontario, Canada</td>
<td>(Evans Ogden and Stutchbury 1975)</td>
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<tr>
<td>Ovenbird</td>
<td>24%</td>
<td>Michigan</td>
<td>(Hann 1937)</td>
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<td></td>
<td>29%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td></td>
<td>70%**</td>
<td>Central Illinois</td>
<td>(Robinson 1992)</td>
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<tr>
<td>Worm-eating Warbler</td>
<td>21%</td>
<td>Arkansas</td>
<td>(Martin 1993a)</td>
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<tr>
<td>Orange-crowned Warbler</td>
<td>33%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Virginia's Warbler</td>
<td>31%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Red-faced Warbler</td>
<td>40%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>MacGillivray's Warbler</td>
<td>49%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Yellow-rumped Warbler</td>
<td>38%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Western Tanager</td>
<td>45%</td>
<td>West-Central Idaho</td>
<td>(Hovis et al. 1997)</td>
</tr>
<tr>
<td></td>
<td>30%</td>
<td>Northeastern New Mexico</td>
<td>(Goguen and Mathews 1998)</td>
</tr>
<tr>
<td></td>
<td>46%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Scarlet Tanager</td>
<td>69–78%**</td>
<td>Illinois</td>
<td>(Brawn and Robinson 1996)</td>
</tr>
<tr>
<td>Green-tailed Towhee</td>
<td>61%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>White-throated Sparrow</td>
<td>35%</td>
<td>Adirondack Park, New York</td>
<td>(Tuttle 1993)</td>
</tr>
<tr>
<td></td>
<td>45%</td>
<td>Algonquin Park, Canada</td>
<td>(Falls and Kopachena 1994)</td>
</tr>
<tr>
<td>Dark-eyed Junco</td>
<td>31%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
<tr>
<td>Indigo Bunting</td>
<td>75%</td>
<td>Indiana</td>
<td>(Carey and Nolan 1979)</td>
</tr>
<tr>
<td>Black-headed Grosbeak</td>
<td>23%</td>
<td>Arizona</td>
<td>(Martin 1993a)</td>
</tr>
</tbody>
</table>
Breeding Seasons
Breeding Seasons

I. Factors affecting breeding seasons
   • Most intriguing feature is the periodicity of reproduction
   • Why are Mountain Bluebirds paired and ready to breed in late March and early April every year?
What factors affect the breeding season of a particular species in a particular place at a particular time?

A. Hypotheses
   1. Food availability
   2. Habitat
   3. Temperature
   4. Photoperiod
B. Types of Answers
Proximate vs. Ultimate

Notice that the central question can be answered at two different levels;
At a proximate and at an ultimate level
Proximate Level – explains the how and in what way aspect of the question, describes the mechanistic and physiological aspects.

Ultimate Level – involves an evolutionary explanation and involves an argument about adaptation/survival value
in connection with the study of breeding periodicity notion of proximate and ultimate factors was defined

need to differentiate between factors involved in a phenotypes evolution and factors involved in its physiological expression
Ultimate factors affect the timing of reproduction and proximate environmental factors get birds to the optimal time.
II. Annual Cycle
   A. Annual Energy Budget and the Annual Cycle

   There is an annual energy budget that partitions out the energy demanding events in a bird's life with a certain degree of equity.
White-fronted Goose (migratory)
Molt takes approx. 3½ weeks

Chaffinch (resident)
Molt takes approx. 10–11 weeks

Chaffinch (migratory)
Molt takes approx. 8 weeks

Snow Bunting (migratory)
Molt takes approx. 4 weeks
• Winter Thermoregulation – 90-100kJ/day
• Prebasic Molt 90kJ/day
• Vernal Migration, including premigratory fat deposition or movement to breeding habitat if not a migratory species 100kJ/day
• Reproduction 100kJ/day
  – Gonad development
  – Territory establishment
  – Courtship and copulation
  – Nest building, egg laying
  – Incubation
  – Brooding
  – Post-fledgling care
• Prealternate Molt 90kJ/day
• Migration including premigratory fat deposition, or movement to winter territory if not migratory 100kJ/day
III. Ultimate factors

What are the ultimate factors that function as selective forces in the evolution of breeding periodicity?

A. Factors on the breeding range.
1. Yellow Wagtail (*Motacilla flava*)

All subspecies winter together in Africa under the same environmental conditions,
Period of molt, fat deposition, and gonad development is correlated with latitude of subspecies breeding grounds.
Furthest migrants left last!

Show a differential response that is correlated to the latitude of their breeding range suggesting that it seems to be determined by the latitude hence climate of the breeding area.
What determines the timing of breeding?

Must be factors on the breeding grounds!

Why?

Because all were exposed to the same conditions on the wintering grounds
2. The case of *Zonotrichia leucophyrs*

Subspecies *pugetensis* and *nutallii* both winter in San Francisco Bay area
*nuttallii*, the resident subspecies begins nesting in March

*pugetensis* goes through prebasic molt, puts on fat doesn’t migrate until April – long after *nuttallii* is breeding!!
*nuttallii* responds earlier to same winter environment than *pugetensis*

Timing of reproductive development correlated with seasonal suitability of latitude.
B. Environmental Factors

Hypothesized – timing of breeding season evolved so that breeding occurs under environmental conditions that are most suitable for survival of young.
• Food availability
• Nest site availability — sedge wrens
• Water levels (riverine ducks in Australia)
• Minimal rates of nest predation
  (Clay-colored Robin)
IV. Proximate Control

Cannot wait until food availability or nest sites are optimal before commence reproduction.

Begin before optimal time!
Must be set of environmental factors that affect development of reproductive state

A. Endogenous

Are they endogenous rather than exogenous?
Willow Warbler
(12L/12D)

a. molt expressed in absence of natural environmental cues

b. periodicity of molt affected (drifts out of phase)

c. cycle can be maintained but not sufficient
Input from environment provides Zeitgeber (time giver)

B. Exogenous

Proximate environmental factors affect development of reproductive state.
Factor must reliably predict the advent of the optimum for ultimate factor involved!

1. Photoperiod

Photoperiod is reliable factor.
a. used by majority of temperate species
b. less valuable for tropical species
2. Rainfall

regularity of alternate wet and dry periods provides an alternate predictor – effect may be direct most likely indirect
C. Need for predictability

Species differ in needs for predictive information provided by proximate environmental factors.
1. minimal need due to constancy of environment

ultimate factor present throughout most of year, hence prediction unnecessary
a. Sooty Terns

Ascension Island Populations Breed every 9.7 months
b. Rufous-collared Sparrow

Birds breed every 6 months, associated with 2 rainy seasons
2. minimal need because environment is unpredictable

Characteristic of arid regions

a. Zebra Finches of Australia

breed following irregular rains no matter what time of year
pairs seen copulating within few hours of rainfall

build nest and lays eggs within 1 week!
• adults maintain tonic levels of FSH, LH
• gonads remain at constant size throughout year (not producing gametes)
• upon ingesting water, FSH increases – meiosis completed
• if experimentally dehydrated – gonads shrink
Red-billed Quelea occurs in large flocks and is an agricultural pest, not due to the direct effect of rainfall but the development of green, pliable grasses.
Males use grass for nest building

Provides tactile sensation that affects hypothalamus increasing release of FSH
Red Crossbills – reproduction timed to availability of conifer crops

Roam in large nomadic flocks

When find food they breed no matter what season.
3. Strong dependence

Temperate species use daylength

Obligatory response is modified by other environmental factors

Accelerators & inhibitors
a. Testis size in mild winters 2x larger than in winters with below normal temps

b. White Crowned Sparrow – cool stormy spring delays onset of breeding

LH and Testosterone levels maintained longer than in fair spring
c. habitat condition may also function to accelerate or inhibit lack of nesting cover and poor food availability can cause sexually mature birds to delay reproduction
Male Dickcissels removed from territories and kept under natural photoperiod went into gonadal regression and molted prematurely.
Breeding Territories
Breeding Territories

During breeding season nearly all birds defend some type of territory

Size and function varies widely

- Nest only
- Area which includes food, nest sites, roost sites etc.
A territory is a defended area.

**Type A** (mating, nesting, & feeding territory)

An area within which all activities occur (such as courtship, mating, nesting, & foraging).

also called an 'all-purpose territory'
the type of territory defended by many songbirds
**Type B**, or mating & nesting territory
An area within which all breeding activities occur, but most foraging occurs elsewhere.
the type of territory defended by male Red-winged Blackbirds, Yellow-headed Blackbirds
Type C, or **nesting territory**
A nest plus a small area around it.
the type of territory defended by colonial waterbirds
**Type D**, or pairing & mating territory
the type of territory defended by males in **lekking species**
Type E, or roosting territory

Type F, or winter territory
Winter territories typically include foraging areas & roost sites. May be equivalent (in terms of location), or nearly so, to the Type A territory, or may be, for a migratory species, on the wintering grounds
Functions of Territories

• Evade predators more easily
• Locate / defend food
Functions of Territories

• Reduces chance of interference by others in population
  • nest material
  • destruction of conspecific eggs/young
  • egg dumping / extra-pair copulations
Figure 5. Territory size as a function of male density.
Figure 7. Number of mates of individual males as a function of the vegetation index of their territories.
Why don’t all species defend territories?

A territory is advantageous as long as resources do not become too clumped or too unpredictable.
Territories are a type of interference competition and hence is correlated with abundant resources

1. Resources are aggregated highly aggregated spatially,

the competition for that one best spot would be intense and no single male would probably be able to successfully defend that area and still mate.
2. Resources unpredictable

Similarly if the available resources for nesting are temporally unpredictable it is not productive to maintain a territory in the hopes that somehow resources will develop within the territory boundary.
3. Resources Widely Dispersed

Cost in both time and energy

May also be so widely dispersed that it takes too much time and energy to defend it – e.g. prey populations for many raptors
Thus, territoriality depends on the interaction of resource distribution and the cost of resource defense.