From Hubbard Brook to Chicxulub: Where do our birds come from?

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with contributions from Cody Kent (Tulane), Natalie Sanchez (Univ. Alberta), and Cagan Sekercioglu (Univ. Utah)

Photo
Sara Kaiser
Dedications

• First, to Dick Holmes: You taught me SO MUCH!
  – Science, curiosity, value of data
  – Intellectual generosity
  – Collaborations involving interspecific competition, foraging ecology, population limitation/regulation,
• To Deb Holmes:
  – Magical woodcock evenings in Lyme Center (and great lasagna!)
  – https://www.youtube.com/watch?v=P1g4ZX6crwM
  – innumerable wonderful conversations over the years
  – Mentoring and inspiration in the importance of gender equality, kids, family
“Everything is connected to everything else.”
(Barry Commoner, 1971, *The Closing Circle*)

- Extend this ecological generalization to time?
- Focus here:
  - Connect HBEF birds to Earth history
  - Integrate ecology and evolution
- Dick Holmes inspired the kinds of questions addressed here:
  1. Who are the Hubbard Brook birds?
  2. What controls abundance of Hubbard Brook migratory breeding birds?
  3. What controls abundance of migrants wintering in Caribbean?
  4. Why do *warblers* dominate Caribbean migrants?
Part 1: Who are the Hubbard Brook birds?

**Hubbard Brook Warblers:**
Blk. & Wh. Warbler
Bk.-thr. Green Warbler
Bk.-thr. Blue Warbler
Yellow-r. Warbler
Blackburnian Warbler
Chestnut-sided Warbler
Ovenbird
American Redstart
Canada Warbler

(Yellow = Caribbean Winterers)

Warblers rule!
### Warblers also dominate Caribbean winter bird communities

**Also:** Parulid warblers = 100% of wintering migrant birds surveyed in Jamaica, 1989 (Sliwa; N = 585 point counts, 16 sites, 6,144 total bird individuals, 2,262 total migrant individuals)

<table>
<thead>
<tr>
<th>Warbler</th>
<th>Survey Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rough-winged swallow</td>
<td>infrequent; aerial</td>
</tr>
<tr>
<td>Tree swallow</td>
<td></td>
</tr>
<tr>
<td>Gray catbird</td>
<td></td>
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<tr>
<td>Ovenbird</td>
<td></td>
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<tr>
<td>Worm-eating warbler</td>
<td></td>
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<tr>
<td>Louisiana waterthrush</td>
<td></td>
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<tr>
<td>Northern waterthrush</td>
<td></td>
</tr>
<tr>
<td>Black-and-white Warbler</td>
<td></td>
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<tr>
<td>Prothonotary warbler</td>
<td>infrequent, spotty</td>
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<tr>
<td>Swainson's warbler</td>
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<tr>
<td>Common yellowthroat</td>
<td></td>
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<tr>
<td>Hooded warbler</td>
<td>infrequent</td>
</tr>
<tr>
<td>American redstart</td>
<td></td>
</tr>
<tr>
<td>Cape May warbler</td>
<td></td>
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<tr>
<td>Northern parula</td>
<td></td>
</tr>
<tr>
<td>Magnolia warbler</td>
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<tr>
<td>Chestnut-sided warbler</td>
<td>infrequent, spotty</td>
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<tr>
<td>Black-throated blue warbler</td>
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<tr>
<td>Palm warbler</td>
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<tr>
<td>Yellow-rumped warbler</td>
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</tr>
<tr>
<td>Yellow-throated warbler</td>
<td></td>
</tr>
<tr>
<td>Prairie warbler</td>
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<tr>
<td>Black-throated green warbler</td>
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</tr>
<tr>
<td>Summer tanager</td>
<td>rare</td>
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<tr>
<td>Rose-breasted grosbeak</td>
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<tr>
<td>Indigo bunting</td>
<td>infrequent, spotty</td>
</tr>
<tr>
<td>Baltimore oriole</td>
<td>infrequent, spotty</td>
</tr>
</tbody>
</table>

eBird data, Jamaica winter, 1900-2018
Part 2: What controls migrant bird abundance?

- Populations depend on reproduction & survival!
- Importance of redstart reproduction indicated by long-term data: Nesting success predicts population change
- Notice: variation in nesting success (X-axis)

Sherry et al., 2015, *Journal of Avian Biology*
Nesting success variation?

- Nest predators! (fluctuate annually)
- Baffled nests fledged young at almost double rate of controls
- Squirrel/chipmunk co-vary
- Results support scansorial mammals as most important nest predators – Especially red squirrel
- Weather also impacts nest success, indirectly (via food?)

Sherry et al., 2015, *Journal of Avian Biology*
Winter also limits migrant populations

• Black-throated blue warbler annual survival corresponds to Caribbean El Niño-La Niña (ENSO = SOI) fluctuations in rainfall & probably food (Sillett, Holmes, & Sherry, *Science* 2000)

• Redstart annual survival also impacted by rainfall
  – Insect food reduction \(\rightarrow\) worse body condition, delayed departure Spring migration (Cooper, Sherry, & Marra, 2015, *Ecology*)

![Graph showing survival and SOI over years](image)
Importance of *multiple seasons*

- **Population Ecology:** Winter & summer
  - Winter affects adult survival
  - Winter affects reproduction indirectly via carry-over effects (pioneered by Marra, Holmes, Sillett, Webster)
  - Summer affects reproduction directly

- **Evolution of feeding ecology:** Winter?
  - Winter impacts both annual adult survival AND reproductive success
  - Winter fitness food-limited
  - Summer fitness complicated by reproduction

- MacArthur’s classic 1958 study lacked winter perspective!
Full *life* cycle important

- *Not just summer & winter, not just full annual cycle*
  - *Also full geographic range*
  - *Connectivity*
- *Powerful methods available to probe migrant populations in both time and space*
- *These methods → renaissance of migratory bird population studies*
  - *Started at Hubbard Brook!*

Sherry, 2018, PNAS
Part 3: What controls abundance of wintering migrants in Caribbean?

• Winter food = critical resource!
• This implies competition among species!
• André Dhondt’s conditions for interspecific competition:
  1. Population resource-limited (e.g., food),
  2. Individuals compete within population for that resource
  3. Resource overlap among different species for that resource
• High food overlaps (out of 1.0) among warblers in Jamaican wet limestone forest (Cody Kent & Tom Sherry, unpubl. data)

<table>
<thead>
<tr>
<th></th>
<th>black-throated blue</th>
<th>worm-eating</th>
<th>n. parula</th>
<th>black-and-white</th>
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<tr>
<td>redstart</td>
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<td>0.46</td>
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<td>0.82</td>
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<tr>
<td>n. parula</td>
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<td>0.76</td>
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</table>
Five coexisting wet limestone spps. differ in diet, foraging substrates, morphology:

- Redstart: aerobatic forager in foliage, airspace
- Black-throated blue warbler: gleans live leaves & branches, middle layers
- Black-and-white warbler: creeps along tree trunks & branches
- Worm-eating warbler: probes in dead leaf clusters
- N. parula warbler: gleans live leaves, forest canopy

(Cody Kent & TWS, unpubl. data)

“MacArthur’s Warblers” in winter!
What do wintering warblers eat?

- Birds adapted morphologically to small prey
- Larger-beaked warblers eat larger beetles (wet limestone)!
- Mostly insects, but some species rely on fruit, nectar (e.g., Wunderle talk)
- All migrants we’ve studied eat tiny ants! (1-3 mm)
- Opportunistic on most other small insects: beetles, parasitic wasps, bark lice, tree hoppers, etc. (modal size ~2 mm)

From Kristen Rosamond, Tulane senior honors thesis, 2018
Part 4: Why do warblers dominate Caribbean migrants in winter?

• Evolutionary history, phylogeny!
• Three important questions:
  – Whence the warblers (Parulidae)?
  – Why so many “empty” Caribbean niches?
  – Why the warbler adaptive radiation including Caribbean?

• Preliminary answers…
Whence parulid warblers?

- Warblers = Emberizoids (finches/tanagers), colonized Americas from Asia, ~17 MYA (Miocene warm period; via Beringia)
  - Ultimately from Australia!
- Stem (ancestral) warblers ~12 MYA = Newcomers!
- Ovenbird split from Magnolia (Setophaga) warbler ~6 MYA

Fragment of passerine phylogeny (Fig. 1), Oliveros et al. unpubl. MS
Available feeding niches in Caribbean?

- Caribbean *islands* relatively species-depauperate

- Seasonal rainfall, so residents don’t dominate food (Greenberg’s “Breeding Currency Hypothesis”)
  - Small insects, fruit, nectar available throughout dry season
  - Warblers adapted for small insects

- Caribbean geological history

- Possible role for mainland South and Central America and Chicxulub?
Chicxulub impact re-set planetary history ~66 MYA

- Asteroid ~10-15 miles in diameter slammed into Yucatan, wiped out ~70% of species globally!
- A few mammals survived → humans!
- A few dinosaurs survived → Birds!
- South America at the time was corner of Gondwanaland, tropical, huge, isolated continent (Claramunt & Cracraft 2012)
  - Also geologically complex
  - Speciation rate exceeded extinction rate
  - Species diversified steadily
### Mainland Neotropical insectivores!

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>No. Species</th>
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<td>Piciformes</td>
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<td>Passeriformes</td>
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<td>Pipridae</td>
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<td>Vireonidae</td>
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<td>Corvidae</td>
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<td>Polioptilidae</td>
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<tr>
<td>Mimidae</td>
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</table>

**Numbers in table for just insectivorous species!**
Specialization in mainland tropical insect-feeding birds

(Sherry et al. unpubl. MS.)

- Specialization = evolutionary consequence of competition by so many species & clades

- Tradeoff: Feeding specialization → weak dispersal
  - Some tropical forest understory birds lack stamina to fly a few hundred meters!
  - Greater genetic variability geographically in tropical birds

Fabricicio Vasconselos photo
Caribbean ecological equivalents...

...for absent mainland Neotropical insectivores?

Myioborus “whitestarts” (12 spp.)

43 species of Dendrocolaptidae (tree creepers)

158 species of Furnariidae: (Neotropical ovenbirds)

275 species of tyrannid flycatchers, including canopy spp. like Tyrannulets

158 species of Furnariidae: (Neotropical ovenbirds)

Epinecrophylla antwrens (10 spp.)
So…why do warblers rule the Caribbean?

- Seasonality constrains resident Caribbean populations
- Warblers are small-bodied, opportunistic & tweezer-beaked, ideal to exploit tiny dry season insects, fruit & nectar
- “Empty” Caribbean niches (most older mainland insectivore clades never colonized)
Recapitulation

- Warblers abundant at Hubbard Brook
- HBEF warblers belong as much to Caribbean as temperate forests
- History, ecology, & geography necessary to understand Caribbean warbler adaptive radiation
- Phylogenetic studies provide important insights into origins, timing, circumstances
- Integrating ecology and evolution—space and time—has bright future
Gondwanaland, including South America, starts to break up: OLD, large (and geologically complex) AREA, TROPICAL CLIMATE

- High speciation rate (tropics as “cradle”)
- Low extinction rate (tropics as “museum”)

Release from interspecific competition

Mass extinction ~65 Million Years Ago

Multiple adaptive radiations in South America, Paleocene Epoch to present: Animals, Plants, etc.

- Development of latitudinal diversity gradient
- High tropical species richness, all taxa including Insectivores (birds, mammals, herps, fish, arthropods)

Diffuse exploitative interspecific competition

Extensive genetic geographic variation & ecotypic variation

- Weakened dispersal

Low food abundance for insectivores (“arthropod desert”), particularly in wet tropics

- Insectivorous birds evolve energy-conserving (physiological) life histories

Insects (& other arthropods) evolve diverse anti-predator adaptations

- Predator-prey arms races

Cost of residency, specialization: life-history tradeoff

Insectivorous birds evolve feeding specialization: habitats, substrates, prey types
A few well defended arthropods...

- Stinging—e.g., *Paraponera* ants, warrior wasps, diverse other ants, bees (Hymenoptera)
- Physical—diverse Orthoptera
- Chemical protection, e.g., *Heliconius* butterflies (aposematism) & Batesian & Mullerian mimics
- Diverse escape strategies—flying, jumping, clicking, hard bodies, startle displays
- Camouflage, crypsis,
“Mimicry is much more pervasive in tropical insect communities than the few well-known examples from butterflies would suggest. Although the first examples and much of the current literature implies that mimicry is primarily a property of butterflies, mimicry is common in most taxa of tropical arthropods, including spiders.”

“practically every diurnally active and conspicuous [tropical] arthropod participates in some form of mimicry”.

(Hespenheide, 1996, Occasional Publication of the Midred E. Mathias Botanical Garden 1.)