Offspring Development Mode and the Evolution of Brood Parasitism

the thorny case of Coccyzus cuckoos

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1. Abstract
- Brood parasitism should shift from facultative to obligate when the cost of parental care is high.
- Development mode is coupled with mode of parasitism (see Box 2).
- North American cuckoos appear to contradict this model, as they have altricial offspring but are thought to be facultative interspecific brood parasites (in addition to being parasites of conspecifics).
- Our population genetics model suggests obligate parasitism could spread from rare to predominant in < 3,000 generations.
- We found no parasitism in 10,197 songbird nests, despite varied levels of food and nest predation.
- Egg-rejection experiments reveal that many "hosts" would accept cuckoo eggs if parasitized.
- Previous reports of cuckoos parasitizing songbirds may reflect mistakes by cuckoos trying to parasitize each other.

2. Background: Life History Pattern of Interspecific Brood Parasites

After the origin of facultative interspecific parasitism, a species should evolve obligate parasitism if the cost of parental care is high (i.e., if offspring are altricial rather than precocial; Davies 2000).

Data support theory, with three exceptions (Lyon & Eadie 1991).

<table>
<thead>
<tr>
<th>Parasitism Mode</th>
<th>Species Count</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obligate</td>
<td>86</td>
</tr>
<tr>
<td>Facultative</td>
<td>2</td>
</tr>
</tbody>
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3. Background: North American Cuckoos
- North American cuckoos (Coccyzus americanus and C. erythrophthalmus) are intraspecific brood parasites (Fleischer et al. 1985).
- Anecdotal data indicate that North American cuckoos are also facultative parasites of other species (Darwin 1859, Lorenzana & Sealy 2002), perhaps even having evolved mimetic eggs (Hughes 1997).
- This facultative interspecific parasitism conflicts with theory, as cuckoos have altricial offspring (= expensive parental care).
- Is our theoretical framework wrong? Or does some other factor explain the reports of interspecific parasitism by Coccyzus cuckoos?
- We explored this with an evolutionary model, data from nests of potential hosts, and egg-rejection experiments.

4. Population Genetics Model
How fast would obligate brood parasitism spread in a population of parentally breeding cuckoos?
QUICKLY: it becomes the predominant reproductive mode in 300 to 3,000 generations (depending on model values)

\[ s = \text{selection against parental care} \]
\[ c = \text{cost of parental care} \]
\[ q = \text{frequency of parasites} \]

- Single locus with three phenotypes
  - Fitness: obligate > facultative > parental
  - Parental parasites: \( s \cdot c - q \cdot c \cdot q \)
  - Facultative parasites: \( 1 - c \cdot q \cdot q \)
  - Obligate parasites: \( 1 - c \cdot q \cdot q \)

5. Nest Monitoring Data
How often are songbirds parasitized by North American cuckoos?

ALMOST NEVER: no parasitism in 10,197 songbird nests in Illinois, Missouri, & Pennsylvania

95% CI on parasitism frequency:
0 to 0.0003617
excluding likely rejecter species, 95% CI: 0 to 0.0004132

absence of parasitism is despite:
- spatial and temporal overlap of cuckoos and hosts
- 1,801 'host' nests active during periodical cicada emergences
- variation in likelihood of nest predation (48% - 89% at different site-years)

6. Egg Rejection Experiments
Is apparent absence of parasitism due to widespread egg rejection by hosts?
NO: common hosts accept some or all model cuckoo eggs

- dusk/thrush eastern brown cardinal brown thrasher gray catbird

- added a model cuckoo egg to host nests during incubation
- monitored nests for egg rejection within 5 days

7. Synthesis & New Hypothesis
- The literature includes anecdotal reports of North American cuckoos parasitizing 18 species, predominantly songbirds with blue eggs that "match" those of Coccyzus (Hughes 1997).
- This observation is contrary to theoretical expectations (see Boxes 2 and 3).
- Our model suggests obligate brood parasitism could transition from a very rare strategy to the predominant strategy in < 3,000 generations.
- We found no evidence of Coccyzus cuckoos parasitizing songbirds, despite opportunity and favorable ecological conditions.
- Common "hosts" sometimes or always accepted model cuckoo eggs, suggesting that most parasitic eggs would be accepted if laid.
- A new hypothesis accounts for these observations: Coccyzus cuckoo are not facultative interspecific parasites. Rather, they parasitize each other (Fleischer et al. 1985) and, rarely, make mistakes by parasitizing songbirds whose eggs look like cuckoo eggs.

Acknowledgments
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References
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