

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).

	<i>altricial offspring</i> (high cost of parental care)	<i>precocial offspring</i> (lower cost of parental care)
<i>obligate parasites</i>	86 species (songbirds, etc., as predicted)	1 species (black-headed duck)
<i>facultative parasites</i>	2 species (North America's yellow-billed & black-billed cuckoos, <i>Coccyzus</i> spp.)	33 species (ducks, as predicted)

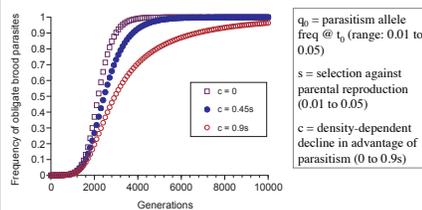
3. Background: North American Cuckoos

- North American cuckoos (*Coccyzus americanus* and *C. erythroptalmus*) 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)



ϕ_0 = parasitism allele freq @ t_0 (range: 0.01 to 0.05)
s = selection against parental reproduction (0.01 to 0.05)
c = density-dependent decline in advantage of parasitism (0 to 0.9s)

- single locus with three phenotypes
- fitness: obligate > facultative > parental
parental females = $1 - s$
facultatively parasitic females = $1 - s/2 - c(q^2 + pq)/2$
obligately parasitic females = $1 - c(q^2 + pq)$

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



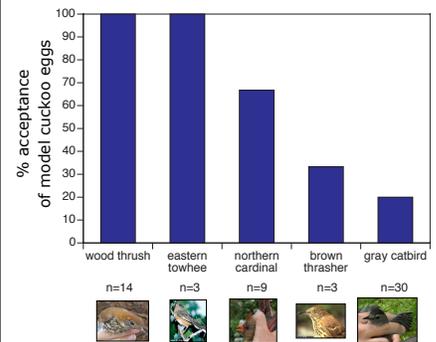
absence of parasitism is despite

- 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



- 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* cuckoos 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

- Darwin C. 1859. On the origin of species by means of natural selection. London: Murray
- Davies NB. 2000. Cuckoos, cowbirds, and other cheats. London: T & AD Poyser
- Fleischer RC, Murphy MT, Hunt LE. 1985. Wilson Bull. 97:125-127
- Hughes JM. 1997. Can. J. Zool. 75:1380-1386
- Lorenzana JC, Sealy SG. 2002. Auk 119:851-854
- Lyon BE, Eadie JM. 1991. Behav. Ecol. 2:309-318