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The Ecology of Avian Brood Parasitism

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Brood parasitic birds lay their eggs in the nests of others, sparing themselves the expense of rearing their own young. The resulting coevolutionary arms race includes sophisticated defenses by hosts and escalating tools of exploitation by parasites.

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Brood Parasitism as a Reproductive Strategy

Avian brood parasitism, or the laying of one's eggs in the nest of another individual, is a reproductive strategy whereby parasites foist the cost of rearing their offspring onto another individual, the host (Davies 2000). Brood parasitism may be facultative at the species or individual levels, with some eggs incubated by the mother and others laid in foreign nests, or obligate. Brood parasitism may also be intraspecific, with eggs laid in other nests of the parasite's own species, or interspecific, with all eggs laid in the nests of other species. Cowbirds and cuckoos are the most commonly studied avian brood parasites (Davies 2000), although obligate interspecific brood parasitism has evolved at least 7 separate times among various avian clades, including cowbirds (*Icteridae*), honeyguides (*Indicatoridae*), Old World cuckoos (*Cuculinae*), twice in the New World cuckoos (*Neomorphinae*), indigobirds and their allies (*Ploceidae*), and the Black-headed duck (*Anatidae*).

For the parasite, benefits include increased fecundity due to greater allocation of resources toward mating and producing more eggs rather than defending nests, incubating eggs, and feeding young. For hosts of brood parasitic birds, the costs of parasitism range from

diminished nestling growth rate, due to competition with larger and more competitive parasitic offspring (cowbirds, whydahs), to total loss of breeding by the abandonment of parasitized broods (cowbirds, cuckoos), the eviction of all host eggs by the early-hatching parasites (cuckoos), or the killing of host hatchlings by parasitic hatchlings (cuckoos, honeyguides) (Kilner 2005; Servedio & Hauber 2006). These costs exert reciprocal natural selection on parasites and hosts, such that in many cases host-parasite interactions result in escalating coevolution between intimately tied and interdependent species (Langmore *et al.* 2003). In turn, many hosts are able to discriminate against and reject foreign eggs or chicks based on visual, acoustic, or multimodal sensory cues (Cassey *et al.* 2008). The eggs of many brood parasites, for example, mimic those of their hosts (to deceive hosts to accept), have harder shells (to impede rejection by puncture), and require slightly shorter incubation times (causing a size advantage for parasitic nestlings) (Davies 2000) (Figure 1).



Figure 1: Common Cuckoos (*Cuculus canorus*) parasitizing Common Redstarts (*Phoenicurus phoenicurus*) in Europe lay eggs whose colors mimic closely host egg colors (the parasite egg is the slightly larger egg). In contrast (inset), Brown-headed Cowbirds (*Molothrus ater*) in North America lay speckled eggs which do not resemble the pure white eggs of one of their many hosts, the Eastern Phoebe (*Sayornis phoebe*).

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Evolution and Maintenance

There are two major hypotheses that have been implemented in attempting to explain the evolution and maintenance of the complex and often paradoxical reproductive strategies that fall under brood parasitism (Rothstein & Robinson, 1998). The evolutionary lag hypothesis posits that rejection is almost always more adaptive than acceptance, so that 1. hosts accept parasitism only because they have not yet evolved mechanisms for defense against parasites and/or 2. parasites fail with certain hosts because they have not yet evolved mechanisms for overcoming existing host defenses. Historically recent contact, due to natural or anthropogenic change (e.g., deforestation, forest fragmentation), the acceptance of foreign eggs even when these do not resemble host eggs (nonmimetic), and a high cost of parasitism without apparent defenses to prevent and recognize parasitism, all suggest that evolutionary lag is the mechanism for host acceptance of parasitic eggs, but as it is difficult to test this hypothesis directly, it is often the default or fall-back explanation (Peer & Sealy 2004).

In contrast, the evolutionary equilibrium hypothesis posits that hosts accept parasitism only because the cost associated with the rejection of parasitic eggs is greater than the cost of rearing cowbird offspring (Klippenstine & Sealy 2008). Rejection costs may be incurred via misrecognition of parasitic eggs, so that hosts mistakenly eject their own eggs, or via rejection costs, when hosts accidentally damage their own eggs while attempting to remove parasitic eggs. Host-egg mimicry and increased eggshell thickness by parasitic eggs have both evolved repeatedly in diverse lineages of obligate parasites, rendering the recognition and removal of parasitic eggs more costly, and thereby increasing selective pressure to accept parasitism or delay the evolution of costly and error-prone discrimination mechanisms to reject parasites.

The Coevolutionary "Arms-Race"

Egg Mimicry

Most host defenses against costly parasitism occur at the egg stage with the recognition and removal of parasitic eggs. This ability may have evolved from behaviors such as nest sanitation (removal of fecal sacs and broken shells), and morphological traits such as large bills, which serve as preadaptations for removal of parasitic eggs (Peer & Sealy 2004). Egg recognition thereby exerts selective pressure on the parasites to lay eggs that mimic in appearance those of their host, and reciprocal pressure on hosts to fine-tune their discriminative abilities. This "arms race" is at the heart of brood parasitism as a coevolutionary phenomenon. The degree of egg mimicry and concurrent host specialization varies dramatically among parasitic clades. A recent study by Klippenstine and Sealy (2008) has shown that grassland cowbird hosts possess the ability to discriminate between and reject foreign eggs when the eggs differ dramatically (in color and maculation) from their own eggs, but these same species do not eject real or model cowbird eggs. This suggests that a more generalized form of egg mimicry than that employed by cuckoos, and that Brown-headed cowbird (*Molothrus ater*) eggs loosely mimic a wide range of potential grassland hosts. In contrast, individual females of many old world cuckoos, lay eggs that are specific to particular hosts — that is, they mimic eggs of a specific subset of their host species. Generalist cowbirds, by contrast, do not lay highly mimetic eggs, and parasitize a wide range of hosts rather than specializing on a particular species of host or host-egg race. Recognition and removal of parasitic eggs is based largely on differences between own and foreign eggs in background color, with size, shape, and maculation acting in various combinations to elicit egg rejection. A major caveat in studies of degree of egg color matching to date has been that eggs are assessed according to the human visual system. As many birds possess a fourth, UV-sensitive photoreceptor type relevant in behavioral decision-making, biologically realistic sensory models should be used in future studies to determine the parameters eliciting egg rejection (Cassey *et al.* 2008; Honza *et al.* 2007).

Nestling Mimicry

If constraints surrounding egg recognition and removal make rejection at the egg stage too costly, the recognition and rejection of nestlings may provide an effective alternative defense strategy for host species, ultimately resulting in plumage, mouth, and begging call mimicry (Langmore *et al.* 2003; Anderson *et al.* 2009). For post-hatching discrimination to evolve, parasitism rates must be sufficiently high to outweigh the cost of recognition errors, and hosts must have sufficiently high fecundity to bear the cost of mistakenly rejecting their own chicks (Langmore *et al.* 2003). Host rejection of parasitic nestlings has been demonstrated in Superb Fairy-wrens (*Malurus cyaneus*), and may have selected for the evolution of nestling begging call mimicry in Horsfield's Bronze-Cuckoos (*Chalcites basalus*) (Langmore *et al.* 2003). Nestling discrimination by hosts is, however, relatively rare, despite hosts having various behavioral and cognitive traits that would enable such behavior. This is likely because nestling discrimination can only evolve when egg discrimination has failed (Grim 2006).

Hosts may discriminate nestlings using cues such as size, color, vocalization, and overall clutch size. Mouth coloration and gape patterns of parasitic nestlings can stimulate higher rates of provisioning by host parents by serving as a supernormal stimulus and enabling parasites to outcompete host young (Kilner *et al.* 1999). In parasitic indigobirds, nestling flange markings may resemble those of healthy hosts in order to stimulate greater provisioning (Hauber & Kilner 2007) and to avoid discrimination through reduced feeding by host parents (Schuetz 2005).

Identity Crisis?

If parasitic nestlings are not exposed to conspecifics during development, then how are they able to identify members of their own species with which to mate? Rather than relying solely on cues learned from parents and nestmates, brood parasites must employ some other mechanism for species recognition in order to avoid mistakenly courting heterospecifics. Brown-headed Cowbirds seem to rely on a combination of self-referent phenotype matching and a "password" like vocal trigger that unlocks learning of species-specific cues at their first encounter with a conspecific (Hauber *et al.* 2000, 2001). Such a combination of developmental paths and recognition mechanism may apply to brood parasites more generally, and could represent a difficult-to-evolve behavioral algorithm, as was seen recently in an

experimental study where male facultative interspecific brood parasitic ducks mistakenly courted females of the host species instead of their own (Sorenson *et al.* 2010).

Conservation Impacts of Brood Parasitism

As a widespread generalist brood parasite, the native Brown-headed Cowbird poses a conservation threat to several of its North American passerine hosts. Selective pressure resulting from cowbird parasitism is likely higher now than in the past, owing to increased suitable habitat provided by deforestation, leaving more and novel hosts vulnerable to parasitism by increasing numbers of cowbirds (Davis & Sealy 2000). For brown-headed cowbird host populations already in decline, such as the endangered Kirtland's Warblers (*Dendroica kirtlandii*), Black-capped Vireos (*Vireo atricapilla*), Least Bell's Vireos (*Vireo bellii pusillus*), and Southwestern Willow Flycatchers (*Empidonax traillii extimus*), the effects of this can be devastating, and human control of cowbird population size may be necessary to prevent local extinctions (Smith *et al.* 2000). This is a particular consideration for conservation biologists working with hosts of generalist brood parasites, because even when a species declines in number it may continue to be parasitized at high rates, since as generalist parasites, the cowbird population will not be impacted reciprocally with that of individual host species. These applied aspects of host-parasite interactions confirm that scientifically informed conservation management is critical for the efficient and productive planning and implementation of long term goals (Hauber 2009; Parker *et al.* 2010).

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