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Author: Peer, Brian D.

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OVERVIEW

EGG DESTRUCTION AND EGG REMOVAL BY AVIAN BROOD PARASITES: ADAPTIVENESS AND CONSEQUENCES

Brian D. Peer[1]

Department of Biological Sciences, Western Illinois University, Macomb, Illinois 61455, USA

Avian brood parasites possess an array of adaptations that help them to succeed at their alternative breeding strategy, and these adaptations reduce host fitness in several ways. Host eggs may not hatch because brood parasites have relatively short incubation periods that allow them to hatch sooner, and this may cause hosts to stop incubating their eggs (Briskie and Sealy 1990, Hauber 2003). If host eggs hatch, their nestlings may be outcompeted by parasitic nestlings that are often larger (reviewed in Lorenzana and Sealy 1999, Peer et al. 2005). Common Cuckoo (*Cuculus canorus*) nestlings eliminate competition by evicting host nestlings or eggs, and Honeyguide (*Indicator* spp.) and Striped Cuckoo (*Tapera naevia*) nestlings have specialized mandibular hooks used to kill host young (Davies 2000). Brood parasites also remove or puncture host eggs, and this reduces the host's clutch size and sometimes causes the host to abandon its nest (Davies and Brooke 1988, Sealy 1992, Peer and Sealy 1999a). Some parasites may occasionally depredate nests, thereby causing total nest failure (Soler et al. 1995, Arcese et al. 1996). Egg removal and egg puncture are among the least understood of these adaptations.

In a study published in this issue of *The Auk*, Astié and Reboreda (2006) investigated the effects of egg puncture by Shiny Cowbirds (*Molothrus bonariensis*). Shiny Cowbirds punctured host eggs in parasitized as well as unparasitized nests, which reveals that the effects that parasites have on hosts are complex and cannot always be fully understood simply by comparing host reproductive success at parasitized and unparasitized nests.

Adaptiveness of Host Egg Destruction and Removal

Eggs that are removed from host nests are carried away by the parasite and may be eaten (Scott et al. 1992). Female Common Cuckoos remove and consume a host egg at the same time they lay their eggs (Davies 2000), possibly because their eggs are mimetic and they may mistakenly remove them if they wait until later. When female Brown-headed Cowbirds (*M. ater*) remove host eggs in conjunction with parasitism, they do so on the day before they have laid their egg, later on the day of laying, or the next day (Sealy 1992). By contrast, cowbirds do not lay mimetic eggs (but see Peer et al. 2000), which may explain why they do not remove eggs at laying, and one would predict that if cowbirds removed host eggs from nests with eggs that resemble their own (e.g. Northern Cardinal [*Cardinalis cardinalis*], Song Sparrow [*Melospiza melodia*]), they would do so prior to laying.

Most evidence suggests that egg removal enhances host incubation. The "host incubation limit" hypothesis proposes that parasites remove host eggs to ensure that the addition of their egg will not exceed the host's ability to incubate the clutch (Davies and Brooke 1988). In support of this hypothesis, Davies and Brooke (1988) found a greater incidence of unhatched eggs in nests from which host eggs had not been removed, and Lerkelund et al. (1993) found that experimentally enlarged clutches were more likely to contain unhatched eggs. Peer and Bollinger (1997, 2000) suggested that egg size and number influence the effectiveness of incubation. The "incubation efficiency" hypothesis predicts that an enlarged clutch volume will decrease the likelihood of a smaller parasitic egg being incubated effectively among

[1]E-mail: bd-peer@wiu.edu

the larger host eggs. This is consistent with the hypothesis that Brown-headed Cowbirds parasitized larger hosts that occupied open habitats more frequently in the past (Rothstein 1975, Peer and Bollinger 2000, Peer and Sealy 2004). These hosts are more likely to reject cowbird eggs, which suggests that they were parasitized more often and had time to evolve defenses (Rothstein 1975, Peer and Sealy 2004). Larger hosts also build nests that may be more readily found, and they may be superior to smaller hosts because they can provide more food and deter predators better (Rothstein 1975, Peer and Sealy 2004).

Brown-headed Cowbirds remove eggs more frequently from nests of large hosts (see Sealy 1992), which may reflect the fact that they parasitized larger hosts more frequently in the past (i.e. egg removal may be an atavistic trait and it may be declining). According to the incubation efficiency hypothesis, removal of eggs from nests of smaller hosts is less critical, because the larger parasitic egg will contact the host's brood patch better (Peer and Bollinger 2000). For example, cowbird eggs in Yellow Warbler (*Dendroica petechia*) nests hatched whether or not a host egg was removed (McMaster and Sealy 1997). At least two potential costs of host egg removal may lead to its decline if removal has no current utility: risk of injury and increased risk of rejection. A cowbird risks being attacked by a host when it comes to lay (Leathers 1956) and, because a host egg generally is not removed at this time, the cowbird may be injured when it returns again to remove an egg. Hosts that observe a cowbird at the nest also may be more likely to reject parasitism (Strausberger and Burhans 2001; but see Peer and Bollinger 1997). If the costs are greater than the current benefits, and because small hosts are parasitized more often than large hosts (Ortega 1998), this behavior should decline.

Early researchers believed that parasites replaced eggs they removed with their own because hosts could count and rejected parasitism if there were too many eggs (see Hamilton and Orians 1965). Hosts apparently assess overall clutch volume, however, rather than counting the number of eggs. Egg removal has no apparent influence on rejection unless too many eggs are removed, which makes hosts more likely to abandon clutches (Rothstein 1986, Hill and Sealy 1994). When eaten, the eggs provide females with much-needed calcium for the production of more eggs (see Scott et al. 1992), but because not all of these eggs are eaten, the primary reason for removal cannot be food for the parasite. Other possibilities include reducing crowding and competition (Scott 1977) and testing the incubation status of nests (Massoni and Reboreda 1999). Whatever its function, host egg removal is costly to hosts, even those that reject parasitism or species that provision their young with food unsuitable for parasites. If parasitism on such hosts continues (e.g. Scott 1977), their clutches will be reduced through egg removal and, although they do not raise a cowbird, rejecters may lose eggs that cannot be recouped until cowbirds no longer parasitize them (Peer et al. 2005).

Shiny, Bronzed (*M. aeneus*), and Screaming (*M. rufoaxillaris*) cowbirds puncture or remove host eggs (Carter 1986, Fraga 1986, Peer and Sealy 1999a, Nakamura and Cruz 2000). Punctured host eggs are left in the nest, where the contents may stick to the bottom and the eggs cannot be turned, thus possibly attracting predators (Peer and Sealy 1999a, Nakamura and Cruz 2000). Evidence suggests that in some locations, when they locate a nest that is too advanced for successful parasitism, Bronzed Cowbirds puncture eggs to force hosts to renest (Peer and Sealy 1999a). Puncturing eggs may also function to decrease competition (Carter 1986), which may be particularly important because Bronzed Cowbirds frequently parasitize larger hosts (Carter 1986, Peer and Sealy 1999a). Egg puncture in Shiny Cowbirds also may promote renesting by hosts (Nakamura and Cruz 2000), reduce competition (Mason 1986), or possibly test the incubation stage of the host clutch to ascertain whether it is suitable for parasitism (Massoni and Reboreda 1999).

Consequences of Egg Destruction and Removal

Although the adaptiveness of egg puncture and egg removal is not fully understood, it is clear that these behaviors have a significant effect on host fitness (e.g. Peer and Sealy 1999a, Nakamura and Cruz 2000, Tewksbury et al. 2002, Peer et al. 2005). Effects of brood parasitism on hosts are commonly measured by comparing reproductive success at parasitized and unparasitized nests. Such estimates indicate that parasitism reduces success, especially in small hosts that sometimes raise only cowbirds (reviewed in Lorenzana and Sealy 1999, Peer et al. 2005).

One obstacle in estimating the costs of egg puncture by Shiny Cowbirds has been that some hosts reject parasitism (Fraga 1985, Mermoz and Reboreda 2003). Rejecters may remove cowbird eggs before researchers inspect nests, therefore leading to an erroneous conclusion that the nests were not parasitized (e.g. Rothstein 1975, Scott 1977). Astié and Reboreda (2006) calculated the costs inflicted by Shiny Cowbirds at parasitized and unparasitized nests of a large host, the Creamy-bellied Thrush (*Turdus amaurochalinus*), which tends to eject immaculate Shiny Cowbird eggs and accept most spotted Shiny Cowbird eggs (Astié and Reboreda 2005). In Argentina, where their study was conducted, Shiny Cowbirds lay primarily spotted eggs, which facilitated accurate estimates of losses at unparasitized nests. Sixty percent of nests were parasitized, but cowbird nestlings did not affect growth or survival of host nestlings, or nest survival (Astié and Reboreda 2006). Adult Creamy-bellied Thrushes are almost twice as heavy as adult Shiny Cowbirds (63 g vs. 35 g; Dunning 1993), and cowbird and host chicks frequently hatched at the same time, which apparently allowed thrush nestlings to outcompete cowbirds, because in more than half the nests cowbird chicks died.

Most loss incurred by Creamy-bellied Thrushes was from punctured eggs (Astié and Reboreda 2006). Puncture holes were triangular and differed from wren punctures that were not observed in thrush nests. Eggs in parasitized nests were punctured 71% of the time, reducing the number of viable host eggs by 49%. Shiny Cowbirds also punctured eggs in 42% of the unparasitized nests, which reduced the number of eggs by 23%. Nests with punctured eggs had a lower chance of surviving than nests with no eggs punctured.

Shiny and Bronzed cowbirds parasitize larger hosts more frequently than Brown-headed Cowbirds currently do (Carter 1986, Mason 1986, Peer and Sealy 1999a, Astié and Reboreda 2006). These large hosts should possess defenses against egg destruction, in addition to ejecting the parasitic egg, because egg destruction may have the greatest effect on their reproductive success. Because of their size, larger hosts should be relatively successful in thwarting egg destruction if they are present at their nests when cowbirds come to remove eggs. For example, although Yellow Warblers are smaller than Brown-headed Cowbirds, they can prevent cowbirds from removing their eggs (Tewksbury et al. 2002). Astié and Reboreda (2005) found that although Creamy-bellied Thrushes were highly attentive at their nests when cowbirds were most likely to puncture eggs, their presence did little to prevent egg puncture. They simply may not have been there when the cowbirds visited the nests. Video cameras at nests would determine whether this is the case (e.g. Tewksbury et al. 2002). Hosts may be better able to defend against cowbirds laying, because it occurs consistently over a few minutes around sunrise in most species (Scott 1991, Peer and Sealy 1999b). By contrast, egg removal and puncture occur over a greater part of the day, which likely makes it difficult for a host to prevent egg puncture. Also, the cowbird's motivation and benefit from laying may be greater than the motivation and benefit of puncturing or removing host eggs (S. I. Rothstein pers. comm.).

When hosts increase nest attentiveness to decrease egg puncture and egg removal, they may increase the chances of loss from nest predators. Yellow Warblers reduced the frequency of host egg removal from Brown-headed Cowbirds by becoming more vigilant at their nests, but males had to make more trips to the nests, which increased predation (Tewksbury et al. 2002). Studies have demonstrated that nest predators reduce nest success more than cowbirds (Schmidt and Whelan 1999). Likewise, Peer and Sealy (1999a) found that 51% of Northern Cardinal nests were parasitized by Bronzed or Brown-headed cowbirds. Twenty-five percent of parasitized and 9% of unparasitized nests had eggs punctured and 81% of all host nests with punctured eggs were deserted. However, the effects from parasitism were negligible compared with the effects of nest predators, given that only 1 of 115 Northern Cardinal nests successfully fledged young (B. Peer unpubl. data). Perhaps traditional nest predators also affect Creamy-bellied Thrushes more than egg puncture, and the thrushes may focus their defenses against them rather than against cowbirds.

The distinction between traditional nest predators and brood parasites has become ambiguous, because parasites also act as nest predators.

At least one species, the Great Spotted Cuckoo (*Clamator glandarious*), may use "mafia" tactics to ensure that its eggs are accepted. It returns to parasitized nests and destroys the host's clutch if its egg is gone, in effect forcing the host to accept parasitism (Soler et al. 1995). Shiny and Bronzed cowbirds puncture host eggs, and this often causes hosts to abandon nests, which suggests that this behavior is intended to "reset" host nesting activity and create another opportunity for parasitism (Peer and Sealy 1999a, Nakamura and Cruz 2000). Eggs punctured by cowbirds are not eaten, as those taken by predators are, but the effects on the host may be the same. One study suggested that cowbirds puncture eggs to determine whether clutches are at appropriate stages for parasitism (Massoni and Reboreda 1999), but this would be more plausible if the parasite removed and examined an egg rather than leaving it in the nest. Egg puncture may have multiple functions depending on the ecological context but, as has been pointed out, this behavior is risky if the intent is for the host to continue tending a nest, because these nests frequently fail (Nakamura and Cruz 2000, Sealy et al. 2000). Indeed, Creamy-bellied Thrushes deserted many nests that contained punctured eggs (Astié and Reboreda 2006). More research on egg destruction is warranted to ascertain its adaptive significance.

Brown-headed Cowbirds sometimes use a similar tactic when they remove host eggs or nestlings from nests they discover that are too advanced for successful parasitism (Elliott 1999). Such depredation forces hosts to renest, thereby providing cowbirds another opportunity for parasitism (Arcese et al. 1996). This behavior is used regularly by cowbirds parasitizing Song Sparrows on Mandarte Island, British Columbia (Arcese et al. 1996). However, McLaren and Sealy (2000) found no evidence that this behavior occurs with another commonly used host, the Yellow Warbler. There is also evidence from video cameras that cowbirds act as nest predators occasionally, but not regularly. Cowbirds depredated 1 nest out of 25 in a study by Thompson et al. (1999), compared with 2 of 26 nests in a study by Pietz and Granfors (2000), 7 of 132 nests in Granfors et al. (2001), 1 of 24 nests in Renfrew and Ribic (2003), and 9 of 59 nests in Stake and Cimprich (2003), but only one in the latter caused nest failure. Even if cowbirds depredate nests regularly, the effects may not be dramatic. In hosts, such as the Song Sparrow, that are common throughout North America, it may even benefit overall community diversity by preventing one dominant species from outcompeting other species (Rothstein and Peer 2005). The defenses hosts use against predatory cowbirds, and whether they differ appreciably from defenses used against other nest predators, is yet another topic that deserves attention.

Conclusions and Directions for Future Research

Astié and Reboreda (2006) have demonstrated an important and sometimes underappreciated facet of brood parasitism, namely that cowbirds have a significant negative effect on the reproductive success of large hosts as well as small hosts, albeit in different ways. Parasitism may affect the success of large hosts less than that of smaller hosts because many large hosts can care for broods containing parasitic young and their own young (e.g. Peer and Bollinger 1997, Astié and Reboreda 2006). However, Astié and Reboreda's (2006) study shows that large hosts are significantly affected by egg puncture, rather than by losses incurred when cowbird nestlings outcompete their own (Lorenzana and Sealy 1999). Whereas several studies have examined host defenses against parasitic eggs (Rothstein and Robinson 1998, Peer and Sealy 2004), scant attention has been focused on means by which hosts deter egg removal and egg puncture by parasites (but see Tewksbury et al. 2002, Astié and Reboreda 2005). In view of the ubiquity and costs imposed by these behaviors, considerably more research is needed to elucidate why parasites exhibit these behaviors and the nature of host defenses used against them. Specifically, what is the function of egg puncture? Does it reset host nesting, test the incubation status of a clutch, reduce nestling competition, or function in some other way? What is the function of egg removal? Is this behavior declining? What is the benefit of removing eggs from nests of small hosts? How often do Brown-headed Cowbirds depredate nests and how widespread is this behavior? Finally, what defenses have hosts evolved to counter these parasite behaviors? No hypothesis is likely to be all-encompassing, because these behaviors vary among parasitic species and even within single species. Egg puncture and removal may be phenotypically plastic with multiple functions, and there may be reasons for these behaviors that are presently unknown.

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