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Shiny cowbirds synchronize parasitism with host laying and puncture host eggs according to host characteristics

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Obligate avian brood parasites lay their eggs in nests of other species, which thereafter provide all parental care. Brood parasites synchronize parasitism with host laying and remove or puncture host eggs to increase their reproductive success, but the benefits of these behaviours may depend on hosts characteristics such as body size. We experimentally analysed the effects of synchronization between parasitism and host laying and reduction in number of host eggs on hatching success and chick survival of shiny cowbirds, *Molothrus bonariensis* (50 g), in two common hosts that differ in body mass: chalk-browed mockingbirds, *Mimus saturninus* (75 g), and house wrens, *Troglodytes aedon* (13 g). We found no effect of synchronization of parasitism or of the number of host eggs removed on parasite hatching success in either host. However, survival of cowbird chicks in mockingbird nests was lower when cowbird chicks hatched after host chicks and when there was no removal of host eggs. In contrast, in wren nests, there was no effect of hatching asynchrony or egg removal on cowbird survival, but asymptotic weight was higher in nests without egg removal. In natural nests, the proportion of cowbird eggs laid during host laying was higher and the number of host eggs punctured per parasitic event was greater for mockingbirds than for wrens. These differences between hosts in the extent of synchronization between parasitism and host laying and the intensity of egg punctures suggest that shiny cowbirds may adaptively adjust these behaviours to host characteristics.

Obligate avian brood parasites, such as cowbirds and cuckoos, lay their eggs in nests of other host species, which thereafter provide all parental care (Ortega 1998; Rothstein & Robinson 1998; Davies 2000). Brood parasitism is an excellent example of coevolutionary interactions, as parasites reduce the reproductive success of the host, which results in selection for host defences. In turn, host defences select for parasite counterdefences that may select for new host defences and therefore result in a coevolutionary process or 'arms race' (Davies & Brooke 1988; Rothstein 1990; Krüger 2007). The best example of this coevolutionary process occurs in the common cuckoo, *Cuculus canorus*, where host egg rejection may cause cuckoo female lineages to lay mimetic eggs that resemble those of the host that they parasitize (Brooke & Davies 1988; Gibbs et al. 2000). In contrast, it has been generally accepted that cowbirds (*Molothrus* spp.) do not present noticeable parasite counterdefences as they rely more on high fecundity (i.e. 'shotgun strategy', Kattan 1997). However, more recent studies (Hahn et al. 1999; Alderson et al. 1999; Strausberger & Ashley 2003; Woolfenden et al. 2003) indicate that realized female fecundity of cowbirds is relatively low compared with previous estimates. As a consequence, the reproductive value of each cowbird egg may be higher than previously supposed, and, therefore, there are likely to be strong selection pressures on cowbirds to evolve behaviours that increase the survival of their eggs and chicks.

The reproductive success of cowbirds depends, among other factors, on eggs completing embryonic development and chicks growing large enough to fledge successfully. Two behaviours that increase the likelihood of egg hatching and chick survival are synchronization between parasitism and host laying (Carter 1986; Strausberger 1998; Mermoz & Reboreda 1999) and removal (Scott et al. 1992; Sealy 1992) or puncture (Carter 1986; Peer & Sealy 1999; Massoni & Reboreda 2002; Astié & Reboreda 2006; Peer 2006) of host eggs.

Synchronization between parasitism and host laying provides cowbird eggs enough time for incubation to ensure successful hatching. Cowbird eggs also have shorter incubation periods than hosts of similar size (Briskie & Sealy 1990; Kattan 1995), so synchronization of parasitism generally results in cowbird chicks hatching before host chicks, giving the parasite an advantage of 1–2 days in the competition for food with their nestmates (Briskie &

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Sealy 1990; Peer & Bollinger 1997; Mermoz & Reboreda 2003). Benefits of synchronizing parasitism with host laying may differ depending on the size of the host. When hosts are smaller than the cowbird, it is not imperative that cowbird chick hatches before the host chicks, because the cowbird's larger size compensates for differences in age (Clark & Robertson 1981; Marvil & Cruz 1989; Petit 1991). However, when hosts are larger than the parasite, it is critical for the cowbird chick to hatch earlier than the host chicks to fledge successfully (Carter 1986; Peer & Bollinger 1997).

In addition to synchronizing parasitism, cowbirds may benefit from eliminating host eggs either by removing them or by pecking and puncturing them. Several hypotheses have been proposed to explain the benefits of egg removal and egg puncture by cowbirds (Sealy 1992; Arcese et al. 1996; Massoni & Reboreda 1999; Peer 2006; Hoover & Robinson 2007). Two of the more accepted explanations propose that the removal or puncture of host eggs may enhance the efficiency of incubation of the parasite egg (incubation efficiency hypothesis: Peer & Bollinger 1997, 2000), or reduce competition for food between parasite and host chicks (competition reduction hypothesis: Carter 1986; Mason 1986a; Sealy 1992). The incubation efficiency hypothesis predicts that hatching success of the parasite in nests of larger hosts will increase as the number of host eggs decreases, because this improves the contact of the smaller parasitic egg with the brood patch of the host (Peer & Bollinger 1997, 2000). This benefit would be reduced or absent, however, when hosts are smaller than the parasite (Wiley 1985; Peer & Bollinger 1997, 2000).

According to the competition reduction hypothesis, by removing or puncturing host eggs, cowbird females increase the survival of their parasitic chicks by reducing the number of competing chicks. Again, this behaviour would be more important when host chicks are larger than the parasite and thus could easily outcompete the parasite for food (Fraga 1985; Lichtenstein 1998). Some studies (Kilner 2003; Kilner et al. 2004) have shown that cowbird chicks may also benefit from sharing the nest with smaller host chicks because begging by host chicks solicits a higher provisioning rate than does begging by the cowbird alone, allowing the parasite to grow more rapidly.

The shiny cowbird, *Molothrus bonariensis*, is a generalist brood parasite that uses more than 200 species as hosts (Friedmann & Kiff 1985; Ortega 1998). Shiny cowbirds usually synchronize parasitism with host laying (Massoni & Reboreda 1998; Mermoz & Reboreda 1999; Fiorini & Reboreda 2006; but see Kattan 1997). In addition, shiny cowbird females regularly puncture one or more host eggs shortly before or on the day that they parasitize a nest (Fraga 1978; Massoni & Reboreda 1999; Mermoz & Reboreda 1999; Astié & Reboreda 2006; Fiorini & Reboreda 2006). Punctures made by shiny cowbirds result in one large, usually triangular hole through the eggshell (Fiorini & Reboreda 2006), which causes the contents of the egg to dry up or leak into the nest. Punctured eggs are frequently removed by the host during nest sanitation (Kemal & Rothstein 1988), reducing the number of host eggs. However, puncturing of host eggs may also increase the probability of nest abandonment by the host, and thus, could be a costly behaviour for shiny cowbirds (Fraga 1978; Massoni & Reboreda 1998; Astié & Reboreda 2006; Tuero et al. 2007). Nevertheless, in nests of large hosts, the benefits of puncturing eggs may outweigh the costs of increasing the probability of nest abandonment. Therefore, cowbirds might puncture eggs of large hosts more often than those of small hosts. In agreement with this prediction, the removal or damage of host eggs by cowbird females varies considerably among hosts (e.g. Friedmann 1963; Smith 1981; Fraga 1985; Kattan 1998; Lichtenstein 1998; Astié & Reboreda 2006), possibly depending on characteristics of the host species that they parasitize (Sealy 1992).

Chalked-browed mockingbirds, *Mimus saturninus* (hereafter mockingbirds), and house wrens, *Troglodytes aedon* (hereafter wrens) are two frequent hosts of shiny cowbirds (Fraga 1985; Kattan 1997; Fiorini & Reboreda 2006; Tuero et al. 2007). Mockingbirds are noticeably larger and have an incubation period that is 1 day longer than that of the parasite, whereas wrens are much smaller and have an incubation period that is 2 days longer than that of the parasite. We experimentally analysed the effects of (1) the extent of synchronization between parasitism and host laying and (2) the reduction in the number of host eggs on hatching success and chick survival of shiny cowbirds in nests of both host species. We expected that the extent of synchronization and the number of host eggs punctured would affect hatching success and chick survival in mockingbirds but not in wrens. We also examined whether synchronization of parasitism and puncturing of host eggs by shiny cowbirds are adapted to host characteristics. In this case, we expected that the extent of synchronization and the number of punctured eggs would be higher in mockingbird nests than in wren nests.

METHODS

Study Area

The study was conducted within an area of approximately 650 ha near the town of Magdalena (35°08′S, 57°23′W), in the province of Buenos Aires, Argentina. The study area was predominately marshy grassland, interspersed with pastures and old-growth and second-growth stands dominated by Tala (*Celtis tala*) and Coronillo (*Scutia buxifolia*). Data collection was conducted during the breeding seasons (October–January) 2002–2003, 2003–2004, 2004–2005 and 2005–2006. We used the data from the first 2 years to analyse differences between hosts in the extent of synchronization between parasitism and host laying and in the intensity of egg punctures. We also used these data to analyse the association of the extent of synchronization and the intensity of egg punctures with cowbird hatching success and chick survival. Nests found during 2004–2005 and 2005–2006 breeding seasons were used to conduct the experiments (see below).

Study Species

Shiny cowbirds

In our study area, shiny cowbirds breed from early October to late January. Cowbird eggs have an average volume of 4.3 cm^3 (Fiorini 2007) and an incubation period of 12.7 days (Fiorini 2007; Tuero et al. 2007). Cowbird chicks weigh approximately 4 g at hatching and 40 g at fledging, when they are 11–12 days old. Adult females and males weight approximately 45 g and 50 g, respectively.

Chalk-browed mockingbirds

Mockingbirds breed from late September to mid-January. This species builds open-cup nests, and most favoured nest sites are shrubs or trees with dense foliage. Mockingbirds have an average clutch size of 3.6 eggs (Fiorini & Reboreda 2006), and eggs have an average volume of 6.1 cm^3 (Fiorini 2007). Incubation starts with the laying of the penultimate egg and lasts 13.7 days (Fiorini 2007). Chicks weigh 6 g at hatching and 50–55 g at fledging, when they are 12–14 days old (Fiorini 2007). Adults weigh approximately 70–75 g. At our study site, approximately 70% of mockingbird nests are parasitized by shiny cowbirds, with an intensity of parasitism of 2.2 eggs per parasitized nest (Fiorini & Reboreda 2006).