



Brood parasites manipulate their hosts: experimental evidence for the farming hypothesis



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Parasites show a wide variety of strategies to maximize the successful transmission of themselves and/or their offspring, by exploiting hosts. One such strategy occurs when parasites manipulate host behaviour in a way that increases their probability of transmission to an uninfected host. Here, we examine whether brood parasitic brown-headed cowbirds, *Molothrus ater*, attack and cause nest failure in late-stage, and hence, inappropriate host nests, which theory suggests they may do to parasitize the replacement nests at an opportune time, effectively manipulating their host's reproductive behaviour and improving their own transmission. Critical to this 'farming' hypothesis, cowbirds must be attuned to the reproductive stage of their host and act accordingly by destroying nonparasitized clutches they find late in the nesting cycle. We conducted a series of experimental manipulations in which we presented captive cowbirds with nests simulating early and late stages. We found that cowbirds caused significantly greater destruction in the late-stage nests. Moreover, our results suggest that cowbirds are capable of using both direct assessment and absolute egg number to assess which clutches to destroy. Corroborating our findings in the laboratory, 10 years of field data show that cowbirds significantly increase the intensity of their attacks (i.e. the proportion of the clutch destroyed) on nonparasitized host nests as the nesting cycle progresses; however, we found no such trend for parasitized host nests. These results indicate that cowbirds evaluate the reproductive stage of their hosts using multiple mechanisms and use this information to vary the intensity of their attacks.

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Parasites, of all sorts, show a wide variety of strategies to maximize the successful transmission of themselves and/or their offspring, by exploiting typically unrelated hosts (Poulin, 2007). One such strategy occurs when parasites manipulate host behaviour in a way that increases their probability of transmission to an uninfected host (Holmes & Bethel, 1972; Poulin, 2000). Examples of parasites altering host behaviour abound, and the effects may be dramatic and often focus on host reproductive behaviour (Moore, 2002). For instance, rodents infected with *Toxoplasma gondii* appear less 'fearful' of the parasite's definitive cat host (Berdoy, Webster, & Macdonald, 2000) and may even seem more sexually attractive to uninfected members of the opposite sex (Vyas, 2013). Host behavioural changes such as these may be considered an adaptive extended phenotype of the parasite (Dawkins, 1982),

when the behavioural change is actually caused by the parasite and can be shown to increase the probability of transmission (reviewed in: Moore, 2002; Poulin, 1995; Thomas, Adamo, & Moore, 2005). Also critical, is the need to identify the mechanisms involved in the behavioural change in order to understand the complexity and sophistication of the supposed manipulation (Nickol, 2005; Thomas et al., 2005). Brood-parasitic birds are functionally indistinguishable from conventional parasites and pathogens in that they may reduce the reproductive success of infected hosts (Davies, 2000; Hauber, 2003; Kilner, 2005; Ortega, 1998; Smith, Taitt, & Zanette, 2002) and their transmission success is wholly dependent on their ability to encounter hosts suitable for parasitism during the infective stage (i.e. during egg laying/early incubation). Nevertheless, instances of adult brood parasites manipulating host behaviour in order to increase the probability of infection have rarely been considered (but see Hoover & Robinson, 2007; Ponton, Biron, Moore, Møller, & Thomas, 2006; Soler, Soler, Martinez, & Møller, 1995).

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Obligate avian brood parasites, such as cowbirds and cuckoos, lay their eggs in the nests of other species ('hosts') whereupon the host parents provide all parental care for the parasitic young (Davies, 2000). To successfully 'infect' a host, a brood parasite must be attuned to its hosts' reproductive stage as there is only a narrow window of time during egg laying and early incubation in which parasitism will be effective (Fiorini, Tuero, & Rebores, 2009). Some brood parasites also attack host nests, destroying eggs/nestlings and causing nest failure of their potential hosts (Arcese, Smith, & Hatch, 1996; Peer & Sealy, 1999; Soler et al., 1995). Such behaviour is perplexing as it appears to be a superficial waste of a laying opportunity on the one hand, but these predatory habits could actually increase the probability of successful transmission (Arcese et al., 1996). The farming hypothesis suggests that brood parasites will destroy, or 'farm', host nests found too late in the nesting cycle to be suitable for parasitism, thereby manipulating those hosts into starting a new reproductive cycle prematurely, ultimately creating future opportunities to parasitize the host's re-nesting attempts (Arcese, Smith, Hochachka, Rogers, & Ludwig, 1992; Arcese et al., 1996). As long as the parasite focuses its attacks on late-stage nests no laying opportunity is wasted. Hence, as with parasitic egg laying, 'farming' behaviour requires that the parasite can assess the host's reproductive stage and acts accordingly by destroying late-stage nests.

We investigated the predatory behaviour of the brood-parasitic brown-headed cowbird, *Molothrus ater* (hereafter cowbird) to determine whether they were consistent with what would be expected from the farming hypothesis. Cowbirds are common throughout North America and are extreme host generalists, successfully parasitizing over 100 species of passerines (Lowther, 1993). To date, most studies of the farming hypothesis have focused on whether or not cowbirds are substantial nest predators because this is one general condition that would be necessary if farming were occurring. While several lines of evidence indicate that they are (Arcese et al., 1996; Clotfelter & Yasukawa, 1999; Granfors, Pietz, & Joyal, 2001; Hoover & Robinson, 2007), the critical prediction that cowbirds focus their attacks on late-stage host nests that are no longer suitable for parasitism remains untested. Moreover, the recognition mechanisms that cowbirds use to discriminate early- from late-stage nests before deciding to attack are largely unknown (King, 1979). Cowbirds are adept at finding hosts and appear to be capable of discriminating appropriate from inappropriate nests when deciding whether to lay in a nest (White, Ho, & Freed-Brown, 2009; White, Ho, de los Santos, & Godoy, 2007). If cowbirds are indeed 'farming' their hosts, then it makes logical sense that the parasite must be attuned to the host's reproductive cycle and use this knowledge to assess whether or not to destroy nests.

Cowbirds typically cause nest failure by either puncturing or removing enough eggs to cause the host parents to abandon. Beyond farming, other hypotheses have been proposed to explain egg removal or egg puncture by cowbirds (Hoover & Robinson, 2007; Peer, 2000; Sealy, 1992). For example, female cowbirds are known to occasionally consume the eggs they destroy (Sealy, 1992). Nutrition does not appear to be the primary motivator for attacking nests, however, as most documented incidents do not involve the cowbird eating any nest contents (Granfors et al., 2001; Scott, Weatherhead, & Ankney, 1992; Sealy, 1992). In cowbird parasitized nests, removal of host eggs may enhance the incubation efficiency of the parasitic egg (incubation efficiency hypothesis: Peer & Bollinger, 2000) or reduce future competition for a parasitic nestling (competition reduction hypothesis: Carter, 1986; Llambias, Ferretti, & Rebores, 2006). Also in parasitized nests, if a host rejects the parasitic egg, the parasite may retaliate by destroying enough of

the nest contents to cause complete failure (mafia hypothesis: Hoover & Robinson, 2007). The incubation efficiency, competition reduction and mafia hypotheses do not, however, explain attacks on nonparasitized nests, which are the focus of the farming hypothesis and our study.

The most direct and reliable way a cowbird could gauge the developmental stage of a host nest is by puncturing a portion of the clutch (Massoni & Rebores, 1999). Conceivably, the degree of development of a single host embryo could easily be evaluated in this way and such information could be used when deciding whether or not to destroy the clutch. Other indirect methods of evaluating nest stage include attending to cues (e.g. absolute egg number) that are indicative of a clutch being complete and most likely late stage (White et al., 2009, 2007). Here, we report the results from a series of experiments in the laboratory demonstrating that cowbirds use both direct and indirect methods to gauge host egg stage and are more likely to destroy evidently later-stage eggs. These experimental results in the laboratory are corroborated by evidence from 10 years of field data suggesting that cowbirds preferentially cause late-stage nests to fail likely in an attempt to 'farm' their hosts.

METHODS

Experimental Procedures

We performed a series of 'cafeteria style' choice experiments designed to test whether female cowbirds preferentially destroy late-stage nests that would no longer be suitable for parasitism (as per the farming hypothesis). We also evaluated whether cowbirds use direct and/or indirect methods of assessing the age of host eggs. Specifically, we examined the tendency of females to approach and attack artificial nests that contained eggs of different developmental stages or different numbers of eggs. We assessed whether female cowbirds would preferentially attack nests that simulated late- versus early-stage nests by comparing nests containing (1) highly developed eggs versus freshly laid and undeveloped eggs, (2) different numbers of eggs, permitting us to determine whether absolute or relative number is important and (3) varying numbers of eggs across days versus a continual 'full' clutch.

We captured 58 adult cowbirds (40 female and 18 male) using mist nets and funnel traps baited with cracked corn at Long Point Bird Observatory and Ruthvin Park Banding Station in Ontario during April 2012. Cowbirds were transported to the University of Western Ontario, Canada, colour-banded for individual recognition and housed in four large outdoor cages at the Advanced Facility for Avian Research (AFAR). Birds were fed a modified Bronx Zoo diet for omnivorous birds daily (see White et al., 2007) and had ad libitum access to white millet, canary seed mix, crushed oyster shells and vitamin-treated water. In order for cowbirds to regularly lay eggs in captivity, they require spacious outdoor aviaries much larger than the cages our birds were housed in (White et al., 2009, 2007). However, we assumed that our birds were in breeding condition because eggs were occasionally found (approximately two per week) within the cages, and males and females continued to perform breeding displays throughout the duration of the study.

Before each trial for each experiment, individual birds were transferred to an outdoor flight chamber and left for 24 h to habituate. We randomly selected a subset of females from the captive population for each experiment, and subjects used multiple times had a minimum 5-day interval between trials (mean \pm SE = 18 \pm 1.7 days). Flight chambers contained natural perches situated across one wall, along with food and water.

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