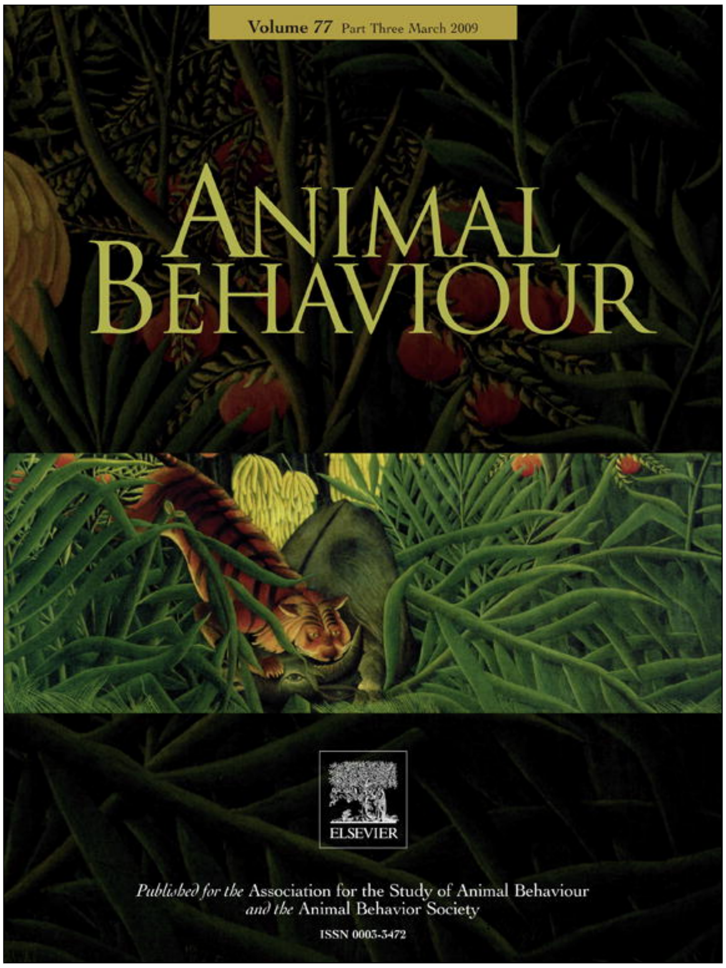
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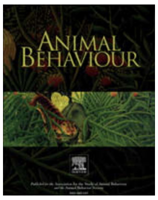

Articles

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).

House wrens

Wrens breed from early October to mid-January. Clutch size averages 5.2 eggs, and eggs have an average volume of 1.6 cm^3 (Tuero et al. 2007). Incubation starts with the laying of the penultimate egg and lasts 14.8 days (Tuero et al. 2007). Chicks weigh 1.5 g at hatching and 13 g at fledging, when they are 14–16 days old. Adults weigh approximately 12–13 g (Tuero et al. 2007). At our study site, approximately 60% of the nests are parasitized by shiny cowbirds, with an intensity of parasitism of 1.7 eggs per parasitized nest (Tuero et al. 2007).

General Methodology

We found mockingbird nests by focusing on individual activity and inspecting potential nesting sites within the territory of the breeding pair. To facilitate wren data collection we placed 100 wooden nestboxes in the study area (see Tuero et al. 2007). We visited mockingbird and wren nests daily or every other day until the chicks fledged or the nest failed. At each visit we recorded the number of host and parasite eggs and the occurrence of punctures in them. We also recorded the laying and hatching date of each egg, and the fate of each egg and chick. We numbered eggs and marked chicks on the tarsus with waterproof ink. We weighed chicks in wren nests with a digital portable balance (Ohaus LS 200) to the nearest 0.1 g and those in mockingbird nests with a Pesola spring scale to the nearest 0.5 g. We weighted chicks until they were 9 days old (hatching day = day 0). We did not visit nests after day 9 to avoid causing chicks to fledge prematurely. We assumed that cowbird chick weight at day 9 was the asymptotic weight (Massoni & Reboreda 1998; Mermoz & Reboreda 2003) and that cowbird chicks that were alive at day 9 fledged successfully. We performed egg and brood manipulations as quickly as possible (usually within 10 min) to minimize disturbance at the nest. There were no cases of nest abandonment associated with our manipulations.

Effects of Synchronization and Egg Punctures

Experimental procedures

We analysed the effects of synchronization between parasitism and host laying and of puncture of host eggs on cowbird hatching success and chick survival. We conducted experiments in which (1) we manipulated synchronization between parasitism and host laying by creating synchronous and asynchronous groups and (2) we manipulated the number of host eggs by creating normal and reduced clutches. In synchronous groups, we added one cowbird egg before the start of incubation, and in asynchronous groups, we added one cowbird egg 3 days after the onset of incubation. We selected this level of laying asynchrony because less than 30% of shiny cowbird parasitic events occur after day 3 of host incubation (Fiorini & Reboreda 2006). For manipulation of clutch size, we left the normal clutch size or removed two host eggs from nests. This manipulation produced mockingbird nests with four host eggs (normal clutches) or two host eggs (reduced clutches), and produced wren nests with five host eggs (normal clutches) or three host eggs (reduced clutches). The number of host eggs removed was similar to the average number of punctured eggs in naturally parasitized nests of mockingbirds and wrens (Fiorini & Reboreda 2006; Tuero et al. 2007). Therefore, we created four experimental groups of nests: (1) synchronous parasitism and normal clutch, (2) synchronous parasitism and reduced clutch (3) asynchronous parasitism and normal clutch and (4) asynchronous parasitism and reduced clutch. Table 1 shows the average number of days elapsed since the onset of incubation and experimental parasitism, and the number of host eggs in the four experimental groups. These manipulations also resulted in four groups of nests during the chick stage: (1) nests with a cowbird chick hatched from a synchronous egg and with the normal number of host chicks; (2) nests with a cowbird chick hatched from a synchronous egg and a reduced number of host chicks; (3) nests with a cowbird chick hatched from an asynchronous egg and the normal number of host chicks; (4) nests with a cowbird chick hatched from an asynchronous egg and a reduced number of host chicks. Table 2 shows the average number of days elapsed between hatching of the cowbird chick and the first host chick in each nest, and the number of host chicks in the four experimental groups.

Table 1
Days elapsed between the onset of incubation and experimental parasitism (synchrony of parasitism), number of host eggs and number of nests in experimental groups of mockingbirds and wrens

Species	Group	Synchrony of parasitism	Number of host eggs	Number of nests
Mockingbird	SR	0.14±0.14	2.00±0.00	7
Mockingbird	SN	0.09±0.06	3.36±0.11	22
Mockingbird	AR	2.40±0.25	1.80±0.20	5
Mockingbird	AN	2.63±0.16	3.58±0.12	19
Wren	SR	0.06±0.06	3.13±0.13	16
Wren	SN	0.16±0.09	4.90±0.07	19
Wren	AR	2.94±0.16	3.12±0.49	17
Wren	AN	2.67±0.19	5.00±0.00	12

SR: synchronous parasitism and reduced clutch size; SN: synchronous parasitism and normal clutch size; AR: asynchronous parasitism and reduced clutch size; AN: asynchronous parasitism and normal clutch size. Values are means ± SE.

Table 2
Days elapsed between hatching of the first host chick and hatching of the shiny cowbird chick (hatching synchrony), number of host chicks and number of nests in experimental groups of mockingbirds and wrens

Species	Group	Hatching synchrony	Number of host chicks	Number of nests
Mockingbird	SR	−0.82±0.30	1.63±0.15	11
Mockingbird	SN	−1.00±0.26	3.83±0.17	6
Mockingbird	AR	1.43±0.30	1.71±0.18	7
Mockingbird	AN	1.75±0.25	3.13±0.13	8
Wren	SR	−2.33±0.20	2.17±0.19	18
Wren	SN	−2.00±0.32	4.60±0.25	5
Wren	AR	1.00±0.31	2.00±0.31	7
Wren	AN	0.75±0.25	4.60±0.25	5

Negative values of hatching synchrony indicate that the parasite chick hatched before the first host chick. SR: synchronous hatching and reduced number of host chicks; SN: synchronous hatching and normal number of host chicks; AR: asynchronous hatching and reduced number of host chicks; AN: asynchronous hatching and normal number of host chicks. Values are means ± SE.

We randomly assigned nests to experimental groups throughout the breeding season, controlling for temporal or spatial variation in food availability. Nests depredated before the nestlings stage were not included in the analysis of hatching success and those depredated before chicks fledged were not included in the analysis of chick survival. When host eggs failed to hatch in 'normal clutch size nests', we reassigned them to the category of 'reduced number of host chick nests'. Thus, some sample sizes in Table 2 are larger than those in Table 1. Shiny cowbird eggs used in these experiments were collected from house wren nests or chalk-browed mockingbird nests.

To avoid natural parasitism and the puncture of host eggs by shiny cowbirds in experimental wren nests, we reduced the nestbox opening from 4.5 to 3 cm in diameter. This opening size allowed wrens but not cowbirds to access to the nestbox (none of our experimental nests was parasitized or had punctured eggs). After hatching, we enlarged the nestbox opening to the original diameter to allow the cowbird chicks to fledge. Cowbird eggs were collected on the same day that they were laid and in all cases they were collected during host laying (i.e. they were not incubated before translocation). Each egg was kept at room temperature (ca. 20 °C) in the laboratory for 24–48 h before translocation to an experimental nest.

In mockingbird nests, most egg punctures occur during egg laying (Fiorini & Reboreda 2006). To minimize natural punctures of host eggs in mockingbird nests, we replaced each host egg with a plaster egg as soon as it was laid. We kept the removed host eggs at room temperature in the laboratory. On day 3 (laying of the fourth mockingbird egg), we returned three host eggs (normal clutches) or one host egg (reduced clutches) to the original nest and removed the plaster eggs and the natural egg laid on that day. On the following day we added the remaining host egg. We considered the day that we first returned host eggs as the onset of incubation. In the synchronous groups, we added the cowbird egg together with first host eggs, and in asynchronous groups, we added the cowbird egg 3 days later. The only measurable effect of this manipulation was to extend by 1 day the incubation period of the host, which is within the normal range of variation of this species, for a clutch size of five eggs. The manipulations performed during the experiments complied with the Argentinean Law of Conservation of Wild Fauna.

Correlational analyses

We used nonmanipulated nests that hatched chicks to analyse the association between cowbird hatching success and (1) synchronization of parasitism and (2) the number of eggs in the nest. Variation in the number of eggs in nonmanipulated host nests resulted from differences in intensities of parasitism and egg punctures. Synchronization of parasitism was estimated as the number of days elapsed between parasitism and the onset of incubation (negative values were considered = 0). To avoid pseudoreplication, in nests with multiple parasitism, we used only one cowbird egg chosen at random. For this analysis we included the number of cowbird eggs as another predictor variable.

Synchronization of parasitism in mockingbird and wren nests

To examine whether the extent of synchronization between parasitism and host laying differed between host species, we compared the proportion of parasitism during host laying in mockingbird and wren nests. For mockingbirds, we used a sample of 180 parasitic eggs laid in 86 nests that were found before or during host laying. In 47% of these cases, we could estimate directly the date of parasitism (i.e. the nest was visited on consecutive days and parasitism occurred between visits). In cases where nests were visited every other day, we assumed that, in half of the cases, the parasitic egg was laid the day before, and in the other half, we assumed that the parasitic egg was laid the same day that we visited the nest. For wrens, we used a sample of 69 parasite eggs laid in 39 nests that were found before or during host laying. In 52% of the cases, we could estimate directly the date of parasitism. In the other cases, we assumed that parasitism occurred between consecutive visits, or we estimated the date of parasitism from the date of hatching of the parasitic egg.

Egg punctures in mockingbird and wren nests

To examine whether egg-pecking behaviour by shiny cowbirds differed between host species, we determined the number of mockingbird and wren eggs that were punctured until the first parasitic event in nests that had at least three host eggs at the time that parasitism occurred. We also examined whether there was an association between the number of host eggs punctured and the number of host eggs present in the nest at the time that the first parasitic event occurred.

Statistical Analysis

When possible we used parametric statistical tests. Otherwise, we used nonparametric tests (Siegel & Castellan 1988). To analyse the effects of the extent of synchronization between parasitism and host laying and of the number of host eggs removed on cowbird hatching success and chick survival, we performed generalized linear models (GLM) with binomial error distribution and logit-link function, using the extent of synchronization and the number of host eggs as categorical predictor variables, and hatching success of the cowbird egg (0–1) or survival of the cowbird chick (0–1) as response variables. The predictor variables were entered simultaneously in the main effects model. Significance was tested using the Wald statistic, which follows a chi-square distribution. Because some host eggs did not hatch, the number of host chicks varied between groups. Therefore, in the analyses of chick survival, we used the number of host chicks as a continuous predictor variable. We analysed differences in asymptotic weight between treatments using ANOVA. To compare the synchronization of parasitism between hosts, we used a chi-square test, and for comparing differences in the intensity of egg punctures between hosts, we used a Mann–Whitney *U* test. We tested the association between the number of host eggs punctured and the number of host eggs present in the nest at the time that parasitism occurred using Spearman correlations. Statistical tests were performed using Statistica 6.0 (StatSoft, Tulsa, OK, U.S.A.) with $P < 0.05$ (two-tailed).

RESULTS

Effects of Synchronization and Egg Punctures

Experimental results

We found no effect of the extent of synchronization or of the number of host eggs present on cowbird hatching success in mockingbird nests (GLM: synchronization: $\chi^2_1 = 0.76$, $P = 0.38$; host eggs: $\chi^2_1 = 0.001$, $P = 0.13$) or in wren nests (GLM: synchronization: $\chi^2_1 = 2.28$, $P = 0.13$; host eggs: $\chi^2_1 = 0.31$, $P = 0.58$; Fig. 1).

In mockingbird nests, survival of cowbird chicks was lower in asynchronous groups than in synchronous groups, and was negatively affected by the number of host chicks (GLM: synchronization: $\chi^2_1 = 7.28$, $P = 0.01$; host chicks: $\chi^2_1 = 4.10$, $P = 0.04$; Fig. 2). We also

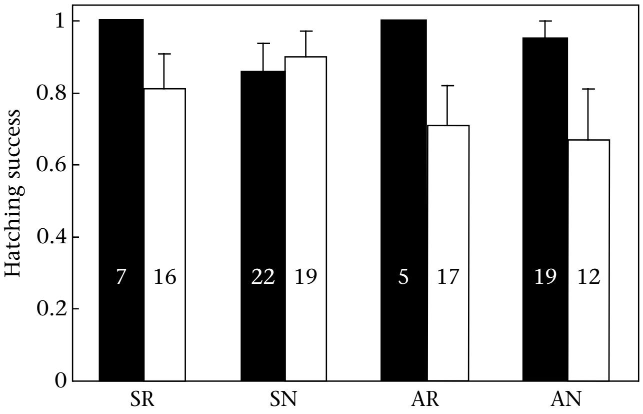

Figure 1. Mean + SE hatching success of shiny cowbirds in the four experimental groups of mockingbirds (solid bars) and wrens (open bars). Sample size (number of nests) is indicated within each bar. SR: synchronous parasitism and reduced host clutch, SN: synchronous parasitism and normal host clutch, AR: asynchronous parasitism and reduced host clutch, AN: asynchronous parasitism and normal host clutch.

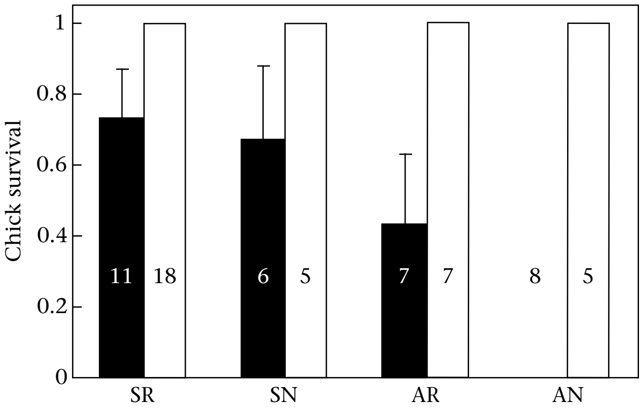

Figure 2. Mean + SE survival of cowbird chicks in the four experimental groups of mockingbirds (solid bars) and wrens (open bars). Sample size (number of nests) is indicated within each bar. SR: synchronous hatching and reduced number of host chicks, SN: synchronous hatching and normal number of host chicks, AR: asynchronous hatching and reduced number of host chicks, AN: asynchronous hatching and normal number of host chicks.

analysed the asymptotic weight of cowbird chicks. In asynchronous groups, most cowbird chicks died, so we evaluated differences in asymptotic weight only between synchronous nests with normal and reduced numbers of mockingbird chicks. The asymptotic weight did not differ between cowbird chicks reared in nests with reduced ($\overline{X} \pm \mathrm{SE} = 37.03 \pm 2.55$ g, $N = 6$) or normal numbers of mockingbird chicks ($\overline{X} \pm \mathrm{SE} = 35.25 \pm 0.84$ g, $N = 4$; ANOVA: $F_{1,8} = 0.30$, $P = 0.60$). However, the power of this analysis was very low (8%).

In wren nests, the survival of cowbird chicks was not affected by the extent of hatching synchrony between cowbird and host chicks or by the number of host chicks (all cowbird chicks survived in the four experimental groups; Fig. 2). In addition, the asymptotic weight of cowbird chicks was not affected by hatching synchrony, but cowbird chicks reared in nests with normal numbers of host chicks were significantly heavier than those reared in nests with a reduced number of host chicks (two-way ANOVA: hatching synchrony: $F_{1,23} = 0.1$, $P = 0.8$; number of host chicks: $F_{1,23} = 4.3$, $P = 0.05$; interaction between hatching synchrony and number of host chicks: $F_{1,23} = 0.14$, $P = 0.71$; Fig. 3).

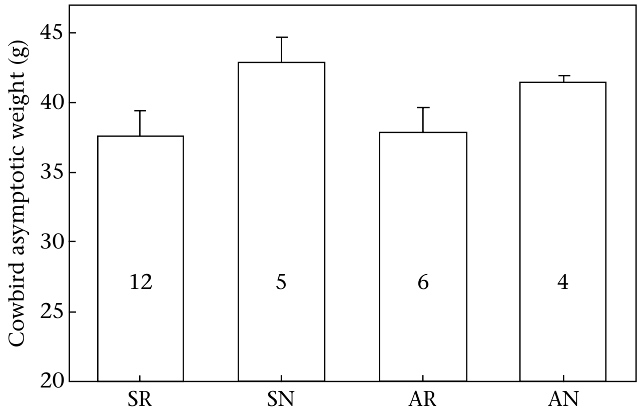

Figure 3. Mean + SE asymptotic weight of cowbird chicks in the four experimental groups of wren nests. Sample size (number of nests) is indicated inside each bar. SR: synchronous hatching and reduced number of host chicks, SN: synchronous hatching and normal number of host chicks, AR: asynchronous hatching and reduced number of host chicks, AN: asynchronous hatching and normal number of host chicks.

Correlational results

The variability in synchronization of parasitism and in the number of host eggs that we used in our experiment was lower than the one observed in nonmanipulated nests. In our experimental nests, asynchronous eggs were added 3 days after the onset of incubation (early incubation), but in nonmanipulated nests, parasitism also occurred during mid and late incubation. Similarly, in experimental nests, the difference in the number of host eggs between normal and reduced clutches was two eggs, but in nonmanipulated nests, the number of host eggs varied between one and four eggs in mockingbird nests and between one and six eggs in wren nests. Therefore, we analysed the association between cowbird hatching success and synchronization of parasitism and number of host eggs taking into account the variability that occurred in natural nests. Because there were cases of multiple parasitism in these nests, we also included in our analysis the number of cowbird eggs. In mockingbird nests, hatching success was negatively associated with the day that parasitism occurred (GLM: $\chi^2_1 = 3.85$, $P = 0.05$), but there was no significant association between hatching success and the number of host eggs (GLM: $\chi^2_1 = 0.81$, $P = 0.37$) or the number of cowbird eggs (GLM: $\chi^2_1 = 0.86$, $P = 0.35$). Similarly, cowbird hatching success in wren nests was negatively associated with the day that parasitism occurred (GLM: $\chi^2_1 = 4.73$, $P = 0.03$), and there was a tendency towards a negative association between hatching success and the number of cowbird eggs (GLM: $\chi^2_1 = 3.42$, $P = 0.06$), but no effect of the number of host eggs (GLM: $\chi^2_1 = 0.01$, $P = 0.93$).

Synchronization of Parasitism in Mockingbird and Wren Nests

In mockingbirds, 3.3% of parasitic events occurred before the host began laying, 73.9% occurred during host laying (days 0–3) and 22.8% occurred during incubation (days 4–16; Fig. 4a). In wrens, 56.5% of parasitism events occurred during host laying (days 0–4) and 43.5% occurred during incubation (days 5–18; Fig. 4b). Cowbirds laid significantly more eggs during host laying in mockingbird nests than in wren nests (chi-square test: $\chi^2_1 = 6.39$, $P = 0.01$).

Egg Punctures in Mockingbird and Wren Nests

Significantly more host eggs were punctured per parasitic event in mockingbird nests than in wren nests (mockingbirds: $\overline{X} \pm \mathrm{SE} = 1.7 \pm 0.3$ eggs, wrens: $\overline{X} \pm \mathrm{SE} = 0.7 \pm 0.2$ eggs; Mann–Whitney U test: $U = 182$, $N_1 = 14$, $N_2 = 17$, $P = 0.009$). There was a significant positive association between the number of host eggs at the first occurrence of parasitism and the number of host eggs punctured in mockingbird nests (Spearman rank correlation: $r_S = 0.56$, $N = 35$, $Z = 3.28$, $P = 0.001$; Fig. 5), but no relation between these variables in wren nests ($r_S = 0.03$, $N = 18$, $Z = 0.11$, $P = 0.91$; Fig. 5).

DISCUSSION

Effects of Synchronization and Egg Punctures

There was no effect of synchronization of parasitism on cowbird hatching success in experimental nests of mockingbirds and wrens. However, in nonmanipulated nests of both hosts, there was a negative association between hatching success and the day that parasitism occurred. This discrepancy was probably due to the differences in the extent of synchronization between experimental and nonmanipulated nests, because in the experimental nests, we added the asynchronous cowbird egg 3 days after the onset of incubation, whereas in nonmanipulated nests, some parasitism

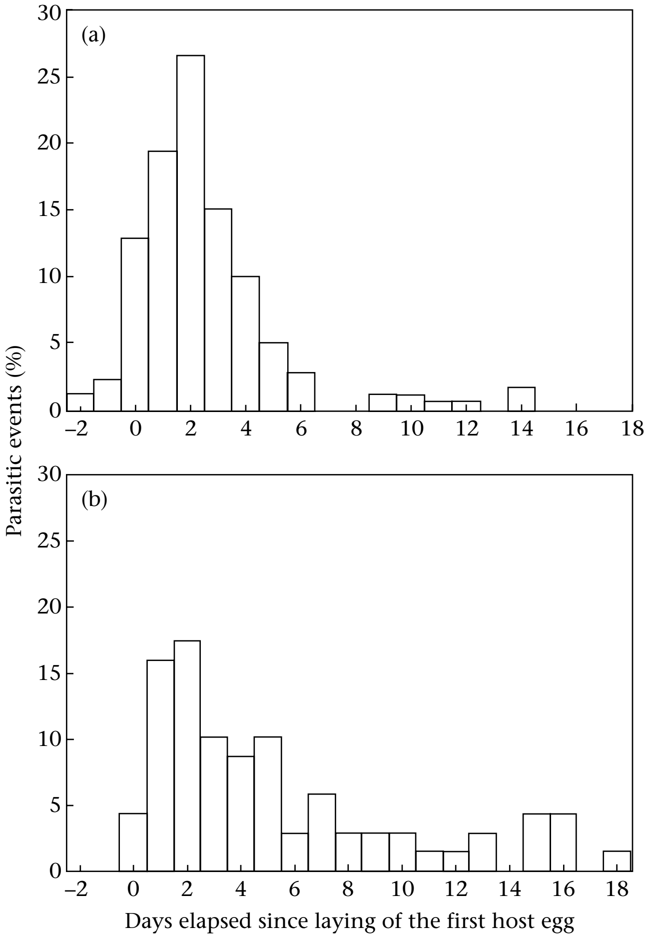

Figure 4. Percentage of cowbird eggs laid in (a) mockingbird ($N = 180$ eggs) and (b) wren ($N = 69$ eggs) nests during host prelaying, laying and incubation. Day 0 corresponds to the laying of the first host egg.

occurred during mid and late incubation. Therefore, the greater degree of asynchrony in nonmanipulated nests probably depressed cowbird hatching success.

In both hosts, the efficiency of incubation of the cowbird egg was not affected by experimental reduction in the number of host eggs. Similarly, in nonmanipulated mockingbird and wren nests, reduction of the clutch as a result of egg punctures did not improve the hatchability of parasitic eggs. The incubation efficiency hypothesis predicts that a decrease in the number of host eggs will increase hatching success of the parasite egg in nests of larger hosts but not in nests of smaller hosts, because removal of larger host eggs improves contact of the smaller parasitic egg with the host's brood patch, whereas in nests of smaller hosts, the cowbird egg is the largest egg in the clutch. In agreement with this hypothesis, Peer & Bollinger (1997) observed that brown-headed cowbird, *M. ater*, eggs added to nests of a large host, the common grackle, *Quiscalus quiscula*, had higher hatching success when host eggs were removed, and McMaster & Sealy (1997) found no difference in hatching success of brown-headed cowbird eggs in nests of a small host, the yellow warbler, *Dendroica petechia*, when one or no host egg was removed. One important difference between Peer & Bollinger's (1997) study and our study is that common grackle eggs are 120% larger than brown-headed cowbird eggs, while mockingbird eggs are only 50% larger than shiny cowbird eggs (see Methods). Chalk-browed mockingbirds are one of the largest hosts used by shiny cowbirds (Mason 1986b). Therefore, our results suggest that the enhancement of efficiency of incubation of the parasite egg would not be an important selective pressure responsible for maintaining the pecking behaviour of shiny cowbirds.

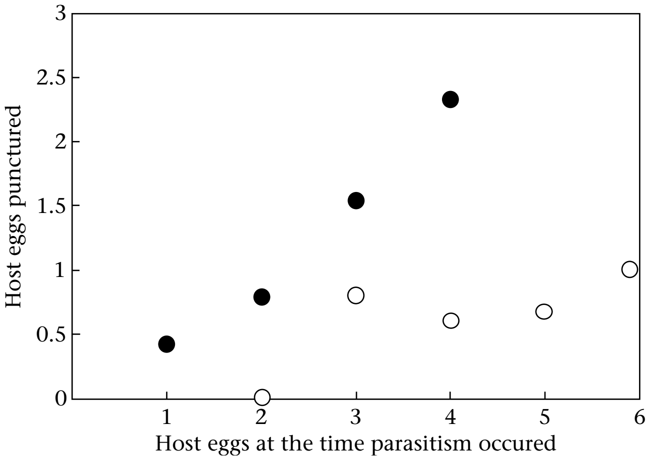

Figure 5. Average number of host eggs punctured until the first parasitic event in mockingbird (solid symbols) and wren (open symbols) nests as a function of the number of host eggs in the nest when the first event of parasitism occurred.

Synchronization between parasitism and host laying increased the survival of cowbird chicks in mockingbird nests but not in wren nests. Mockingbirds have an incubation period that is 1 day longer than that of cowbirds. Therefore, parasite eggs laid before the onset of incubation should hatch 1 day before the host eggs, giving cowbird chicks a 1-day head start, which would increase their chance of successfully competing for food with their larger nestmates. In contrast, although wrens have an incubation period that is 2 days longer than that of cowbirds, wren chicks weigh less at hatching and do not reach the hatching weight of a cowbird chick until they are 3 days old. This difference in hatching weights provides cowbirds with a wider time window for parasitizing wren nests without affecting the survival of their chicks. Other authors have also found that when the host is smaller than the parasite, the parasite does not have to hatch before the host chicks to fledge successfully (Clark & Robertson 1981), but when hosts are larger than the parasite, parasites that hatch simultaneously with or before the host chicks have increased survival (Carter 1986). Note, however, that the wren–mockingbird contrast is not a typical small–large host comparison, because larger birds usually have longer incubation periods than smaller birds. This means that some of the costs that a cowbird faces by parasitizing a large host are ameliorated by the longer incubation period of large hosts. But cavity nesting (as in house wrens) is also linked to longer incubation periods. Therefore, in the present case, cowbirds get a double benefit from parasitizing the wren instead of the mockingbird because the wren is smaller than the cowbird and its eggs take longer to hatch.

Removal of host eggs increased survival of the cowbird chick in experimental mockingbird nests but not in experimental wren nests. This result is consistent with the reduction of competition hypothesis, which predicts an increase in the survival of the cowbird chick in nests where host eggs are removed. However, contrary to the predictions of this hypothesis, we observed a positive association between the number of wren chicks and the asymptotic weight of the cowbird chick. This result is similar to that of Kilner et al. (2004), who found that brown-headed cowbird chicks reared with chicks of a small host (the eastern phoebe, *Sayornis phoebe*) grew faster than those reared without host nestmates. These authors proposed that the combined begging of parasitic and host chicks evoked a higher level of provisioning by the parents than did begging by the parasite alone, and that the larger cowbird chicks were able to capitalize on parental feedings and obtain a higher provisioning rate.

Our results indicate that the main benefit that shiny cowbirds obtain from synchronizing parasitism with host laying is to enhance the survival of their chicks in nests of the larger host. Similarly, by puncturing host eggs, female cowbirds increased the survival of their chicks in nests of the larger host but not in nests of the smaller host, where sharing the nest with smaller nestmates increased the asymptotic weight of the cowbird chick. Puncture of host eggs may increase the likelihood of nest abandonment (Fraga 1978; Massoni & Reboreda 1998; Astié & Reboreda 2006; Tuero et al. 2007), so it would be adaptive to peck host eggs only when this behaviour increases the survival of cowbird chicks.

Synchronization and Egg Pecking in Mockingbird and Wren Nests

We found that the proportion of synchronized parasitism in nonmanipulated nests was higher in mockingbirds than in wrens. We also found that the number of host eggs punctured per parasitic event was larger in mockingbirds than in wrens, and that the number of host eggs punctured was positively associated with number of host eggs in mockingbirds but not in wrens. These results indicate that laying synchrony and egg-pecking behaviours of female cowbirds are associated with the benefits that they produce in the hosts that they parasitize, because synchronizing parasitism and puncturing host eggs is important for the survival of the parasite chick in mockingbird nests but not in wren nests. Kattan (1998) also reported a low incidence of punctured eggs in wren nests that had high frequencies of shiny cowbird parasitism. In addition, several authors (Blankespoor et al. 1982; Røskaft et al. 1990; Sealy 1992) reported that brown-headed cowbird females removed more host eggs from nests of large hosts than from nests of small hosts. Similarly, in the greater honeyguide, *Indicator indicator*, the number of punctures per host egg is higher in large hosts than it is in small hosts. In this species the difference in behaviour is associated with the likelihood that greater honeyguide chicks can kill host chicks (Spottiswoode & Colebrook-Robjent 2007). Also, Soler et al. (1997) found that the number of magpie, *Pica pica*, eggs destroyed by great spotted cuckoos, *Clamator glandarius*, increases with the number of eggs laid by this large host. In this case, egg damage reduces the number of competing host chicks and increases hatching success of late-laid cuckoo eggs. In addition, Kleven et al. (1999) found that common cuckoos, *Cuculus canorus*, lay larger eggs when they parasitize larger hosts. Because cuckoo females have host-specific races (Gibbs et al. 2000), these authors suggested that variation in egg size in cuckoos would be an adaptation to parasitizing larger hosts.

Lower synchronization between parasitism and host laying in wren nests would also be expected if cowbirds have more difficulty monitoring cavity nests than they do open-cup nests, because the contents of cavity nests may only be determined when cowbirds enter the cavity. Similarly, cowbirds might destroy fewer eggs from the nests of one host because that species defends its nests more strongly. Tewksbury et al. (2002) showed that increased nest attentiveness by female yellow warblers, *Dendroica petechia*, reduces egg removal by brown-headed cowbirds. Therefore, if wrens defend their nests better than mockingbirds, shiny cowbirds might be less likely to puncture wren eggs than mockingbird eggs. However, mockingbirds have a higher level of nest attentiveness than wrens do and they are more aggressive towards experimental models of shiny cowbirds placed close to their nests (Fiorini 2007). Therefore, the differences in the number of host eggs punctured between mockingbirds and wrens are unlikely to be the result of differences in the intensity of host defences. Nevertheless, although we can draw inferences from the differences in the behaviour of cowbirds when parasitizing mockingbird nests and wren nests, we cannot conclude that these differences in behaviour arose exclusively from differences in body mass between these hosts, and thus, other differences between hosts (i.e. nest type) should be considered.

Our results may be consistent with the hypothesis that shiny cowbirds adaptively adjust their laying and pecking behaviours according to host characteristics. This host specialization could be the result of individual females parasitizing one host species and thus forming host-specific lineages (Brooke & Davies 1988; Gibbs et al. 2000; Avilés & Møller 2004; Starling et al. 2006), with each lineage presenting behaviours adapted to host characteristics. Recent studies (Mahler et al. 2007) showed that, in our study area, the population of shiny cowbird females that parasitizes wrens is genetically differentiated in the mitochondrial control region from the population that parasitizes mockingbirds, suggesting nonrandom host use by the parasite and thus providing a simple explanation for the differences between hosts in laying and puncturing behaviours.

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