

## EGG-LAYING BEHAVIOR IN SCREAMING COWBIRDS: WHY DOES A SPECIALIST BROOD PARASITE WASTE SO MANY EGGS?

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**Abstract.** Obligate brood parasites should synchronize parasitism with host laying to maximize egg hatchability and chick survival. While the generalist Shiny (*Molothrus bonariensis*), Brown-headed (*M. ater*), and Bronzed (*M. aeneus*) Cowbirds frequently synchronize parasitism with host laying, specialist Screaming Cowbirds (*M. rufoaxillaris*) very often fail to do so in nests of their main host, the Bay-winged Cowbird (*Agelaioides badius*). The poor synchronization of Screaming Cowbird parasitism may be the result of low availability of host nests at the time of laying, higher nest attentiveness by the host during laying, or unpredictable host laying behavior. We used a large set of observational data to test these hypotheses. The rate of Screaming Cowbird parasitism occurring during host prelaying was 31%, while during laying and incubation, it was 50% and 19%, respectively. Synchronization of parasitism was not associated with availability of host nests at laying or with changes in host nest attentiveness through the nesting cycle. The length of the prelaying period varied from one to 19 days and was not associated with latency of parasitism after nest completion. Nests with prelaying periods of 4–6 days received fewer eggs than nests with shorter or longer periods. Shiny Cowbirds also parasitized Bay-winged Cowbirds during prelaying more frequently (48%) than in other studied hosts (1%–8%). Our results indicate that Bay-winged Cowbird prelaying behavior precludes synchronization between parasitism and host laying and therefore may act as an antiparasitic defense, as it decreases the incidence of successful parasitism.

**Key words:** *Agelaioides badius*, Bay-winged Cowbird, brood parasitism, egg laying, *Molothrus rufoaxillaris*, Screaming Cowbird.

### Comportamiento de Puesta de *Molothrus rufoaxillaris*: ¿Por qué un Parásito Especialista Desperdicia Tantos Huevos?

**Resumen.** Los parásitos de cría obligados deberían sincronizar el parasitismo con la puesta del hospedador para maximizar el éxito de eclosión de sus huevos y la supervivencia de sus pichones. Mientras que los parásitos generalistas *Molothrus bonariensis*, *M. ater* y *M. aeneus* frecuentemente sincronizan el parasitismo con la puesta del hospedador, el especialista *M. rufoaxillaris* suele no hacerlo en nidos de su principal hospedador, *Agelaioides badius*. La baja sincronización del parasitismo de *M. rufoaxillaris* en este hospedador puede ser el resultado de una baja disponibilidad de nidos en puesta, una mayor defensa del nido por parte del hospedador durante la puesta, o un comportamiento de puesta impredecible del hospedador. Se utilizó un gran conjunto de datos observacionales para poner a prueba estas hipótesis. La frecuencia de parasitismo de *M. rufoaxillaris* durante la prepuesta fue del 31%, mientras que durante la puesta e incubación las frecuencias fueron del 50 y 19%, respectivamente. La sincronización no estuvo asociada a la disponibilidad de nidos en puesta ni a cambios en la atención del nido por parte del hospedador a lo largo del ciclo de nidificación. La duración del periodo de prepuesta varió entre un y 19 días, y no mostró asociación con la latencia en el parasitismo desde que el nido estuvo completo. Los nidos con periodos de prepuesta de 4-6 días recibieron menos huevos que aquellos con periodos más largos o más cortos. *Molothrus bonariensis* también parasitó a *Agelaioides badius* durante la prepuesta más frecuentemente (48%) que a otros hospedadores estudiados (1-8%). Nuestros resultados indican que el comportamiento de *Agelaioides badius* durante la prepuesta dificulta la sincronización entre el parasitismo y la puesta del hospedador, y puede actuar como defensa antiparasitaria al disminuir la incidencia del parasitismo.

## INTRODUCTION

Cowbirds, like cuckoos and other obligate brood parasites, lay their eggs in nests of other birds (i.e., hosts), which raise the parasitic offspring until independence (Ortega 1998, Rothstein

and Robinson 1998, Davies 2000). As a consequence of this reproductive strategy, brood parasites face the problem of synchronizing parasitism with host laying. If parasitism occurs before host laying, parasite eggs can be more likely to be rejected (Rothstein 1986, Sealy 1992, 1995; but see Moskát

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and Hauber 2007). Similarly, if parasitism occurs after the onset of incubation, parasite eggs have a low probability of success, as they may not hatch or may hatch too late, the latter case increasing the probability that the parasite chicks will be outcompeted for food by host chicks (Lichtenstein 1998, Hauber 2003).

On the basis of many studies reporting high fecundity in Brown-headed (*Molothrus ater*; Payne 1965, Scott and Ankney 1980, 1983, Jackson and Roby 1992) and Shiny (*M. bonariensis*; Kattan 1993) Cowbirds, it has been argued that the reproductive success of female cowbirds may depend on their spreading a large number of eggs among the available nests, rather than on the accurate timing and location of each parasitic egg (Kattan 1997, Lea and Kattan 1998). Alternatively, recent studies in Brown-headed Cowbirds involving genetic parentage analyses (Aldersson et al. 1999, Hahn et al. 1999, Strausberger and Ashley 2003, Woolfenden et al. 2003) indicate that cowbird fecundity is lower than previously estimated. Consequently, the potential value of each egg is greater for a female cowbird than previously thought.

If the success of a parasite's eggs and chicks depends on the timing of parasitism, and actual fecundity is relatively low, there are likely to be strong selection pressures on parasitic females to synchronize parasitism with host laying. In agreement with this view, some studies have reported that Shiny, Brown-headed, and Bronzed (*M. aeneus*) Cowbirds lay most of their eggs at the time of host laying, rarely parasitizing before that stage or in abandoned nests (Massoni and Reboresda 1998, Strausberger 1998, Mermoz and Reboresda 1999, Ellison et al. 2006, Fiorini and Reboresda 2006; but see Sealy 1995, Kattan 1997). Similarly, Moskat et al. (2006) found high synchrony of laying patterns between the Common Cuckoo (*Cuculus canorus*) and its local primary host, the Great Reed Warbler (*Acrocephalus arundinaceus*). In contrast, the specialist Screaming Cowbird (*M. rufoaxillaris*), for which, over most of its range, the Bay-winged Cowbird (*Agelaioides badius*) is its main host (Fraga 1998, Ortega 1998), frequently parasitizes before host laying (Hoy and Ottow 1964, Mason 1980, Fraga 1986). Bay-winged Cowbirds always reject parasitic eggs by ejecting them from the incubation chamber or by burying them with new nest-lining material. In addition, this host sometimes prematurely deserts parasitized nests without laying (Fraga 1998).

There is no clear explanation for this nonadaptive timing of laying behavior by Screaming Cowbirds. Mason (1980) estimated that the laying of 87% of Screaming Cowbird eggs was not synchronized with Bay-winged Cowbird laying and attributed this to the high degree of unpredictability in the laying behavior of the host, based on the observation that it delayed laying for as much as five weeks after the nest was ready. Fraga (1986, 1998) described the breeding behavior of Bay-winged Cowbirds as "cryptic," but he did not analyze its

relationship with premature parasitism. He pointed out that synchronization may be difficult for Screaming Cowbirds, as the host often breeds in close, dark nests whose content is rarely visible from the outside (Fraga 1998). Thus, it is not clear whether the unpredictable laying behavior of Bay-winged Cowbirds or their nest type is the main cause of the poor timing of Screaming Cowbird parasitism. In addition, there are other hypotheses to explain the poor synchronization of Screaming Cowbird parasitism with host laying. The parasite depends almost exclusively on the availability of Bay-winged Cowbird nests. Therefore, if the number of laying-stage Bay-winged Cowbird nests is low, the synchrony between parasitism and host laying may also be low as a result of a lack of suitable nests at the time Screaming Cowbirds are laying. The effect of nest availability on timing of parasitism would be more intense if individual females avoided parasitizing the same nest more than once, as in other cowbird species (Ellison et al. 2006, but see McLaren et al. 2003). Another possible explanation for the disparity in timing between Screaming and Bay-winged Cowbird laying is that higher nest attentiveness by the host during laying precludes parasite females from accessing the nest. This would be expected because the consequences of successful parasitism during laying are more severe for the host than in other stages of the nesting cycle (Briskie and Sealy 1989, Fraga 1998). Bay-winged Cowbirds have been described as fierce defenders of their nests against Screaming Cowbirds, even before laying (Hudson 1920, Friedmann 1929, Mason 1980, Fraga 1998), but there are no data in the literature on the extent of nest attentiveness through the nesting cycle and its association with parasitism.

The aim of our study was to disentangle the factors affecting synchronization of Screaming Cowbird parasitism with Bay-winged Cowbird laying. We tested the hypotheses outlined above using a large set of observational data. We predicted that, if poor synchronization is the result of 1) a shortage of suitable host nests, then synchronization should be positively associated with availability of host nests at laying; 2) differences in host nest attentiveness along the nesting cycle, then nest attentiveness should be higher during laying than during prelaying or incubation, and intensity of parasitism should be negatively associated with nest attentiveness; and 3) unpredictability of Bay-winged Cowbird laying, then the frequency distribution of the lengths of prelaying periods should fit a negative exponential distribution (as expected under a Poisson process; Bednekoff and Lima 1998), and intensity of synchronized parasitism should vary with length of prelaying period. We also analyzed synchronization of host laying and Shiny Cowbirds parasitism of Bay-winged Cowbirds and Screaming Cowbird parasitism of two alternative hosts, the Chopi Blackbird (*Gnorimopsar chopi*; Fraga 1996) and the Brown-and-yellow Marshbird (*Pseudoleistes virescens*; Mermoz and Reboresda 1996, Mermoz and Fernández 2003).

## METHODS

### STUDY SITE

Our study was conducted at Reserva El Destino, near the town of Magdalena (35°08'S, 57°23'W), in the province of Buenos Aires, Argentina, during the 2003–2005 breeding seasons (November–February). The study area is near flat and marshy grassland, with implanted pastures and old and second growth stands dominated by tala (*Celtis tala*) and coronillo (*Scutia buxifolia*). Our study site comprised an area approximately 600 ha in size, which is included within the Biosphere Reserve (MAB-UNESCO) Parque Costero del Sur, an area approximately 30 000 ha in size.

### DATA COLLECTION

Bay-winged Cowbirds normally breed in old closed or domed nests built by other species such as thornbirds (*Phacellodomus* spp.), spinetails (*Synallaxis* spp.), Rufous Horneros (*Furnarius rufus*), Firewood-gatherers (*Anumbius annumbi*), and Great Kiskadees (*Pitangus sulphuratus*; Friedmann 1929). They often recondition nests by adding nest-lining material (typically grasses) before laying their own eggs (Fraga 1986). To facilitate data collection, we placed 50 wooden nest boxes in our study area. The boxes were 30 × 20 × 16 cm, each with an entrance hole 4.5 cm in diameter and a roof opening that allowed us to monitor the progress of the nest it contained. Based on preliminary observations, all nest boxes were located close to known Bay-winged Cowbird nesting sites. Because Bay-winged Cowbirds use nests built by other species, we partially filled each nest box with nest material, making a nest cup of plant fibers. Bay-winged Cowbirds used these nest boxes, but not very often (only 5–8 boxes were occupied each year), showing a preference for natural nests that were usually easy to find by following the alarm calls of the owners. Most nests were found along the edges of woodland patches (i.e., talaes) or in isolated tala trees, at heights of 1.3–12 m. About half of the nests found were too high to be accessible. Thus, we limited our study to those built at a height of less than 5 m, which could be reached with a portable ladder. We found a total of 114 nests with these characteristics: 35 in 2003, 39 in 2004, and 40 in 2005. Seventy-seven of these nests were found during prelaying, 16 during laying, 20 during incubation, and one after hatching.

We checked the nests daily or every two days until they fledged young or failed. Nest content was determined at each visit by taking all the eggs or nestlings out of the nest. In the few cases where a nest chamber was too deep to be accessible through the entrance hole (i.e., nests of the Firewood-gatherer), we made an additional hole near the chamber to facilitate egg and chick handling. The additional hole was closed after each visit. This disturbance did not cause any nest desertion. At each visit, we recorded if the host had completed the nest lining, and after that, the number of host and parasite eggs present

in the nest. A nest was considered parasitized if it contained Screaming or Shiny Cowbird eggs at any stage of the nesting cycle. Bay-winged and Screaming Cowbird eggs are spotted and similar in size but can be distinguished from each other. We identified the eggs as those of host or parasite on the basis of the background color (predominantly greenish or bluish for Bay-winged, and reddish or pinkish for Screaming Cowbird eggs), presence of dark scrawls (characteristic of Screaming Cowbird eggs), and spotting pattern (more heterogeneous for Screaming than for Bay-winged Cowbird eggs; Fraga 1983). Shiny Cowbird eggs, although highly polymorphic in color, are easy to distinguish from those of Bay-winged and Screaming Cowbirds by their rounded shape, background color, and clearly defined spots. We marked newly detected eggs with waterproof ink and measured the length and width of each to the nearest 0.1 mm with calipers. Nest checking lasted at most 5–10 min. During our visits, both members of the breeding pair always remained close to us, and individuals usually resumed incubation as soon as we left the nest. This host usually lays at around 07:00 (MCDM, pers. obs.). To avoid interference with host laying, we visited the nests from 07:30 to 18:00.

### INCIDENCE OF SCREAMING COWBIRD PARASITISM

To study the incidence of Screaming Cowbird parasitism, we analyzed independently the parasitic events that occurred before and after the host began laying, as they have different effects on parasite and host reproductive success. The variable used in this analysis was number of Screaming Cowbird eggs laid per nest. This variable accounted for the frequency and intensity of parasitism, as it equals zero when the nest is not parasitized and indicates the actual number of parasitic events in parasitized nests. Nests found during incubation were excluded from this analysis.

### TIMING OF SCREAMING COWBIRD PARASITISM

We estimated the timing of Screaming Cowbird parasitism from a sample of 273 parasite eggs laid in 58 Bay-winged Cowbird nests that were found before or during host laying. In 128 cases (47%), we could establish directly the date of parasitism (i.e., nests were visited daily, and parasitic eggs appeared between two consecutive visits). In the remaining cases, we did not know the exact date of parasitism because nests were visited every other day. We assumed that in half of these cases, the parasite egg was laid the same day the egg was found, and in the other half, that it was laid the day before. The number of nests that we observed at different stages of the nesting cycle differed as a result of different probabilities of encounter, desertion, or predation. To correct for these differences, we calculated an average daily intensity of parasitism by dividing the number of Screaming Cowbird eggs laid in a given day of the nesting cycle by the number of Bay-winged Cowbird nests that we observed on that day of the nesting cycle.

#### NEST AVAILABILITY

We analyzed the relationship between availability of host nests at laying and intensity and timing of parasitism using polynomial regression. Given that 29% (33 of 114) of Bay-winged Cowbird nests were depredated or deserted before clutch completion, we estimated the actual availability of nests at laying using nest-days as the unit of measure, where 1 nest-day equals one day of nest activity during laying (Mayfield 1975). The number of nest-days at laying also varied among nests because of differences in clutch size (mean  $\pm$  SE:  $3.8 \pm 0.7$  eggs, range: 3–5 eggs,  $n = 62$  nests). To standardize our estimate of nest availability, we considered days 0–4 of the nesting cycle (day 0 corresponds to the laying of the first host egg) as laying period. All parasite eggs laid in Bay-winged Cowbird nests during this period were considered synchronized with host laying, as they hatched one day before or simultaneously with host eggs. Non-synchronized parasitism included all Screaming Cowbird eggs laid during prelaying, incubation (from day 5 onwards), and after hatching, as well as those eggs laid in previously abandoned nests or in nests where the host never laid. We divided the breeding season into five-day periods and calculated for each period the number of parasitic events per nest-day at laying and the proportion of synchronized parasitism (i.e., number of parasitic events in nests at laying divided by total number of parasitic events).

#### NEST ATTENTIVENESS

To assess the extent of nest attention by Bay-winged Cowbirds and the frequency of nest visits by Screaming Cowbirds, we made focal observations of nests through the nesting cycle. We observed 13 nests during prelaying and laying (two in 2004 and 11 in 2005) and 12 nests during incubation (five in 2004 and seven in 2005). We decided to use independent subsets of nests for focal observations during incubation because during our study, 60%–77% of the nests failed shortly after laying due to desertion or nest predation. Therefore, if we had used the same nests throughout the nesting cycle, our sample size would have been very small. We observed nests separated from one another by at least 70–100 m. This distance exceeds the minimum distance observed between an active Bay-winged Cowbird nest and the next closest nest in our study area (MCDM, pers. obs.). Therefore, it seems unlikely that we observed different nesting attempts of the same breeding pair during the same breeding season. We made the observations using  $7 \times 50$  binoculars at a distance approximately 20 m from nests, hidden in the surrounding vegetation or covered with a blind. Before beginning the observations, we estimated the distance from each nest to nearby tree branches to use them as points of reference. Observations lasted  $76 \pm 3$  min (range: 50–124 min) and were conducted during the morning (from 07:30 to 11:00) because previous studies reported that Screaming Cowbirds lay their

eggs in the morning hours until 11:00 (Hoy and Ottow 1964, Scott 1991) and inspect host nests throughout the day (Mason 1987, Fraga 1998). Data were recorded using a portable tape recorder. We obtained the following variables: number of Bay-winged Cowbirds present, time spent by the host inside the nest, time spent by the host within 5 m of the nest, frequency and duration of parasite's visits, and number of parasites in each visit. We defined nest attentiveness as the proportion of time with at least one Bay-winged Cowbird within 5 m of the nest. Preliminary observations showed that within this radius, Bay-winged Cowbirds detected and responded quickly to intruders approaching the nest. We assumed that a nest was unattended when there were no Bay-winged Cowbirds within 5 m of the nest.

#### LENGTH OF PRELAYING PERIOD

We measured the length of the prelaying period in a subset of 44 nests found before nest lining was completed and visited daily or every other day until the host began laying. We considered a nest to be complete when we did not detect differences in its lining between two consecutive visits. The length of prelaying was estimated as the number of days elapsed from nest completion to the laying of the first host egg. Similarly, we estimated the latency of Screaming Cowbird parasitism as the number of days elapsed from nest completion to the laying of the first parasite egg. For this estimation, we excluded four nests—one because it was not parasitized and three because the estimated date of the first parasitic event had a considerable error. To analyze the relationship between length of prelaying and the intensity of parasitism during prelaying and laying, we divided the period lengths into four categories: 1–3 days, 4–6 days, 7–9 days, and more than 10 days. Observations in another icterid (i.e., the Red-winged Blackbird, *Agelaius phoeniceus*; Holcomb and Twiest 1968) and in species sympatric to Bay-winged Cowbirds that are hosts of Shiny Cowbirds (i.e., the Southern House Wren, *Troglodytes musculus* and Chalk-browed Mockingbird, *Mimus saturninus*; MCDM, pers. obs.) indicate that length of the prelaying period varies from one to three days. Therefore, to reflect a decreasing degree of predictability of host laying, we defined categories two, three, and more than three times longer than the most common category of length of the prelaying period.

#### STATISTICAL ANALYSIS

When possible, we used parametric statistical tests. To meet parametric assumptions, we transformed proportions using the arcsine of the square root of the data (Zar 1996). When transformation did not produce normally distributed data, we used nonparametric tests (Siegel and Castellan 1989). Statistical tests were performed using StatView 5.0 (SAS Institute 1998) with an alpha level  $< 0.05$  (two-tailed). Data are presented as means  $\pm$  SE.

TABLE 1. Characteristics of Bay-winged Cowbird nests parasitized by Screaming Cowbirds in 2002–2005 at Reserva El Destino, Argentina. Nests are grouped by whether Bay-winged Cowbirds did or did not begin laying, and intensity refers to the number of parasitic eggs per parasitized nest (mean  $\pm$  SE). Range values are given in parentheses.

Year	Host began laying			Host deserted before laying		
	<i>n</i>	Frequency (%)	Intensity	<i>n</i>	Frequency (%)	Intensity
2003	32	97	4.5 $\pm$ 0.8 (0–12)	3	33	3
2004	33	91	4.2 $\pm$ 0.6 (0–10)	6	83	5.2 $\pm$ 0.8 (4–8)
2005	36	92	4.4 $\pm$ 0.4 (0–9)	4	100	4.5 $\pm$ 2.0 (1–10)

## RESULTS

### INCIDENCE OF SCREAMING COWBIRD PARASITISM

The mean frequency of Screaming Cowbird parasitism in nests in which Bay-winged Cowbirds began laying was 93% ( $n = 101$  nests). Screaming Cowbirds also parasitized 10 of 13 nests in which the host never laid (Table 1). There were no significant differences among years in the number of parasitic eggs laid per nest during prelaying or laying (Kruskal-Wallis tests:  $H_2 = 0.2$ ,  $n = 67$  nests,  $P = 0.93$  and  $H_2 = 2.5$ ,  $n = 84$  nests,  $P = 0.28$ ). For the analysis of intensity of parasitism through the breeding season, we combined data from the three years. We compared intensity of parasitism over 15–16 day intervals from 1 December to 31 January because during our study, more than 90% of the nesting attempts ( $n = 90$  nests with known initiation date) occurred within this period (Fig. 1). The number of Screaming Cowbird eggs laid before and during the host's laying period did not differ through the breeding season (Kruskal-Wallis tests:  $H_3 = 5.0$ ,  $n = 64$  nests,  $P = 0.17$  and  $H_3 = 4.8$ ,  $n = 81$  nests,  $P = 0.18$ , respectively).

### TIMING OF SCREAMING COWBIRD PARASITISM

We observed laying of parasite eggs up to 17 days before the start of host laying (Fig. 2). On average, Screaming Cowbirds laid more eggs per nest-day during laying ( $0.52 \pm 0.06$ ,  $n = 5$ ) than during prelaying ( $0.27 \pm 0.03$ ,  $n = 17$ ) or incubation ( $0.08 \pm 0.02$ ,  $n = 13$ ), and during prelaying than during incubation (Kruskal-Wallis test,  $H_2 = 20.2$ ,  $P < 0.001$ , post hoc contrasts  $P < 0.05$ ). The cumulative number of parasite eggs laid per nest during laying (days 0 to 4) was 2.6, while during incubation (days 5 to 17), it was 1.0. Considering that the average length of the prelaying period was 6.4 days (see below), the total number of eggs laid during this period was on average 1.6. Therefore, 31%, 50%, and 19% of Screaming Cowbird eggs were laid during prelaying, laying, and incubation, respectively, as estimated from daily intensities of parasitism.

### NEST AVAILABILITY

The number of parasitic eggs laid during the period of host laying fit a quadratic function of the availability of

host nests (polynomial regression:  $F_{2,57} = 65.4$ ,  $r^2 = 0.69$ ,  $P < 0.0001$ , linear term:  $t_{57} = 1.4$ ,  $P < 0.0001$ , quadratic term:  $t_{57} = -0.03$ ,  $P = 0.02$ ; Fig. 3A). However, we did not find any relationship between the proportion of synchronized parasitism and the number of nest-days in laying (polynomial regression of arcsine transformed data:  $F_{2,35} = 0.8$ ,  $P = 0.46$ ; Fig. 3B).

### NEST ATTENTIVENESS

The proportion of time that a nest was attended was  $0.91 \pm 0.09$  during prelaying,  $0.84 \pm 0.03$  during laying, and  $0.89 \pm 0.04$  during incubation. Attentiveness did not differ between prelaying and laying in nests observed at both stages (Wilcoxon signed rank test:  $Z = -1.4$ ,  $n = 13$  nests,  $P = 0.15$ ). Likewise, attentiveness in nests observed at laying was similarly high to that observed at incubation (Mann Whitney U-test:

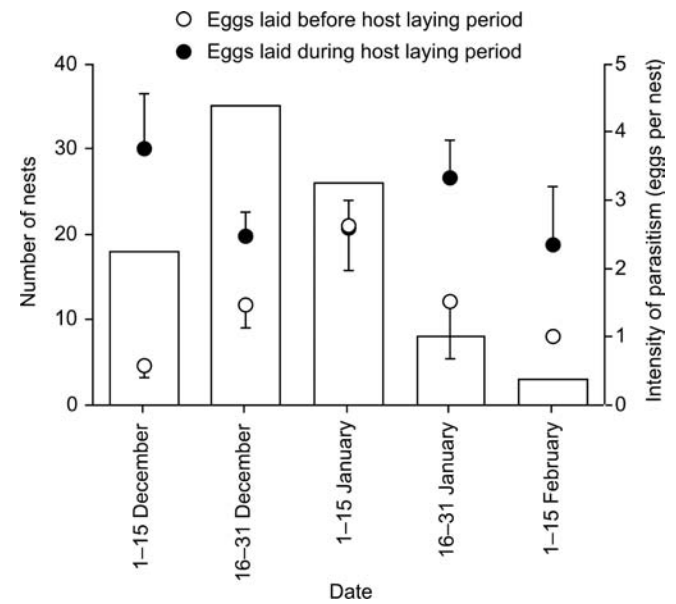


FIGURE 1. Screaming Cowbird parasitism through the breeding seasons 2002–2005 at Reserva El Destino, Argentina. Bars indicate the number of Bay-winged Cowbird nests that started laying within the given time intervals. Circles represent the mean numbers of screaming cowbird eggs laid before or during the host laying period.

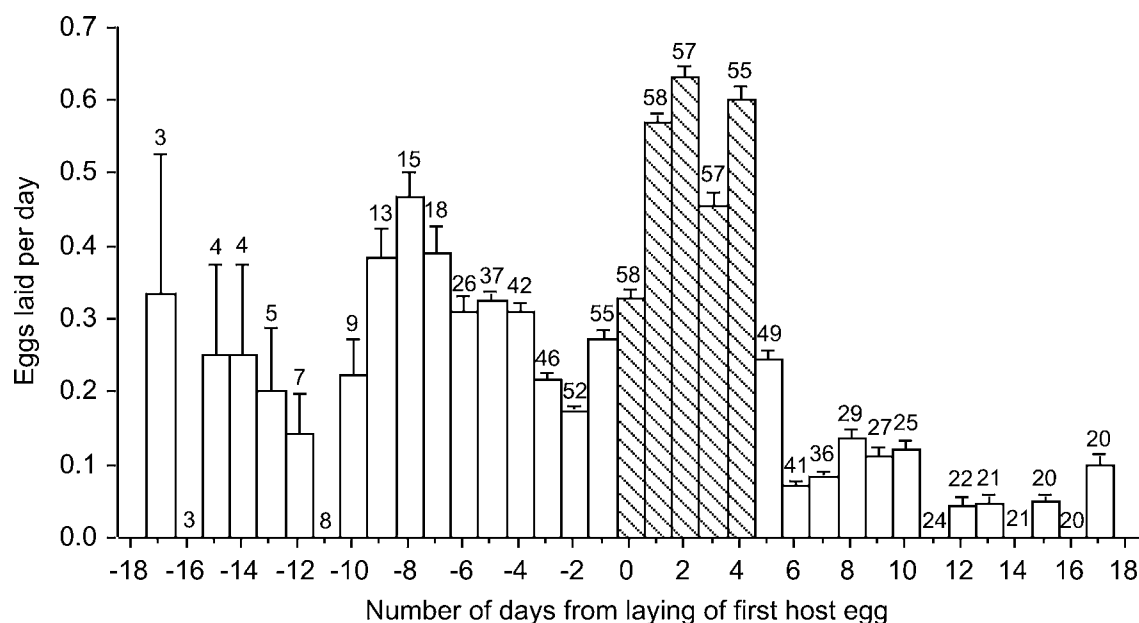


FIGURE 2. Average number of Screaming Cowbird eggs laid per day in active Bay-winged Cowbird nests through the nesting cycle in 2002–2005, at Reserva El Destino, Argentina. Day 0 corresponds to the laying of the first host egg. Striped bars indicate the laying period of the host. Clutch size in this species ranges from 3–5 eggs, and incubation begins with the laying of the penultimate egg, and lasts 13 days. The number of active nests visited each day is indicated above bars.

$U = 78$ ,  $n_1 = 13$  nests,  $n_2 = 12$  nests,  $P > 0.99$ ). There was no association between intensity of parasitism and nest attentiveness during prelaying (Spearman rank correlation:  $r_s = -0.13$ ,  $n = 13$  nests,  $P = 0.66$ ) or laying (Spearman rank correlation:  $r_s = -0.09$ ,  $n = 13$  nests,  $P = 0.76$ ).

We observed Screaming Cowbirds visiting Bay-winged Cowbird nests in 31 out of 38 observation sessions. Parasites approached nests in pairs in all but two occasions, in which solitary individuals visited nests that were in advanced stages of incubation. Most visits involved 1–2 pairs of Screaming Cowbirds, but in some cases, we observed 6–8 individuals arriving together. The mean number of individuals per visit was  $2.9 \pm 0.3$ , and the average number of visits per hour was  $2.3 \pm 0.3$ . The frequency of visits did not differ between prelaying and laying (prelaying:  $3.2 \pm 0.6$ , laying:  $2.5 \pm 0.6$ ; Wilcoxon signed rank test:  $Z = -0.8$ ,  $n = 13$  nests,  $P = 0.41$ ), but it decreased during incubation (laying:  $2.5 \pm 0.6$ , incubation:  $1.3 \pm 0.4$ ; Mann Whitney  $U$ -test:  $U = 42$ ,  $n_1 = 13$ ,  $n_2 = 12$ ,  $P = 0.05$ , 95% confidence interval for the median difference: 0–1.2).

#### LENGTH OF PRELAYING STAGE

The mean length of the prelaying period (number of days elapsed since nest completion until the laying of the first host egg) was  $6.4 \pm 0.7$  days (range: 1–19 days; Fig. 4A) and tended to increase through the breeding season (Spearman rank correlation:  $r_s = 0.30$ ,  $n = 44$ ,  $P = 0.06$ ). The frequency distribution of the prelaying periods departed significantly from

the negative exponential function expected if the start of host laying were to occur unpredictably following nest completion (Kolmogorov-Smirnov test:  $d = 0.6$ ,  $P < 0.01$ ). Latency of Screaming Cowbird parasitism (number of days elapsed since the nest was completed until the laying of the first parasite egg) was 1–3 days in nearly 50% of cases (Fig. 4B). Latency was not associated with length of the Bay-winged Cowbird's prelaying period (Spearman rank correlation:  $r_s = 0.22$ ,  $P = 0.17$ ,  $n = 40$  nests; Fig. 4C).

Overall, there were significant differences among the four categories of prelaying period length in intensity of parasitism during prelaying (Kruskal-Wallis test:  $H_3 = 7.9$ ,  $n = 44$  nests,  $P = 0.05$ ), laying (Kruskal-Wallis test:  $H_3 = 9.4$ ,  $n = 44$  nests,  $P = 0.02$ ), and prelaying and laying combined (Kruskal-Wallis:  $H_3 = 13.2$ ,  $n = 44$  nests,  $P = 0.003$ ; Fig. 5). Nests with prelaying periods of 4–6 days received fewer cowbird eggs during prelaying and laying than those with periods of 10 or more days (post hoc contrasts  $P < 0.05$ ). When we considered intensity of parasitism during prelaying and laying combined, nests with prelaying period lengths of 4–6 days received significantly fewer Screaming Cowbird eggs than those that had shorter or longer prelaying periods (post hoc contrasts  $P < 0.05$ ).

#### TIMING OF SHINY COWBIRD PARASITISM

The frequency of Shiny Cowbird parasitism in Bay-winged Cowbird nests was 15% (17 out of 114 nests), and its intensity  $1.35 \pm 0.05$  eggs per parasitized nest ( $n = 17$  nests). Out of 23

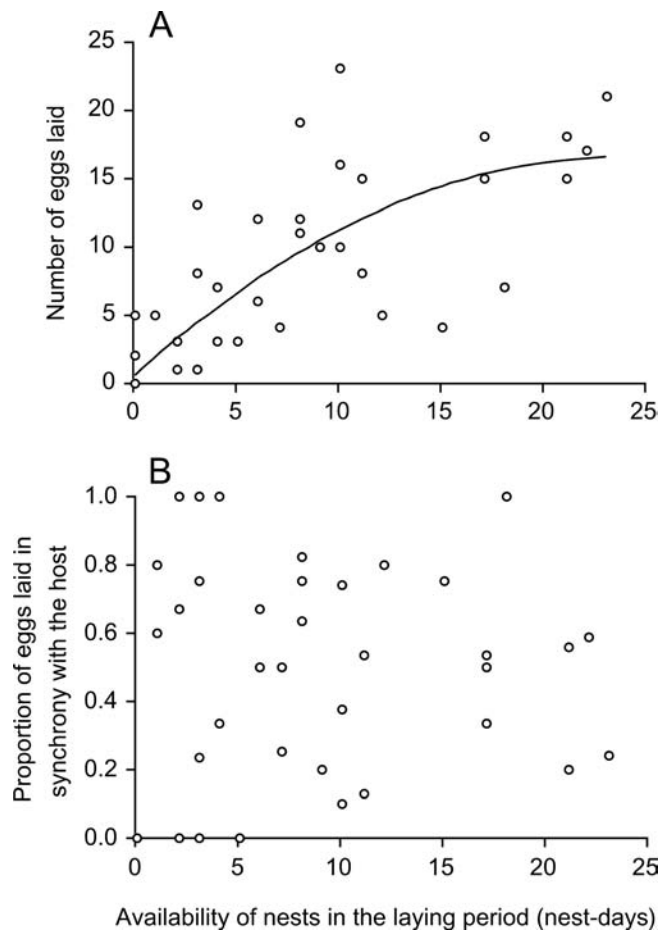


FIGURE 3. (A) Number of parasitic events and (B) proportion of parasitic eggs laid in synchrony with host laying by Screaming Cowbirds as a function of the availability of Bay-winged Cowbird nests at laying stage (expressed in nest-days; one nest-day equals one day of nest activity during laying). Data correspond to 37 periods of five days during the 2002–2005 breeding seasons at Reserva El Destino, Argentina. Events of parasitism with zero nest availability correspond to those that took place in inactive nests or in active nests during prelaying or incubation stages.

Shiny Cowbird eggs, five were laid in two nests where the host did not begin laying, and the other 18 in 15 nests with host laying (seven during prelaying and 11 during laying). The proportion of parasitism synchronized with Bay-winged Cowbird laying did not differ between Shiny and Screaming Cowbirds (Screaming: 137 of 299, Shiny: seven of 18, Heterogeneity test:  $\chi^2_1 = 0.3$ ,  $P = 0.57$ ; Table 2).

TIMING OF SCREAMING AND SHINY COWBIRD PARASITISM IN OTHER HOSTS

Screaming Cowbird parasitism during prelaying was more frequent in Bay-winged Cowbirds (91 of 299 eggs laid

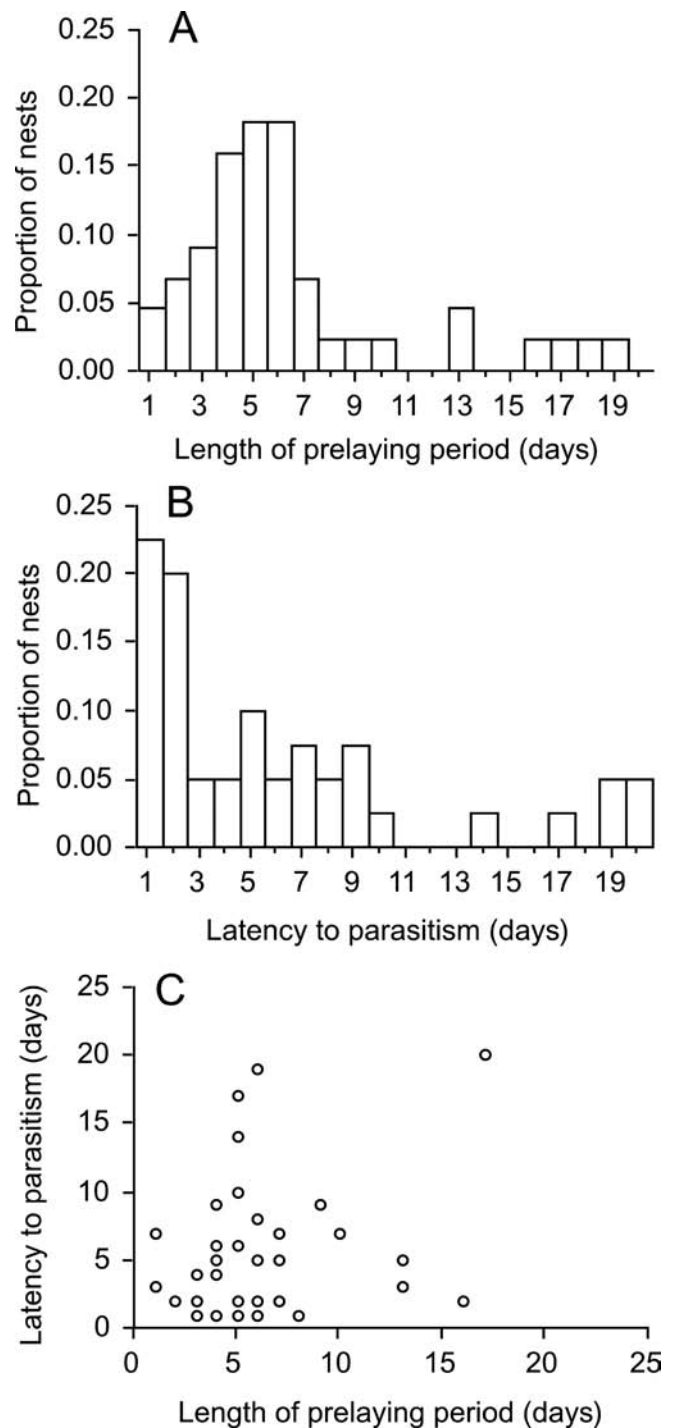


FIGURE 4. Frequency distribution of Bay-winged Cowbird (A) prelaying period lengths ( $n = 44$  nests) and (B) latencies from completion of nest lining until the first event of Screaming Cowbird parasitism ( $n = 40$  nests). (C) Association between the latency to the first Screaming Cowbird parasitic event and length of Bay-winged Cowbird prelaying period. Data are from 2002–2005, Reserva El Destino, Argentina.

TABLE 2. Percentage of Screaming and Shiny Cowbird eggs laid during prelaying and laying in nests of Bay-winged Cowbirds and other hosts in 2002–2005 at Reserva El Destino, Argentina. Total numbers of eggs are given in parentheses.

Cowbird species	Host species	Eggs laid before host laying (%)	Eggs laid during host laying (%)	Nest type
Screaming	Brown-and-yellow Marshbird <i>Pseudoleistes virescens</i> <sup>a</sup>	0.0 (17)	64.7 (17)	Open cup
Screaming	Chopi Blackbird <i>Gnorimopsar chopi</i> <sup>b</sup>	9.6 (52)	59.6 (52)	Cavity
Screaming	Bay-winged Cowbird <i>Agelaioides badius</i>	30.4 (299)	46 (299)	Closed, domed
Shiny	Southern House Wren <i>Troglodytes musculus</i> <sup>c</sup>	1.1 (93)	53.8 (93)	Cavity
Shiny	Chalk-browed Mockingbird <i>Mimus saturninus</i> <sup>d</sup>	3.3 (180)	73.9 (180)	Open cup
Shiny	Brown-and-yellow Marshbird <i>Pseudoleistes virescens</i> <sup>e</sup>	7.6 (157)	64.3 (157)	Open cup
Shiny	Bay-winged Cowbird <i>Agelaioides badius</i>	38.9 (18)	61.1 (18)	Closed, domed

<sup>a</sup>Mermoz and Fernández 2003.

<sup>b</sup>A. G. Di Giacomo, Departamento de Conservación/Aves Argentinas Asociacion Ornitologica del Plata (pers. comm.).

<sup>c</sup>Tuero et al. 2007.

<sup>d</sup>Fiorini and Reborada 2006.

prematurely) than in two alternative hosts, the Chopi Blackbird (five of 52 eggs) and the Brown-and-yellow Marshbird (zero of 17 eggs; heterogeneity chi-squared test: Bay-winged Cowbird vs. other Screaming Cowbird's hosts combined:  $\chi^2_2 = 16.3$ ,  $P < 0.001$ ; Table 2). Likewise, Shiny Cowbirds often parasitized Bay-winged Cowbirds prematurely (seven of 18 eggs laid before host laying). However, this parasite seldom parasitizes other hosts during prelaying (Brown-and-yellow Marshbird: 12 of 157 eggs laid prematurely, Chalk-browed Mockingbird: six of 180 eggs, and Southern House Wren: one of 93 eggs; heterogeneity chi-squared test: Bay-winged Cowbird vs. other Shiny Cowbird's hosts combined:  $\chi^2_3 = 42.8$ ,  $P < 0.0001$ ; Table 2).

## DISCUSSION

Our results confirm that Screaming Cowbird parasitism is poorly synchronized with Bay-winged Cowbird laying. The frequency of parasitism during host prelaying estimated from daily intensities of parasitism was 31%, while during laying and incubation, it was 50% and 19%, respectively. Our values during prelaying are intermediate to the 14% reported by Fraga (1998) and the 87% reported by Mason (1980). The differences between our results and those of Fraga (1998) could be attributed to his estimation being based on fewer nests and his not correcting for the different number of nests observed through the nesting cycle. Regarding Mason's (1980) estimation, it is possible that he had misidentified Bay-winged Cowbird eggs, as suggested by Fraga (1998). This host often removes the whole clutch from the incubation chamber when it is highly parasitized. Therefore, if Bay-winged Cowbird eggs were misidentified as parasite eggs, nonsynchronized parasitism was overestimated.

The frequency of asynchronous Screaming Cowbird parasitism that we observed in nests of its primary host is one of the highest reported for brood parasites. High figures were also reported by McLaren et al. (2003), who found that 30% of Brown-headed Cowbird eggs were laid before the start of host laying in Song Sparrow (*Melospiza melodia*) nests. In that study, the Song Sparrow was the most frequently parasitized species within the host community, with a high proportion of parasitized nests containing multiple cowbird eggs. If parasitic females are relatively selective regarding the host species they exploit within each avian community, as certainly occurs with the specialist Screaming Cowbird, then a higher frequency of misplaced parasitic eggs may reflect the trade-off between laying at the inappropriate stage and trying to locate a more suitable nest of the preferred host.

Poor synchronization between parasitism and host laying might increase if suitable nests are in short supply at the time

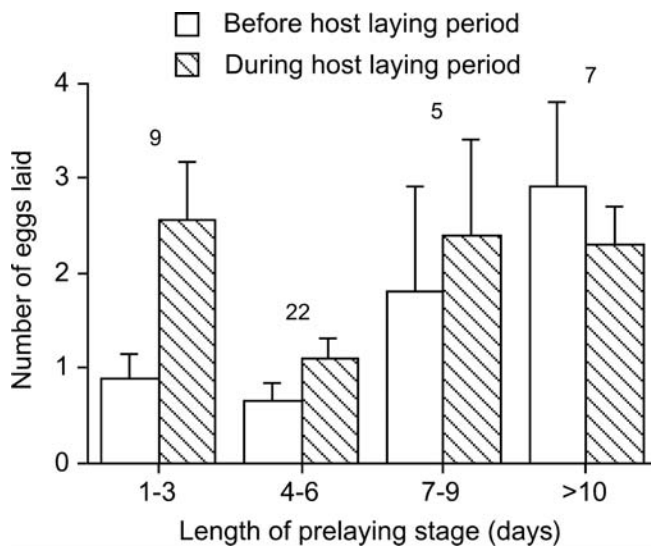


FIGURE 5. Number of Screaming Cowbird eggs per parasitized nest (i.e., intensity of parasitism; mean  $\pm$  SE) as a function of length of prelaying period in 2002–2005 at Reserva El Destino, Argentina. The number of nests in each category is indicated above bars.



parasitic females are ready to lay. This hypothesis implies that females who lay eggs asynchronously make the best of a bad situation, and therefore, synchronization should improve when more nests are available. However, we failed to find a positive association between the proportion of synchronized parasitism and the number of nests at laying. Hence, asynchronous parasitism by the Screaming Cowbird cannot be attributed to a low availability of host nests. Similarly, higher levels of nest defense cannot explain poor synchronization during host laying, as nest attentiveness was equally high before, during, and after laying. Moreover, we did not find a negative association between nest attentiveness and the number of Screaming Cowbird eggs laid during prelaying or laying. Some authors have pointed out that to properly assess the effectiveness of nest attentiveness in deterring parasitism, it should be evaluated at the time parasitic females come to lay their eggs (Sealy et al. 1998). Screaming Cowbirds parasitize Bay-winged Cowbirds from before sunrise (MCDM, pers. obs.) until approximately 10:00–11:00 (Hoy and Ottow 1964, Scott 1991). We found that, in addition, they visit Bay-winged Cowbird nests and monitor host activities throughout the morning, presumably using the information acquired during their visits to decide whether to parasitize particular nests. Therefore, we consider nest attentiveness during the morning to also be informative about the effectiveness of this defense.

Fraga (1998) argued that timing of parasitism could be influenced by nest structure because it is more difficult for the parasites to monitor closed or covered nests, like those used by Bay-winged Cowbirds, than open nests. However, the extent of synchronization between parasitism and host laying is higher when Screaming Cowbirds use nests of Chopti Blackbirds (who are cavity nesters) than when they use those of Bay-winged Cowbirds. Thus, nest architecture per se does not explain the poor synchronization between Screaming and Bay-winged Cowbird laying.

Our results corroborate previous works that mention great variation in the length of the prelaying period in this host species (Hoy and Ottow 1964, Mason 1980, Fraga 1986, 1992). However, Bay-winged Cowbird laying cannot be regarded as strictly unpredictable. If it is equally probable that the host start laying at any time interval after nest completion, then the frequency distribution of the prelaying periods should fit a negative exponential distribution, as is expected in Poisson-like processes (Bednekoff and Lima 1998). Contrary to this prediction, we found that the frequency distribution of prelaying periods significantly departed from a negative exponential distribution. On the other hand, our results indicate that for Screaming Cowbirds, it was not possible to predict the beginning of host laying from cues associated with nest appearance, as latency to the first event of parasitism was not associated with length of prelaying. In approximately 50% of the nests, Screaming Cowbirds laid their first eggs 1–3 days after nest lining was completed, but in only 20% of the nests did hosts begin

laying within this period. We found some support for an effect of length of prelaying period on the intensity of parasitism, as nests with prelaying period lengths of 4–6 days received fewer eggs during prelaying and laying than nests with shorter or longer prelaying periods. Therefore, our results were consistent with Mason's (1980) suggestion that the Bay-winged Cowbird prevents synchronization of Screaming Cowbird parasitism by postponing the beginning of laying. Further indirect evidence supporting this hypothesis arises from the comparison of synchronization of Shiny Cowbird parasitism with Bay-winged Cowbirds and with other hosts. Nearly 50% of Shiny Cowbird eggs were found in Bay-winged Cowbird nests before host laying, while this phenomenon was rare in other hosts, regardless of whether in open or closed nests (Table 2). These results suggest that variability in the length of Bay-winged Cowbird prelaying period also precludes synchronization of Shiny Cowbird parasitism.

Why do Screaming (and Shiny) Cowbirds respond to Bay-winged Cowbird prelaying behavior if it is not a reliable predictor of host laying? During prelaying, this host ferociously guards the nest against parasites and does not show any apparent change in its behavior once it begins laying. If a parasitic female uses the activity of the host as a cue to locate and parasitize suitable nests, as reported in other studies (Wiley 1988, Kattan 1997, Clotfelter 1998, Robinson and Robinson 2001, Honza et al. 2002), then the behavior of Bay-winged Cowbirds during prelaying may act as a signal that elicits a false alarm, namely, premature laying. Signaling theory predicts that if receivers attempt to decrease false alarms by being less receptive to signals, they will increase the risk of misdetections (Wiley 1994). Given that Screaming Cowbirds depend almost entirely on the availability of Bay-winged Cowbird nests for breeding, it is possible that the benefit of being less receptive when deciding to parasitize is outweighed by the cost of not responding to a suitable opportunity for parasitism. In accordance with this interpretation, the high rate of nest visits by Screaming Cowbirds before and during host laying may be a response to the problem of timing parasitism in such a confusing host (Fraga 1998). On the other hand, more than one Screaming Cowbird female usually parasitizes Bay-winged Cowbird nests before, during, or after host laying. Although Bay-winged Cowbirds typically remove premature parasitic eggs within 24 hr, their nests may receive up to five parasite eggs in a single day (MCDM, pers. obs.). If Screaming Cowbird females do not discriminate between conspecific eggs laid prematurely and host eggs, then the encounter of a parasitic egg during prelaying by another cowbird female might act as a cue that triggers premature parasitism. Mason (1980) speculated that if naive females were more likely to lay prematurely, then their erroneous laying could stimulate premature laying by more experienced females.

To summarize, Screaming Cowbirds synchronize parasitism poorly with host laying when they parasitize

Bay-winged Cowbirds but not alternative hosts. Similarly, Shiny Cowbirds show lower synchronization of parasitism with Bay-winged Cowbirds than with other hosts, suggesting that some characteristic of Bay-winged Cowbirds precludes synchronization of parasitism with host laying. Our results indicate that the extent of this synchronization is associated with the length of the prelaying period, which in Bay-winged Cowbirds is highly variable. Thus, the high variance of the prelaying period in this host appears to act as an antiparasitic defense, as it decreases the extent of synchronization between parasitism and host laying, and therefore the costs of parasitism.

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