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Timing is everything: accurate parasitism timing is critical to cowbird nestling success

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Obligate brood parasitism is a reproductive strategy whereby the parasitic parent leaves its offspring to be raised by a host of a different species. This has resulted in specialized adaptive behaviours selected to improve the survival of parasitic progeny. The timing of when to leave a parasitic propagule with the host can be paramount to the parasite's success, and erring in this decision could have dire fitness consequences. Brown-headed cowbirds, *Molothrus ater*, are North America's most widespread avian obligate brood parasite and, as generalists, successfully parasitize over 170 host species. Female cowbirds are cryptic and difficult to monitor, and much of how they make parasitic egg-laying decisions is not well understood. Despite the diversity in potential host species, cowbirds nearly always parasitize nests during a narrow window of the host's egg-laying period just before the onset of incubation, resulting in their offspring typically hatching before the host's own young. How important is it to get this timing right, and what are reproductive costs to parasitizing nests 'late' (i.e. after the onset of host incubation)? We simulated three different parasitic egg-laying timing decisions by adding cowbird eggs to the nests of a locally common host, the prothonotary warbler, *Protonotaria citrea*, at different stages of the host's laying and incubation periods and monitored the subsequent effects on cowbird hatching success, hatching asynchrony relative to host eggs, nestling size, haematocrit, a health proxy, and survival. Our experiment established the costs of delayed parasitic egg laying: late egg addition produced cowbird nestlings that hatched at the same time or later than their host nestmates, had smaller same-age body size and showed markedly lower survival compared to those placed in the pre-incubation window, supporting our hypothesis that parasitism timing is a behaviour under strong selection in this, and perhaps other, obligate brood parasites.

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Obligate brood parasites are a rare but phylogenetically widespread group of organisms that do not provide parental care and instead leave their progeny with an unrelated parental host. This life history strategy has evolved in diverse taxa, including spiders, insects, fishes, frogs and birds (Soler, 2017). Although obligate brood parasites do not engage in 'traditional' parental care, there is growing evidence that many brood-parasitic species make complex decisions and adopt labour-intensive behaviours that optimize offspring survival and reproductive success (White, 2019).

For example, every parasite must decide when to parasitize a host, as erring in this timing decision could have dire fitness consequences, such as hatching failure due to shortened incubation periods of late-laid parasitic eggs (Geltsch et al., 2016), resulting in potentially strong selection for specific parasitism-timing behaviours (e.g. when to leave a propagule with a host relative to the host's own breeding cycle). Males of *Ranitomeya variabilis*, a facultatively brood-parasitic frog, carry their tadpoles to new pools once they hatch and preferentially deposit their tadpoles into pools that already contain conspecific eggs, which its offspring can then consume. Crucially, host pools must be at the correct stage, because if the host eggs have already hatched, a larger host tadpole could cannibalize the smaller parasitic young

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(Brown et al., 2008). The parasitic cuckoo catfish, *Synodontis multipunctatus*, has an even narrower parasitism window, with mere seconds to successfully deposit their eggs with those of their host cichlid species before they are transferred to the breeding female host's buccal cavity (Blažek et al., 2018). The precision of, and by extension the importance of, the timing of parasitism varies by parasite and is dependent on factors like virulence (effects on hosts) and host usage (e.g. Kilner, 2005; Pollock et al., 2021).

Unlike specialists that tailor their parasitism strategy to a single host species, generalist brood parasites instead use multiple hosts (Antonson, Rubenstein, et al., 2020; Kennerley et al., 2022). Lacking consistent coevolutionary pressure from parasitizing a single host, they must adopt a more flexible 'one size-fits-most' approach to parasitism to successfully contend with a diverse set of host characteristics and environments (Antonson, Hauber, et al., 2020; Medina & Langmore, 2016). The brown-headed cowbird, *Molothrus ater* (hereafter, 'cowbird'), North America's most widespread avian brood parasite, is a hypergeneralist known to successfully parasitize more than 170 different host species (Lowther, 2020). Both cowbird nestlings and adults use a wide array of behaviours and adaptations to exploit hosts that range in size, diet, nest shape, clutch size and incubation period. Cowbird nestlings frequently outcompete their host nestmates (Hauber, 2003; Kilner, 2003); they have faster embryonic development and thus shorter incubation periods and hatch earlier than most hosts (Dearborn & Lichtenstein, 2002; Kattan, 1995). They are larger than 80% of their hosts in the egg, nestling and adult stages (Antonson et al., 2022, 2025; Dearborn & Lichtenstein, 2002), have a fast, flexible nestling growth rate (Kilpatrick, 2002; Remeš, 2010; Winnicki et al., 2021) and exhibit intense, prolonged begging (Dearborn, 1998; Hauber & Ramsey, 2003; Rivers, 2007; but see Rivers et al., 2013), all of which help them successfully adapt to and compete in most host nest environments. Brown-headed cowbirds are also sexually dimorphic, with adult males being 25% larger than females (Weatherhead, 1989), although it is not known precisely when during ontogeny this size dimorphism occurs (Kasumovic et al., 2002; Weatherhead, 1989). When sexual dimorphism occurs early in ontogeny, many of these brood-parasite advantages may be mediated by sex (Hauber & Ramsey, 2003; Tonra et al., 2008).

Regardless of the many cowbird nestling adaptations, adult female cowbirds should still make decisions while selecting hosts and laying eggs (i.e. host species choice, site, timing, clutch manipulation) that optimize cowbird nestling success long before they hatch. Despite the commonly held stereotype that cowbird egg laying is indiscriminate or random (i.e. shotgun model; Woolfenden et al., 2003), many studies have shown that female cowbirds invest time and energy, make complex decisions and plan ahead to create ideal conditions for their offspring in highly variable host nest conditions (Merrill et al., 2017). Specifically, female cowbirds prospect, sometimes extensively, for host nests, and have evolved excellent spatial memory (the 'bookkeeping hypothesis'; Clayton et al., 1997; Scardamaglia et al., 2017) for remembering nest locations. They are known to monitor the progression of host nests, counting eggs and perhaps even targeting a specific day to parasitize a nest (Guigueno et al., 2025; White et al., 2009). Cowbird females also monitor the success of their offspring in host nests (Hahn, Sedgwick, Painter, & Casna, 1999; Hoover & Robinson, 2007) and select future hosts based on past outcomes (Loudner et al., 2015). Indeed, individual cowbird females may have host preferences and selectively parasitize hosts they know to be of higher quality (Hahn et al., 1999; Hauber, 2001).

In addition to searching for, finding and selecting targeted host species and nest types, female cowbirds must identify individual nests at the appropriate stage for parasitism. The ideal timing for

parasitism seems to be during the host's laying period before the start of incubation, and most female cowbirds lay during this window (~90% of eggs; Kilner, 2005; McLaren et al., 2003; White et al., 2009). This pre-incubation timing, coupled with their rapid embryonic development, usually results in cowbird eggs hatching earlier than the host's, imparting a significant advantage to the cowbird nestling (Dearborn, 1998; Hauber, 2003; Kilner, 2003; Tonra et al., 2008; Winnicki et al., 2021). This head start allows the cowbird nestling time to grow and develop in advance of the host, and in combination with the many developmental advantages, monopolize parental care (Lichtenstein & Sealy, 1998). Other brood parasites across diverse nonavian lineages also benefit from hatching early: cuckoo catfish (Blažek et al., 2018), brood-parasitic dart frogs (Brown et al., 2008) and some cuckoo bee species (Megachilidae) (Litman, 2019) also must hatch first to be successful, suggesting that this advantage may be a common evolutionary feature as well as behavioural adaptation in brood parasites. But how important is the timing of parasitism, and by extension hatching early, to cowbird nestling success?

Cowbird females are often limited by the availability of suitable host nests at the pre-incubation stage, resulting in suboptimal laying decisions (e.g. multiple parasitism, laying in empty nests, laying far into host incubation, etc.) (Hoover et al., 2006; McLaren et al., 2003; Strausberger, 1998). However, given their rapid embryonic development and other adaptations as parasitic nestlings, a cowbird egg added 'late' (i.e. after the host laying period) could still theoretically receive adequate incubation (but see Peer & Bollinger, 1997, for the parasitic egg's hatching failure as a cost of late parasitism), develop quickly enough and hatch synchronously with, or perhaps a day or two later than, its host nestmates and survive. Other brood parasites are known to undergo compensatory growth (the acceleration of growth rate following a period of low food supply; Hector & Nakagawa, 2012) like common cuckoos, *Cuculus canorus* (Geltsch et al., 2012), and cowbirds are known to speed up and slow their growth and development in different host nest environments (Remeš, 2010; Winnicki et al., 2021). Compensatory growth could be especially useful to a cowbird added late to a host nest, helping them to overcome the initial disadvantages of hatching late and increasing the viability of late parasitism. As such, adult female cowbirds could expand laying opportunities even during periods of low host availability by adding eggs to host nests 1–2 days into the incubation period with presumably little to no cost. However, host nests are infrequently parasitized by cowbirds after the host starts incubation (McLaren et al., 2003; Strausberger, 1998; Woolfenden et al., 2003), and most other avian brood parasites also lay during the pre-incubation window (e.g. common cuckoos: Honza et al., 2020; Moskát et al., 2010; great spotted cuckoos, *Clamator glandarius*: Soler et al., 2015; bronzed cowbirds, *Molothrus aeneus*: Ellison et al., 2006; shiny cowbirds, *Molothrus bonariensis*: Fiorini & Reboreda, 2006; Fiorini et al., 2009; but see some subspecies of shiny bronze cuckoos, *Chalcites lucidus*: Attisano et al., 2023), suggesting that there are likely costs when violating the precise parasitism timing window. To our knowledge, no previous study has quantified experimentally the costs associated with late laying in brown-headed cowbirds.

In this experiment, we studied a locally common, synchronously hatching cowbird host, the prothonotary warbler, *Protonotaria citrea* (hereafter 'warbler'), to investigate the outcomes and potential fitness costs to the parasite associated with altered timing of parasitism. We experimentally varied when cowbird eggs were added to host nests in relation to the onset of host incubation (prior to onset, i.e. pre-incubation; day 2 of incubation; or day 4 of incubation) to simulate three different parasite egg-laying decisions. We then monitored the effects of the different egg-

laying scenarios on cowbird egg hatching success and asynchrony with host eggs, a physiological health metric (represented by haematocrit scores), body size and survival to fledging of cowbird nestlings. We hypothesized that there would be strong selective pressure for cowbird females to lay before the start of host incubation because of potential negative reproductive costs incurred by laying late. We predicted that cowbird eggs placed during the pre-incubation window (the natural condition) would be the most successful (e.g. have higher hatching success, larger body size, better health and higher survival) than eggs placed later, as they would receive adequate incubation and hatch earlier, and therefore be more advanced than their host nestmates. We predicted that the reproductive costs of late egg addition (e.g. lower hatching success, smaller body size, declining health, higher mortality) would be cumulative, worsening the later the egg was placed into the host's incubation period.

METHODS

Study Site and System

We conducted this experiment within a population of prothonotary warblers during two breeding seasons from April–July in 2023 and 2024 in the Cache River watershed in southern Illinois, U.S.A. Prothonotary warblers are Neotropical migrant songbirds that breed throughout eastern North America and prefer to nest in cavities over water in bottomland forests, swamps or forested wetlands (Petit & Petit, 1996). Our study system includes forested wetlands surrounded by primarily upland forests and agriculture (Hoover, 2003b). We used six discrete areas of suitable breeding habitat (i.e. separated by >1 km of unsuitable breeding habitat) as experimental study sites, using three sites in the first year and all six in the second (latitude/longitude of field sites: 37.3550834, 88.9201802; 37.3076522, 88.9721852; 37.3139583, 88.9811716; 37.2978250, 89.0531065; 37.3406410, 89.0728157; 37.2844062, 89.114365). As obligate secondary cavity nesters, warblers readily use nestboxes (Hoover, 2003b) and are typically double-brooded, laying an average of five eggs in the first clutch and four in the second (Hoover, 2003b). On each study site, we used existing or replacement nestboxes constructed of 1.9-litre beverage cartons with 44 mm openings attached to conduit poles and placed approximately 1.7 m above the ground (Hoover, 2003b), although water levels underneath varied seasonally. We placed approximately 260 boxes 50 m apart, spray-painted them brown or black, and greased the conduit poles to reduce access by terrestrial predators, thereby reducing nest loss to predation. These boxes allowed for reliable access to large numbers of active nests and provided practical and convenient means of monitoring and experimental manipulation (Loudner et al., 2015). Female warblers usually begin incubation after the last egg is laid, and their broods hatch synchronously in approximately 12 days (Petit, 2020).

In southern Illinois, the prothonotary warbler is a common host of brown-headed cowbirds, and throughout our study sites, up to 50% of warbler nestboxes are parasitized (Hoover, 2003b). Like 80% of cowbird host species, prothonotary warblers are smaller than cowbirds at the egg, nestling and adult stages (Antonson et al., 2022), although they often successfully raise several of their own offspring alongside cowbird nestlings (Hoover, 2003b; Hoover & Reetz, 2006; Kilner, 2005). Despite frequent cowbird parasitism, these warblers are an 'acceptor' host, seeming to display no anti-parasite behaviours or physiological responses (Hoover, 2003a; Scharf, Abolins-Abols, et al., 2021), and tolerating the addition of cowbird eggs into their clutches with little abandonment (Scharf, Hauber, et al., 2021).

Brown-headed cowbirds have faster embryonic development than the warbler hosts (i.e. 10–12 days incubation time versus 12–14 days), and usually their eggs hatch a day earlier when laid prior to the onset of incubation (Antonson et al., 2022; Hoover, 2003b). Cowbird females in our study system occasionally remove a warbler egg when parasitizing a nest (Hoover, 2003b), but this occurs rarely (approximately 25% of parasitized nests; Hoover, 2003b). Prothonotary warblers are robust cowbird hosts, and at our study site, over 70% of cowbird eggs laid in these nests survive to fledging (Hoover, 2003b).

Manipulation of Hatching Asynchrony and Egg Placement

In late April each year, which is the beginning of the warbler nesting season, we monitored nestboxes on all study sites every 3 days to record nest construction status and content and determined the onset of egg laying. To simulate three different parasitism timing decisions made by female cowbirds, we added a single cowbird egg to host nests (Scharf, Hauber, et al., 2021) at one of three times during the host's laying and incubation periods. The pre-incubation ('PI') eggs were added during the host's laying period before the start of incubation (mode = 1 day before start of incubation, median = 2 days before start of incubation, range 1–4 days before start of incubation), simulating the typical cowbird egg-laying timing. The incubation day 2 (D2) and day 4 (D4) treatment eggs were added after the start of incubation on the second and fourth days, respectively. Because prothonotary warblers generally begin incubating after the last egg is laid, all eggs placed during pre-incubation started incubation at the same time (i.e. the day the warbler female started incubating), ensuring equal 2-day intervals for the onset of incubation between each treatment. We also included a procedural control treatment that consisted of a warbler egg, rather than a cowbird egg, being placed in the nest during pre-incubation only. The procedural control served as a comparison for hatching success as well as to verify that early hatching of the cowbird egg, when added experimentally to a nest during the laying period, was a function of a cowbird egg's short incubation period and not just an artefact of the experimental procedures.

We collected unincubated cowbird and warbler eggs from active nests prior to the onset of incubation for their use in experimental treatments (see below). The eggs were uniquely labelled with a felt-tip pen regarding the nest of origin and the date of collection, and cowbird eggs were kept at room temperature for up to 7 days (mode = 2, median = 3, range 0–7). Warbler control eggs were kept at room temperature for up to 2 days (mode = 0, median = 0, range 0–2). For all experimental nests, all naturally laid cowbird eggs (if any) were removed from treatment nests and replaced with a treatment cowbird egg even if it aligned with the assigned treatment. After experimental parasitism, we inserted two-dimensional panels that reduced the opening of the nestbox from 44 mm to 32 mm to exclude interference and access by adult female cowbirds (Hoover & Robinson, 2007; Scharf, Hauber, et al., 2021). Only one cowbird egg was added to each treatment nest. We did not consider multiple parasitism in this experiment as the power to detect differences between treatments would have been greatly reduced. Nest attempts where warbler eggs were collected for our procedural control were not used for any other part of the experiment.

We assigned experimental treatments to nests in rounds consisting of four active nests (i.e. those in which the female warbler began laying). For each round we randomly assigned one of the four treatments (PI, D2, D4, control) to the first active nest in that group. We then assigned the remaining three treatments to nests by continuing to cycle through the treatment order given above.

We then repeated this process for each new round of nests. The procedural control treatment was de-emphasized in the second field season and was only included in every third round of treatment assignments. The last full round of treatments assigned in a season was considered the cutoff for inclusion in the study, resulting in a total of 122 nests (PI: $N = 36$; D2: $N = 32$; D4: $N = 31$; control $N = 23$) over the 2 years of the study. Each treated nest was assigned an ordinal date representing the commencement of incubation, defined as the first day after clutch completion, assuming one egg was laid per day per warbler. The ordinal dates associated with nests did not differ among treatment categories (Kruskal–Wallis test: $H_3 = 4.2611$, $N = 122$, $P = 0.2346$), and treatments were represented similarly across study sites (Fisher's exact test: $N = 122$, $P = 0.99$).

After the experimental eggs were placed in nests, we calculated the projected hatch date for the cowbird and warbler eggs based on the known incubation periods of each species (i.e. 10–12 days for cowbirds, 12–14 days for warblers). All nests were checked once every 3 days, and daily within 24 h of expected hatching. On each check, the number of cowbird and warbler eggs were noted. Once hatching started, the number of cowbird and warbler nestlings was noted as well as their ages. Of the 122 nests, six were abandoned and two were depredated before hatching and thus were removed from any further statistical analyses. We considered a nest to be abandoned if the clutch was never incubated or incubation ceased before hatching. We considered a nest to be depredated pre-hatch if there was damage to the nestbox (claw marks, tears, etc.), broken eggshells (prior to the hatching window) and/or nesting material pulled up into the opening. The resulting sample size was 114 nests across the four treatment groups (PI: $N = 33$; D2: $N = 28$; D4: $N = 31$; control: $N = 22$).

Hatching Success and Asynchrony

We determined the hatching outcomes of 92 cowbird eggs (PI: $N = 33$; D2: $N = 28$; D4: $N = 31$). Hatching success was defined as a cowbird nestling successfully emerging completely from its egg. If an egg went missing from a nest within the predicted hatching window and no eggshells or signs of predation were apparent, we assumed that the nestling hatched successfully but died and was removed by a host adult (i.e. nest sanitation) before being observed. Eggs not hatched 48 h past their expected hatch date were tested in the field for viability (i.e. heartbeat present) using an EggBuddy (Buddy heart rate monitoring system, Avian Biotech, Cornwall, U.K.; see Di Giovanni et al., 2023) and collected if no embryonic heart rate was detected ($N = 22$). Collected unhatched eggs were stored at 4 °C until dissection, during which embryonic tissue was collected and preserved (when present) in 98% ethanol for later genetic analyses.

We recorded hatch dates for all cowbird and warbler eggs. Hatching asynchrony was defined as the offset in days between the cowbird egg and the first warbler egg hatching. Most warbler eggs hatched synchronously (i.e. the same day). For example, a cowbird hatching a day earlier than the warblers would be noted as having an asynchrony of '−1', hatching the same day would be noted as '0', hatching 2 days later would be noted as '+2', etc. We determined asynchrony for 69 of the 70 hatched cowbird eggs (PI: $N = 27$; D2: $N = 22$; D4: $N = 20$). The asynchrony for one cowbird egg could not be determined because the nestbox was inaccessible due to flooding around the day of hatch.

Body Size

Once the cowbird egg hatched, we visited the nest every 3 days to document nestling survival and measured all nestlings within a

brood on days 3 and 6 of the cowbird nestling's life (hatch day = day 0). We measured tarsus length and wing chord to the nearest 0.01 mm using dial callipers and mass to the nearest 0.01 g using a digital scale. On day 3, 41 of the original 70 hatched cowbird nestlings were alive, and we measured 39 of them (PI: $N = 24$; D2: $N = 12$; D4: $N = 3$). Flooding made two nests (one D2 nest and one D4 nest) inaccessible. By day 6, only 27 of the original 70 hatched cowbird nestlings were alive, and 25 were measured (PI: $N = 15$; D2: $N = 8$; D4: $N = 2$) with two (both PI nests) also inaccessible due to flooding.

As a proxy for body size, we conducted a principal component analysis (PCA) on the morphological metrics obtained (i.e. tarsus length, wing chord length, mass) to combine measurements that were highly positively correlated (all $r > 0.9$). All measurements loaded heavily onto a single principal component (PC1), which accounted for 95% of the total variance. PC1 was used as a composite score of body size in further statistical analyses. Due to high mortality leading to small sample sizes in the D4 treatment, this treatment was removed from the PCA; final sample sizes for the remaining PCA for both nestling day 3 and day 6 were $N = 39$ for PI treatment and $N = 20$ for D2 treatment.

Haematocrit

On cowbird nestling day 6, we banded all nestlings (if aged day 4 or older) with U.S. Geological Survey metal leg bands and collected ~40 µl of blood from each cowbird nestling via puncture of the brachial vein (Owen, 2011). Blood samples were stored in heparinized microcapillary tubes on ice in the field and then spun down within 6 h at 6900 g for 5 min in the ZipCombo Centrifuge (LW Scientific, Lawrenceville, GA, U.S.A.) to measure haematocrit. Haematocrit is a measurement of the volume of red blood cells compared to the overall blood volume and can serve as a physiological health indicator as it represents an organism's ability to transport oxygen (sensu Bowers et al., 2014; Owen, 2011). The haematocrit score was measured using an EZ microhaematocrit reader (LW Scientific). Intermediate haematocrit scores are most associated with good health and survival, and both low and high scores may indicate adverse health conditions or outcomes (e.g. anaemia or a high parasite burden and dehydration, respectively) (Bowers et al., 2014). We collected haematocrit samples from 20 of the 27 cowbirds alive on day 6 (PI: $N = 10$; D2: $N = 8$; D4: $N = 2$). Seven samples were not collected due to inaccessibility during flooding ($N = 2$), tube breakage during transport ($N = 2$), sample processing issues ($N = 2$) and one nestling not yielding a suitable blood sample ($N = 1$). Again, due to high mortality in the D4 treatments causing low sample sizes, this treatment was removed from analysis of haematocrit, with final sample sizes for the remaining analysis being $N = 10$ for PI treatment and $N = 8$ for D2 treatment.

Survival

To determine survival and the timing of mortality, we monitored hatched nestlings every 3 days until fledging or nest failure. Due to the frequency of nest checks, the timing of mortality could only be assigned with an average uncertainty of 1.5 days. We determined whether a nest was depredated posthatch by observing damage to the nestbox (claw marks, tears, etc.), bird body parts in or around the nestbox and/or nesting material pulled from the nestbox opening. Nonpredation-related death was assigned if a nestling was found dead or was missing from the nest (before expected fledging window) with no evident external cause. If a fledging event was not directly observed, we assumed nestlings fledged if the preceding visit noted nestlings 'ready to fledge' (i.e.

developed and aged as old enough) and the nest was empty but undisturbed with faeces in the nest cup, parents calling and feeding fledglings and/or seeing fledglings nearby. We determined survival for all 70 cowbirds, but one PI treatment nest had to be excluded from overall survival model analysis due to predation after nestling day 3 (PI: $N = 26$; D2: $N = 22$; D4: $N = 21$). This nest was included in the Kaplan–Meier survival analysis but was censored after nestling day 3.

Sex

We were interested in the potential effects of sex in this experiment and had planned to include it as a variable in some analyses, as some studies have found sexual size dimorphism in cowbird nestlings at the later nestling and fledgling phases (brown-headed cowbirds: Hauber & Ramsey, 2003; Scott & Lemon, 1996; Tonra et al., 2008; Winnicki et al., 2021; shiny cowbirds, a close relative: Tuero et al., 2013). But, as reported in Boldrick (2025), no sexual size dimorphism was detected in brown-headed cowbirds in this study during the early nestling period when we measured them (nestling day 3 and day 6), and therefore sex was not examined further in this study. We also detected no sex difference in haematocrit. These patterns are supported by several other studies that also found no sexual dimorphism in cowbird size until later in the nestling phase than what was examined in this study or until after fledging (Scharf et al., 2022; Scott & Lemon, 1996; Tuero et al., 2013; Weatherhead, 1989; Winnicki et al., 2021). Additionally, neither Tuero et al. (2013) nor Weatherhead (1989) found a sex difference in survival to fledging.

Statistical Analyses

To evaluate the effects of treatment on cowbird hatching success, we used a generalized linear mixed model (GLMM) with a binomial response (hatched: yes = 1; no = 0) and a logit link function with treatment (ordinally: PI = 1; D2 = 2; D4 = 3) as a fixed effect and site as a random effect and plotted the result as a logistic curve.

To evaluate the effects of treatment on cowbird egg hatching asynchrony relative to host eggs, we used a GLMM with a gamma distribution because the data had right skew, with cowbird hatching asynchrony as a response variable, treatment as a fixed effect and site as a random effect.

To examine whether experimental treatment affected whether a cowbird egg hatched later than predicted, we annotated which cowbird eggs resulted in greater hatching asynchrony between cowbird and host eggs than would have been expected based on known cowbird incubation times (e.g. took longer to hatch). Eggs placed in the PI treatment were predicted to hatch 1 day before the warbler eggs, D2 eggs were expected to hatch 1 day later than the warbler eggs and D4 eggs were expected to hatch 3 days later than the warbler eggs. If their resulting asynchrony exceeded this estimation, the egg was noted as hatching later than predicted. We then used a GLMM with a binomial response (hatched later than predicted = 1; hatched on time or earlier = 0) with a logit link function with treatment as a fixed effect and site as a random effect.

To test for differences in body size among cowbird treatment groups, we used PC1 from the morphological traits as a response variable to represent the body size composite score in a linear mixed model (LMM) (Scharf et al., 2022) with treatment and nestling age at measurement as fixed effects and site as a random effect. We tested for an interaction between treatment and age at measurement but found no interaction (ANOVA: $\chi^2_2 = 0.818$,

$P = 0.366$) and removed it from the model. To determine whether cowbirds exhibit compensatory growth (sensu Winnicki et al., 2021), we tested whether the percentage change in mass differed between treatments. Percentage change in mass was calculated for all cowbirds that had measurements for both nestling day 3 and day 6, and a two-sample t test was performed. For this analysis, measurements for 23 cowbirds were included (PI: $N = 15$; D2: $N = 8$).

To evaluate the potential for a nonlinear relationship (as described in Bowers et al., 2014) between haematocrit and body size (PC1) and test for an effect of treatment on haematocrit, we constructed a linear model with a quadratic term. Specifically, we included haematocrit score as the response variable and the day 6 PC1 values from the body size analysis, day 6 PC1 values squared and treatment as fixed effects.

To evaluate the effects of treatment on cowbird nestling survival, we performed a logistic curve using a GLMM with a binomial response (survived: yes = 1; no = 0) with a logit link function with treatment (ordinally: PI = 1, D2 = 2, D4 = 3) as a fixed effect and site as a random effect. We also used a Kaplan–Meier survival estimate to examine cowbird egg survival over time between treatments (event = cowbird egg/nestling death). The time intervals were as follows: placement of egg (day 0) to hatch (day 1), where hatch day = day 1 in this analysis to include hatching failure; placement of egg to day 3; placement of egg to day 6; placement of egg to fledge (day 10). For this analysis, 91 of the 92 placed cowbird eggs were included (PI: $N = 33$; D2: $N = 28$; D4: $N = 30$), with one D4 nest being excluded due to inaccessibility that made determining the time of death impossible. This individual was included in the overall survival model, however, as the fate was known. We visited nests every 3 days and recorded cowbird egg/nestling survival as 0 (the cowbird egg was placed but failed to hatch), 1 (the cowbird egg hatched but the nestling died before day 3), 3 (the cowbird was alive on day 3 but died before day 6), 6 (the cowbird was alive on day 6 but died before fledging) or 10 (the cowbird fledged from the nest).

We conducted all statistical analyses in R (version 4.4.2) using the 'car' (Fox & Weisberg, 2019), 'dplyr' (Wickham et al., 2023), 'emmeans' (Lenth, 2023), 'ggplot2' (Wickham, 2016), 'gvlma' (Peña & Slate, 2006), 'lme4' (Zeileis, 2002), 'MuMIn' (Barton, 2023), 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova et al., 2017), 'nlme' (Pinheiro et al., 2023), 'performance' (Lüdtke et al., 2021), 'rstatix' (Kassambara, 2023), 'survival' (Therneau, 2023), 'survminer' (Kassambara & Kosinski, 2021), 'survMisc' (Marazzi, 2013) and 'ggsurvfit' (Sjoberg et al., 2021) packages. We inspected residuals for normality and evaluated models to ensure data adhered to statistical assumptions. Data are represented as means and 95% confidence intervals (CIs) unless otherwise specified. All post hoc pairwise comparisons were calculated using a Tukey adjustment unless otherwise specified.

Ethical Note

This research was conducted in compliance with ASAB/ABS guidelines for the ethical treatment of nonhuman animals in research, the University of Illinois Institutional Animal Care and Use Committee (IACUC protocol 22020) and permits from Fish and Wildlife Service Cypress Creek National Wildlife Refuge (special use 2023-007R and 2024-008R), Illinois Department of Natural Resources Scientific Research (NH23.5777 and NH24.5777), Migratory Bird and Eagle Scientific Collecting (MB30850D), Bird Banding Laboratory, U.S. Geological Survey (23931) and Illinois Nature Preserves Commission (SS23-031). We only removed nestlings from the nest for handling and measurement for a few minutes at a time and immediately returned them to their nests to

reduce stress for both the nestlings and the parents. We avoided visits to nests containing nestlings of fledgling age to reduce the chance of force-fledgling nestlings. We collected no more than ~40 µl of blood (far less than 1% of the bird's body weight) from an individual on a given day. All blood collection was performed after proper training and using methodology to reduce excess bleeding or stress as recommended in Owen (2011). All eggs collected for placement in this experiment were unincubated. We removed only one host egg from a given nest, and never the first laid to avoid nest abandonment. We experimentally parasitized host nests using cowbird eggs collected in the same study system and therefore did not contribute to an overall increase in parasitism.

RESULTS

General

For the pre-incubation treatments, there was no difference between hatching success of cowbird eggs (mean ± 95% CI hatching success proportion: 0.818 ± 0.133 , $N = 27$) and warbler eggs (0.955 ± 0.085 , $N = 22$) placed into the target nests during pre-incubation (Fisher's exact test: $P = 0.223$). As predicted, cowbird eggs placed during pre-incubation hatched earlier than warbler eggs (Mann–Whitney U test: $U = 242$, $N_1 = 27$, $N_2 = 22$, $P < 0.001$), with cowbirds hatching on average ($\pm$ SE) 0.63 ± 0.33 days earlier. All control eggs ($N = 22$), excluding one that failed to hatch, hatched synchronously with the remaining host eggs. Although we did not control for the number of host eggs or nestlings, neither warbler clutch size (Kruskal–Wallis: $H_2 = 1.043$, $N = 92$, $P = 0.594$), nor maximum number of warbler hatchlings (Kruskal–Wallis: $H_2 = 3.106$, $N = 92$, $P = 0.212$) in the nest differed among the four treatment groups. As a random effect, site also accounted for a negligible amount of variation in the data.

Hatching Success

Hatching success did not differ significantly with treatment (likelihood ratio test: $\chi^2_1 = 1.70$, $N = 92$, $R^2 = 0.032$, $P = 0.193$; Fig. 1, Table 1).

Hatching Asynchrony

The timing of egg addition significantly affected the asynchrony of hatching between cowbird and host eggs (likelihood ratio test: $\chi^2_2 = 138.91$, $N = 69$, $P < 0.001$; Fig. 2). All three cowbird treatments differed in the degree of asynchrony, with PI hatching the earliest and D4 hatching the latest (PI versus D2: $t_{66} = 6.81$, $P < 0.001$; PI versus D4: $t_{66} = 11.65$, $P < 0.001$; D2 versus D4: $t_{66} = 4.79$, $P < 0.001$). The timing of egg addition did not affect whether a cowbird egg hatched later than predicted (Wald chi-square test: $\chi^2_2 = 0.648$, $N = 69$, $P = 0.723$).

Body Size

Overall, there was a significant effect of treatment (ANOVA: $F_{1,55,122} = 7.131$, $N = 59$, $R^2 = 0.811$, $P = 0.01$) and nestling age (ANOVA: $F_{1,53,061} = 133.117$, $N = 59$, $P < 0.001$) on cowbird nestling body size (Fig. 3). Three-day-old cowbirds were smaller than 6-day-old cowbirds regardless of treatment (pairwise comparison: $t_{52,9} = 15.85$, $P < 0.001$), but cowbirds in the PI treatment were larger overall than those in the D2 treatment (pairwise comparison: PI versus D2: $t_{55,1} = 2.54$, $P = 0.014$) when controlling for nestling age. The percentage change in mass between day 3 and day 6 did not differ between PI (mean ± 95% CI = 52.8 ± 5.11 g) and

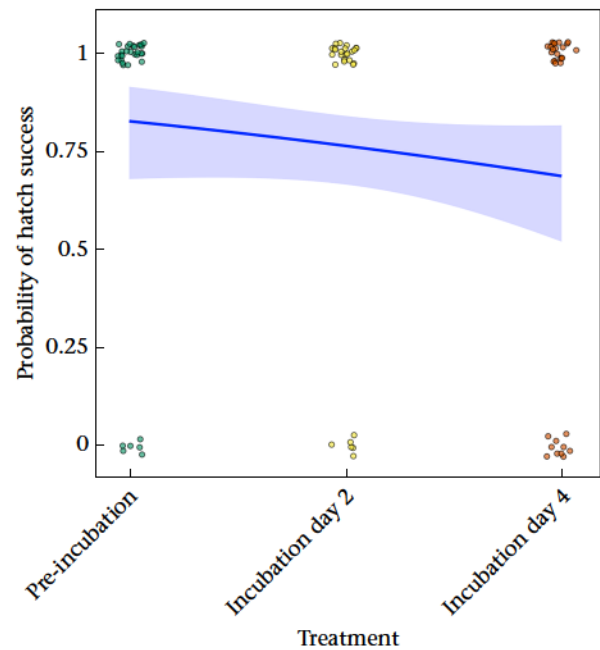


Figure 1. Logistic curve of the probability of hatching success of experimentally placed cowbird eggs among three treatments representing different parasitism timings. Shaded area represents 95% confidence intervals. Colour-coded circles depict raw binomial data (1 = hatch success; 0 = hatch failure).

Table 1

Proportion of experimentally placed cowbird eggs that hatched and proportion of cowbird nestlings that survived to fledging by treatment

Treatment	Proportion hatched (N)	Proportion survived to fledging (N)
Pre-incubation (PI)	0.818 (33)	0.515 (26)
Incubation day 2 (D2)	0.786 (28)	0.286 (22)
Incubation day 4 (D4)	0.677 (31)	0.067 (21)

D2 nestlings (mean ± 95% CI = 49.2 ± 7.79 g) (two-sample t test: $t_{14,30} = 0.889$, $N = 23$, $P = 0.389$).

Haematocrit

There was no significant linear (ANOVA: $F_{1,14} = 0.480$, $N = 18$, $P = 0.50$) or nonlinear (ANOVA: $F_{1,14} = 0.778$, $N = 18$, $P = 0.393$) effect of cowbird nestling day 6 PC1 metric for body size on haematocrit score. There was also no effect of treatment on cowbird nestling haematocrit score (ANOVA: $F_{1,14} = 1.87$, $N = 18$, $P = 0.193$) (mean haematocrit score ± 95% CI: PI: 55.8 ± 11.1 ; D2: 45.6 ± 11.7).

Survival

In the overall survival model, treatment had a significant effect on cowbird nestling survival (likelihood ratio test: $\chi^2_1 = 12.453$, $N = 69$, $R^2 = 0.303$, $P < 0.001$; Fig. 4, Table 1).

Kaplan–Meier survival analysis showed differences in mean survival to fledging by treatment (log-rank test: $\chi^2_2 = 20.2$, $P < 0.001$; Fig. 5), with cowbird eggs in the PI treatment having the highest proportion surviving to fledging (0.545, 95% CI: 0.399–0.745), followed by D2 with intermediate survival (0.286, 95% CI: 0.159–0.513) and D4 with the lowest survival (0.067, 95% CI: 0.018–0.254). Most of the mortality occurred in the first 3 days

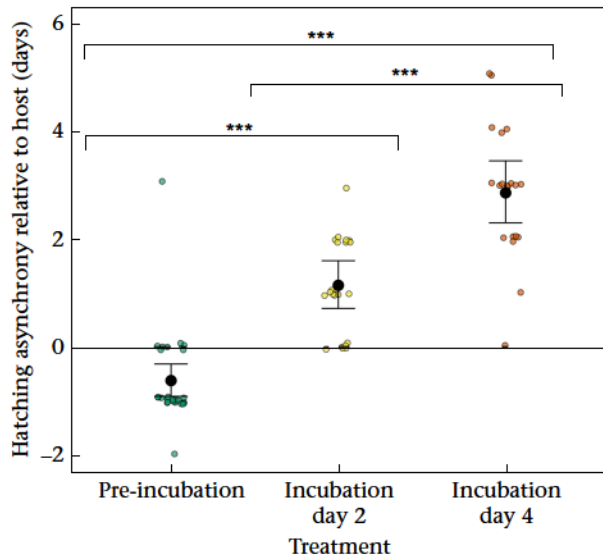


Figure 2. Hatching asynchrony of experimentally placed cowbird eggs relative to warbler host eggs among three treatments representing different parasitism timings. The horizontal line at 0 denotes warbler clutch hatch day, with values below it indicating cowbirds hatching earlier than warbler host eggs and those above indicating hatching later than warbler host eggs. Black circles with whiskers indicate means and 95% confidence intervals. Colour-coded circles depict raw data. *** $P < 0.001$ (pairwise comparisons).

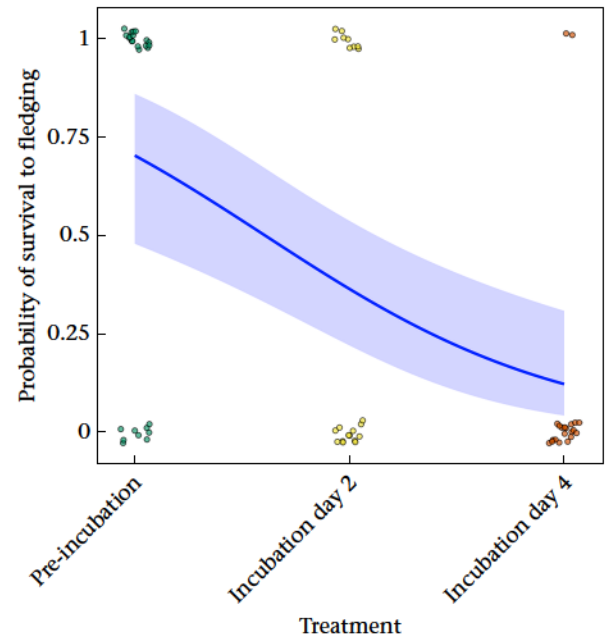


Figure 4. Logistic curve of the probability of survival to fledging of experimentally placed cowbird eggs among three treatments representing different parasitism timings. Shaded area represents 95% confidence intervals. Colour-coded circles depict raw binomial data (1 = survived to fledging; 0 = died).

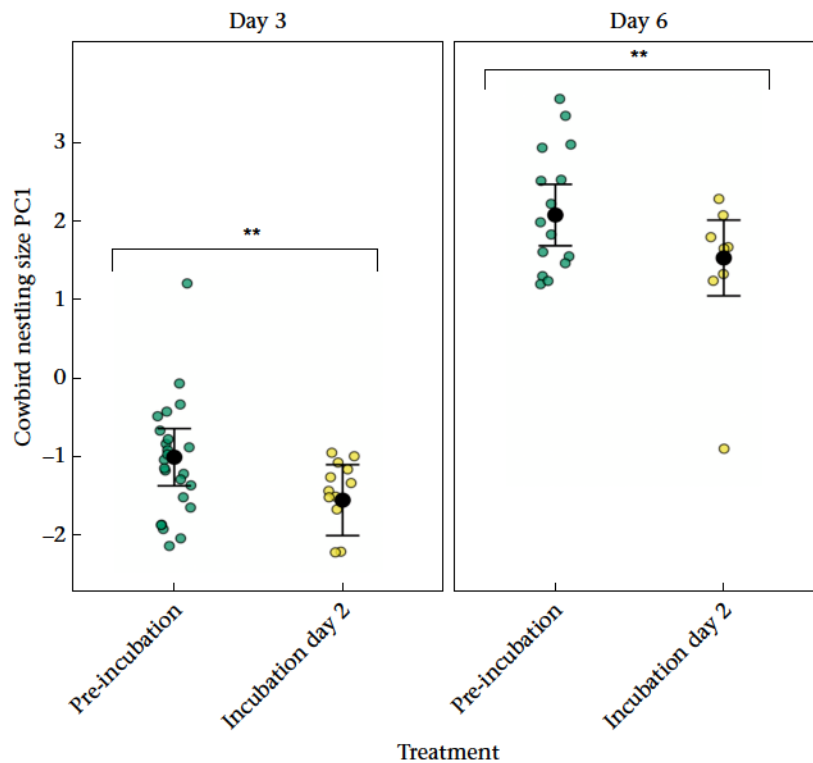


Figure 3. Mean PC1 eigenvalues of cowbird nestling body size at day 3 and day 6 across two treatments. Black circles with whiskers indicate means and 95% confidence intervals. Colour-coded circles depict individual PC1 values. ** $P < 0.01$.

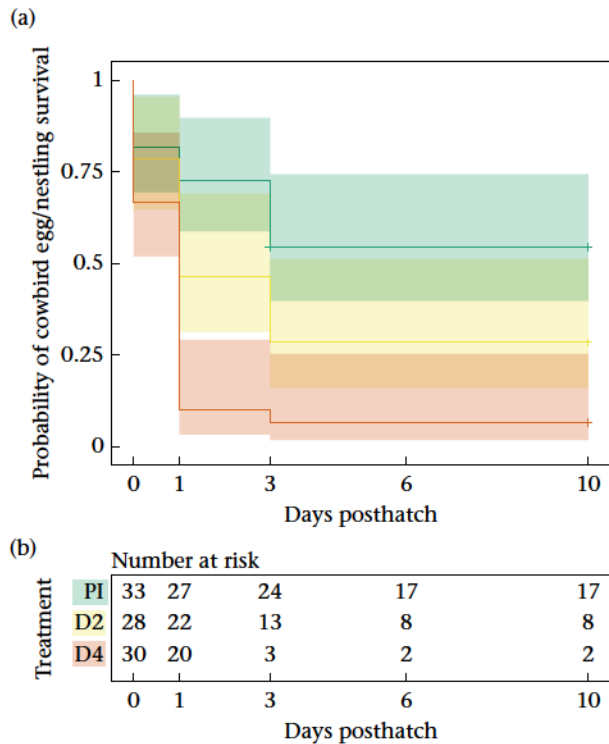


Figure 5. (a) Kaplan–Meier survival curve showing survival probabilities of cowbird eggs/nestlings in the pre-incubation (PI), incubation day 2 (D2) and incubation day 4 (D4) treatments over time. The lines indicate the proportion of cowbirds surviving on a given day for a given treatment. Day 0 to day 1 represents hatching success. Day 10 represents survival to fledging. Shaded areas represent 95% confidence intervals (log–log transformed). (b) The hazard table depicts the number of cowbirds in each treatment alive on a given day.

posthatch, with survival falling by 9.1% for PI nestlings, 32.3% for D2 nestlings and 56.7% for D4 nestlings by this age.

Survival estimates over time differed significantly between treatments (log-rank test, Benjamini–Hochberg adjustment), with cowbird eggs/nestlings surviving significantly longer in the PI treatment than in the D2 (log-rank test: $P = 0.040$) and D4 (log-rank test: $P < 0.001$) treatments. D2 cowbird eggs/nestlings survived significantly longer than those in the D4 treatment (log-rank test: $P = 0.018$).

DISCUSSION

The timing of parasitism is an important factor for cowbird reproductive success, and our study reveals the escalatory reproductive costs of parasitizing host nests later into the incubation period. Unlike in other studies (e.g. [Geltsch et al., 2016](#)), the timing of parasitism did not influence the probability of cowbird egg hatching, but we did find that cowbird eggs added later into incubation hatched later than their host nestmates, as expected. However, later-hatching same-age cowbirds had statistically similar haematocrit scores to those that hatched earlier, indicating similar red blood cell concentrations and oxygen transport abilities. Cowbird nestling growth did not appear to compensate for the hatching delay as the percentage change in mass from nestling day 3 to nestling day 6 did not differ statistically between treatments. In contrast, cowbirds hatching later were smaller and suffered higher mortality, usually within the first 3 days of the nestling period, with only 6% of cowbird eggs placed 4 days into incubation surviving to fledge. Together, these results demonstrate that the timing of parasitism is critical to cowbird reproductive

success and suggest little allowance for flexibility with this timing despite the many other adaptations that make cowbird nestlings competitive among their varied host species (e.g. [Antonson et al., 2022](#); [Kilner et al., 2004](#)).

Although we anticipated a reduction in hatching success with later cowbird egg addition, particularly for cowbird eggs added on day 4 of incubation where the warbler eggs hatched first, we found no such effect. In contrast to our study, others have found reduced hatching success when incubation was altered or disrupted from the typical natural pattern. For example, within this same study system, [Hoover \(2003b\)](#) earlier reported an increase in prothonotary warbler hatching failure with the presence of a cowbird egg and posited that the larger parasitic egg interfered with host eggs' physical contact with the brood patch (the featherless patch of skin used to warm eggs). Similarly, [Hauber \(2003\)](#) found that increased levels of hatching asynchrony between cowbirds and eastern phoebes, *Sayornis phoebe*, resulted in decreased hatching success for the host, hypothesizing that the female host's provisioning of the first-hatched cowbird nestling disrupted the female's incubation efficiency for the rest of the clutch. Such patterns of hatching failure were not reflected in our study, perhaps because cowbird eggs are already larger than the warbler eggs (as in most cowbird hosts; [Dearborn & Lichtenstein, 2002](#)), and small eggs are more likely to bear the brunt of hatching failure if incubation is insufficient or interrupted. When parasitizing a host with larger eggs, cowbird hatching failure may be a more prevalent cost to late egg addition ([Peer & Bollinger, 1997](#)), but with a smaller host, like prothonotary warblers, this cost was not apparent and did not influence the hatchability of the cowbird eggs.

Cowbird eggs placed in the nest later into incubation hatched later relative to the host eggs, confirming that the timing of parasitic egg laying is one of the main drivers of hatching asynchrony among brood parasites and their hosts. [Winnicki et al. \(2021\)](#) suggested that cowbird embryos may speed up their growth and development in the nests of host species with shorter incubation and nestling periods. This flexibility in development would be advantageous to a late-placed cowbird egg. In our study we saw no evidence of accelerated development in later-placed cowbird eggs. However, the [Winnicki et al. \(2021\)](#) study did not examine eggs placed late, and it is possible that under the less-than-ideal conditions of late placement and hatching, these adaptations cannot be used or their effects are negligible. It may also be that different cowbird populations adapted to parasitizing hosts with shorter or more varied incubation periods must maintain this flexible embryonic growth rate, whereas it may not be as critical for the cowbirds in our study system. At our study site, female cowbirds regularly use the same female prothonotary warblers as hosts ([Hoover & Hauber, 2007](#); [Louder et al., 2019](#); [Schelsky et al., 2015](#)) and use social information to inform future parasitism decisions ([Louder et al., 2015](#)). This informed and consistent host use may lead to more accurate parasitism timing, and, thus, may not require accelerated embryonic growth because their eggs already hatch prior to their host in most scenarios.

When cowbird eggs were added after the onset of host incubation, they typically hatched after the host eggs and suffered high nestling mortality, most notably during the first 3 days posthatch. On average, cowbird eggs that hatched before the host eggs (PI treatment) were 47.5% more likely to survive and fledge than those hatching just 1 day later than hosts (D2 treatment) and 87.7% more likely to survive and fledge than those hatching 3 days later than hosts (D4 treatment). Same-age cowbird nestlings that hatched before the host were also larger than those hatching after, suggesting that later placement, and thus later hatching, presents a formidable disadvantage to growth and survival that most cowbird

nestlings cannot overcome. Many other studies have confirmed the advantage of hatching first for the cowbird, finding higher growth and survival when they hatch before host nestlings (Kilner, 2003; Lichtenstein & Sealy, 1998; Winnicki et al., 2021). In contrast with cowbird eggs placed in the host's nest 4 days into incubation, which experienced near complete mortality, some of cowbirds that were placed in the host's nest 2 days into incubation and that hatched synchronously or slightly later than the hosts were still able to survive to fledging. These nestlings, while not having the advantage of hatching earlier than the host, may have still been able to leverage their other parasitic nestling traits (e.g. vigorous begging, rapid growth; reviewed in Dearborn & Lichtenstein, 2002) to successfully compete in the host brood. This suggests that there may be a degree of 'lateness' that still represents a viable, but less than ideal, parasitism opportunity (McLaren et al., 2003). If a female cowbird must lay an egg (e.g. cannot delay by holding it in the oviduct as some cuckoos can; Soler, 2017) and cannot find a nest at the ideal stage to parasitize, then perhaps parasitizing slightly late in certain nests (like those of prothonotary warblers) is better than no opportunity at all.

In our study, the main bottleneck for cowbirds that hatched after the host was surviving the first 3 days of the nestling period. Every cowbird nestling that survived to day 6 fledged successfully regardless of treatment category. This further emphasizes the strong selection for fast growth and highly competitive traits in cowbird nestlings as well as the immediate challenges in the early nestling period for cowbirds that hatch after the host nestlings. If nestlings surviving to day 6, when we measured haematocrit, were the healthiest, strongest and largest individuals within their treatment cohort, then perhaps this is why we found no effect of treatment group or body size on haematocrit. Specifically, by measuring haematocrit on day 6, the age at which no further mortality occurred in any treatment, we may have missed any differences in this health metric present soon after hatching. Bowers et al. (2014) also found no definitive linear relationship between haematocrit and survival, recruitment or reproduction in passerines and recommended also evaluating body condition (size-adjusted mass) to better assess a nestling's overall fitness.

Same-age cowbird nestlings that hatched earlier than the host nestlings were larger than those that hatched later, with their size advantage likely allowing them to monopolize parental provisions. Indeed, Tonra et al. (2008) found hatching asynchrony to be the most important ecological variable affecting the age-adjusted size of cowbird chicks. The advantages of hatching first are well documented for birds in general and for brood parasites: first-hatched nestlings are nearly always larger, more competitive and more likely to survive (Howe, 1976; Lipar et al., 1999; Magrath, 1989; Węgrzyn et al., 2023) than those that hatch later. Nestlings with a head start are afforded time to eat, grow and develop before their other nestmates hatch. Even after they hatch, most host parents, including prothonotary warblers (Petit, 1991), will preferentially feed the biggest (oldest) nestling (Jeon, 2008; Kilner et al., 2004; Lichtenstein & Sealy, 1998; but see Caro et al., 2016), furthering the disparity, and often leading to differences in survival. Despite being adapted to competing against hosts of varying sizes, cowbird nestlings hatching just 1 day later than the hosts in our study were smaller throughout most of the nestling period, meaning the setbacks they faced from hatching late carried on throughout their development. Despite their overall faster growth rate (Kilner, 2003) and their ability to speed up their growth rate in the nests of some hosts (Remeš, 2010; Winnicki et al., 2021), we saw no evidence of compensatory growth in the later-hatching cowbirds through day 6 of the nestling period. It is possible that compensatory growth was present in this study but occurred later in the nestling period or after fledging (outside the age range of

this study's measurement). However, despite the potential advantages of compensatory growth to a late-hatching cowbird, the fact remains that most cowbirds that hatched late in this study simply did not live long enough to benefit from them, as most mortalities occurred in the first 3 days, meaning this trait may only be useful in situations where late parasitism is less costly. Similarly, a cowbird's exaggerated, extended begging (Dearborn, 1998; Hauber & Ramsey, 2003; Rivers, 2007) and overall larger size (Antonson et al., 2022; Dearborn & Lichtenstein, 2002) may not translate to success without the head start afforded to early-hatching cowbirds. In the treatments where cowbirds hatched after the host's, cowbird nestlings most likely struggled to secure adequate food, and subsequently experienced higher mortality.

The most important factor in determining which nestling gets fed in most parasitized broods is size and/or height to secure ideal positioning close to the provisioning parent (Lichtenstein & Sealy, 1998; also see Bortolato et al., 2019 with shiny cowbirds). The cowbird nestling's amplified begging signals alone do not act as a supernormal stimulus (as it does in great spotted cuckoos; Soler et al., 1995). Although we did not measure provisioning rates in our study, Petit (1991) found that prothonotary warblers use the common strategy (Rydén & Bengtsson, 1980) of preferentially feeding the largest nestling, and Lichtenstein and Sealy (1998) found that when cowbirds hatched the same day as their yellow warbler, *Setophaga petechia*, nestmates, the cowbirds received significantly less food than when they hatched before their host nestmates.

We studied just one of the brown-headed cowbird's 170+ potential and viable host species (Lowther, 2020). Although single-host studies tend to allow for more careful control of confounding variables such as those that arise from variation in host traits (e.g. Antonson et al., 2022; Kilner et al., 2004), it can reduce the generalizability of the conclusions being drawn (Antonson et al., 2025). Prothonotary warblers represent a 'middle ground' given their intermediate body size, clutch size and incubation period relative to other cowbird hosts, but the outcomes and importance of parasitism timing would most likely vary with any of these factors. Even with the usually high success rates of cowbirds in prothonotary nestboxes (Hoover, 2003b), hatching from a later-placed egg still presented significant challenges to cowbird nestlings. A larger host or one with a shorter incubation time than cowbirds, such as a northern cardinal, *Cardinalis cardinalis*, would be potentially even more disadvantageous for cowbird nestlings hatching from later-placed eggs. In contrast, the use of a smaller host, or one with a longer incubation period than the prothonotary warbler, like an eastern phoebe, could represent a less costly outcome for later-placed eggs.

Conclusion

Offspring are affected by the choices and behaviour of their parent(s), and decisions that parent organisms make can significantly affect the outcomes for their offspring (Tonra et al., 2008), even in species with little to no 'traditional' parental care. The cowbird female uses many tactics to optimize her offspring's success, like expending energy to prospect for host nests, selecting hosts species, removing host eggs and monitoring nests for post-parasitism outcomes. Our study demonstrates that the timing of parasitism is clearly another, potentially critical, behaviour in this repertoire and fills a key gap in understanding the evolution of brood parasitism behaviours associated with host selection and the timing of egg laying. Conducting a similar study on different host species that vary in traits like body size, clutch size and incubation period would help to determine how the costs of late parasitism change with different nest environments and whether

parasitism within the pre-incubation window is a near-universal trait despite these many host differences. If early parasitism is the general rule, then host counteradaptations emphasized during this pre-incubation window should theoretically be selected for, and more studies should focus on the likelihood of their occurrence such as increased nest vigilance by hosts during the critical parasitism window. These kinds of behaviours are present in a variety of species: yellow warblers are vigilant in response to cowbirds or cowbird-referential alarm calls and will sit on the nest to physically deter cowbird parasitism (Hobson & Sealy, 1989; Lawson et al., 2021); many host species display aggression towards parasites, including red-winged blackbirds, *Agelaius phoeniceus* (Prather et al., 1999), Oriental reed warblers, *Acrocephalus orientalis* (Li et al., 2015), and hosts of both cuckoo catfish (Polačik et al., 2019) and parasitic bees (Litman, 2019). The variation in and extent to which these behaviours are present in other host species is unknown. It would also be relevant to evaluate consistency in parasitism timing behaviour for individual female cowbirds (and other brood parasites) to begin determining how variable this behaviour is and how cowbird breeding experience shapes it (Louder et al., 2015). Nevertheless, despite the many adaptive traits that cowbird nestlings use to outcompete their host nestmates, in this study, these advantages were quickly lost as the timing of parasitism was delayed further into incubation. Perhaps only under extreme scenarios when hosts are limited, or conspecific parasitic competition is at its peak, should female cowbirds add their progeny to nests outside of this 'ideal window'.

Author Contributions

Julia Boldrick: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Wendy Schelsky:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Mark E. Hauber:** Writing – review & editing, Methodology, Conceptualization. **Abigail Tullius:** Writing – review & editing, Investigation, Data curation. **Jeffrey P. Hoover:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Data Availability

Data and R code used for analysis are available for open access on [Figshare.com](https://figshare.com) (data set: <https://doi.org/10.6084/m9.figshare.29420744.v1>).

Declaration of Interest

The authors declare there are no conflicts of interest.

Acknowledgments

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Inclusion and Diversity Statement

This study was conducted with team members of various genders, races and sexual orientations, with an emphasis on field safety and inclusivity.

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