

## The Parasitic Cowbird:

### Ecological Specialization of a Genus of Obligate Brood Parasites

#### Abstract

*The five cowbird species, all contained within the *Molothrus* genus of the Icteridae family of songbirds, are all obligate brood parasites who must lay their eggs within other species' nests so they may successfully produce offspring. This ecological niche has resulted in multiple adaptations by the *Molothrus* species which have been studied, including: thicker eggshells than related heterospecifics, egg-puncturing behavior of host eggs by cowbird parents, high fecundity of females and behavioral adaptations to cope with high fecundity, scouting behavior to discriminate ideal host nests from non-ideal nests, greater hippocampal volume in cowbird parents who participate in said scouting behavior, and competing against heterospecific brood parasites. The *Molothrus* genus of obligate brood parasites is quite varied, but the similarities and differences among the species are what make them such valuable subjects of study within the field of behavioral ecology.*

*Keywords: cowbird, *Molothrus ater*, *Molothrus bonariensis*, *Molothrus aeneus*, *Molothrus oryzivorus*, *Molothrus rufoaxillaris*, Icteridae, parasitism, brood parasitism, memory, hippocampus, egg-laying*

#### Introduction

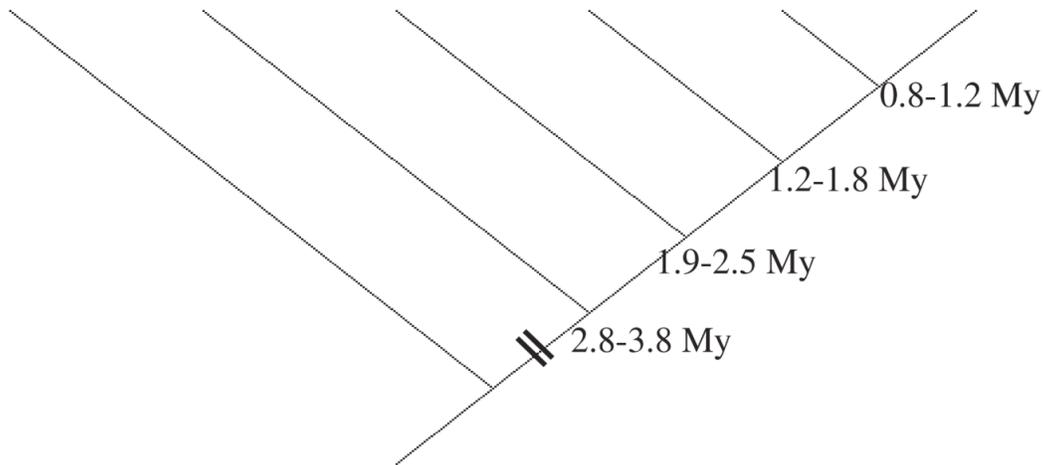
Cowbirds, family *Icteridae* and genus *Molothrus*, are five species of songbirds which include the brown-headed (*M. ater*), shiny (*M. bonariensis*), bronzed (*M. aeneus*), giant (*M. oryzivorus*), and screaming (*M. rufoaxillaris*) cowbirds. All cowbirds are obligate brood parasites, meaning that parents do not raise their own brood: a female cowbird instead finds a nest of another bird species and lays her egg within it so then the host parents will hatch and care for the

resulting cowbird chick (Rueda-Cediel et al. 2008). Screaming cowbirds are specialist brood parasites, primarily laying their eggs in the nests of grayish baywings (*Agelaioides badius*) but also successfully laying in the nests of four other species (Lowther 2019). The eggs, chicks, and juveniles of screaming cowbirds closely resemble those of the grayish baywing, evidence of the close parasite-host relationship (Lowther 2020). Giant cowbirds are somewhat specialized brood parasites, successfully laying their eggs in 11 known species' nests (Lowther 2020). They show some mimicry with their eggs: each of the four egg morphs (excluding a white egg morph) resembles a different host species' eggs, suggesting specialization on a sub-population level (Fleischer & Smith 1992). Bronzed cowbirds are generalists, with eggs found in 103 species' nests and 45 of those species accepting as hosts; shiny cowbirds are broad generalists, with eggs found in 270 species' nests and 97 of those species accepting as hosts; and brown-headed cowbirds are also broad generalists, targeting 249 species and 172 of those species accepting as hosts (Lowther 2019). Phylogenetic examination (Figure 1) has shown that the evolution of brood parasitism within the cowbird family likely started with host specialization (i.e. the screaming cowbird) and then spread to host generalization (i.e. the brown-headed cowbird; Lanyon 1992).

**Figure 1.**

*Phylogeny for Molothrus species* (Ellison et al. 2006). Updated with host data from Lowther 2019.

<i>Agelaioides badius</i>	<i>M. rufoaxillaris</i>	<i>M. oryzivorus</i>	<i>M. aeneus</i>	<i>M. bonariensis</i>	<i>M. ater</i>
	5 hosts	11 hosts	45 hosts	97 hosts	172 hosts



Female brown-headed, shiny, and screaming cowbirds (and also males, in screaming cowbirds) seek out heterospecific nests during the laying season, observing potential host parents and nests before laying in a chosen nest on a subsequent day (Reboreda et al. 1996). This is likely also true for bronzed and giant cowbirds, since obligate brood parasites generally prospect nests before choosing to lay in them, but no specific research has been done on this behavior in these two species. However, bronzed cowbirds have been observed to visit Audubon's orioles while orioles are laying eggs (Flood 1990), which supports the idea of bronzed cowbirds conducting pre-laying nest prospecting behavior. Screaming cowbirds, being the only specialist brood parasite of the *Molothrus* genus, also are the only known cowbird where both parents scout for nests instead of just the female (Reboreda et al. 1996). Due to obligate parasitism, cowbird species have certain ecological pressures that have resulted in adaptations to accommodate these pressures, including host-parasite interaction behavior, egg-laying adaptations, scouting behavior and nest preferences, and greater spatial memory through hippocampal adaptations.

### **Host-parasite interactions**

Obligate brood parasitism naturally results in interactions between parasitic species and their hosts, and this is clearly seen within the *Molothrus* genus. There is evidence for cowbirds puncturing host eggs, for example, in all five cowbird species. Both male and female brown-

headed cowbirds display egg-pecking behavior, preferentially pecking artificial host eggs rather than cowbird eggs when presented with nests that contained one of each (Dubina & Peer 2013). However, females pecked eggs more frequently than males, which is logical considering that male brown-headed cowbirds do not lay eggs; however, the fact that males did display pecking behavior suggests that male brown-headed cowbirds may assist in nest prospecting behavior (Dubina & Peer 2013). Shiny and screaming female cowbirds also preferentially puncture eggs of host species over cowbird eggs (Llambías et al. 2006, Fiorini et al. 2014, Cossa et al. 2017). Bronzed cowbirds display egg-pecking behavior as well, preferentially pecking host eggs over cowbird eggs (Carter 1986). Though brown-headed cowbirds also lived in the area, the punctured eggs found in the field study by Carter 1986 were likely punctured by bronzed cowbirds due to bronzed cowbirds being much more common in the area of study. Giant cowbirds may also engage in egg-puncturing behavior (Fraga 2011). The field study by Fraga 2011 repeatedly found punctured or otherwise destroyed eggs in the nests of red-rumped caciques (a common host of giant cowbirds), including eggs of both hosts and cowbirds. Egg puncturing behaviors seem to be conserved across the *Molothrus* genus, appearing to be important in the coevolution of brood parasites and their hosts.

The reasons for these egg-pecking behaviors may vary between cowbird species. The main two hypotheses for the drive of these behaviors are as follows: cowbirds may peck host eggs to reduce competition (reduction of competition hypothesis), or they may peck host eggs to induce re-nesting in host species (farming hypothesis; Cossa et al. 2017; Dubina & Peer 2013; Fiorini et al. 2014; Hoover & Robinson 2007). Re-nesting hosts in the farming hypothesis would offer another chance for cowbirds to parasitize a nest, which would be valuable to cowbirds if the hosts had previously begun to incubate their nest and therefore had not been available for

parasitism. In screaming and shiny cowbirds, the reduction of competition hypothesis seems to hold true. In Fiorini et al. 2014, shiny cowbirds were presented with artificial nests that contained either one or four eggs, and the eggs were either all mockingbird or all cowbird eggs; mockingbirds, being a large host of shiny cowbirds, pose more competition than cowbirds in this situation. “Complete” nests (four eggs) and single-egg nests were both likely to have at least one egg punctured, though “complete” nests did not have all eggs punctured by cowbirds, and mockingbird eggs were more likely to be punctured than cowbird eggs (Fiorini et al. 2014). This supports a reduction of competition hypothesis rather than a farming hypothesis due to the preferential destruction of mockingbird eggs over cowbird eggs and due to the incomplete destruction of “complete” nests. These findings were corroborated when the experiment was repeated with both shiny and screaming cowbirds by Cossa et al. 2017, but by using three types of eggs of varying shell strength in the 2017 version of the experiment; shiny and screaming cowbirds did not significantly differ in egg-pecking patterns. In brown-headed cowbirds, the farming hypothesis is most supported. Brown-headed cowbirds have been documented to depredate non-parasitized host nests (depredation being defined as destruction of the host nest; Hoover & Robinson 2007). Most importantly, however, in the study conducted by Hoover & Robinson in 2007, brown-headed cowbirds were shown to retaliate in mafia-like behavior when hosts rejected cowbird eggs. The studied host, the prothonotary warbler, had successful nests when cowbirds could not access a parasitized nest after incubation began (when the cowbird egg had been ejected) or when cowbirds could not access the nest whatsoever: these two categories had no depredation. Nests that were non-parasitized but allowed cowbird access were depredated about 20% of the time, and nests that were parasitized and allowed cowbird access were depredated about 6% of the time, significantly different from the 20% rate; nests that were parasitized, allowed cowbird

access, and ejected the cowbird egg were depredated about 56% of the time, a statistically significant difference from the 20% depredation rate (Hoover & Robinson 2007). Brown-headed cowbirds thus conduct both farming and mafia-like retaliatory behaviors against their hosts, behaviors that may have evolved due to the brown-headed cowbirds extreme generalist nature of brood parasitism: having a high number of host species to choose from means that host species cannot quickly evolve defense mechanisms, since a cowbird could simply choose another nest to parasitize.

The most notable instance of host defense against cowbird parasitism lies with the grayish baywing. Since it is the host which the screaming cowbird specializes upon, the grayish baywing has had the most opportunity to evolve defense mechanisms against brood parasitism: and it must evolve defenses, because nearly all of the species' nests suffer from a parasitism event by a screaming cowbird (de Mársico & Reboreda 2008). In de Mársico & Reboreda's study in 2008, 31% of screaming cowbird eggs were laid during the grayish baywing's pre-laying period, a period in which the hosts have their own nest but have not yet begun to lay their own eggs; the remaining 50% and 19% of screaming cowbird eggs were laid during the grayish baywing's laying and incubation periods, respectively. Grayish baywings were more likely to desert their nest if screaming cowbirds had parasitized it during the baywing's pre-laying period (de Mársico & Reboreda 2008). The screaming cowbird prematurely laid eggs in its few, alternate, rare hosts significantly less than it did with the grayish baywing (de Mársico & Reboreda 2008). This signifies that the specialized parasite-host relationship has allowed the host, the grayish baywing, to evolve defense mechanisms against the screaming cowbird, here being its lengthy pre-laying behavior that allows it to desert the nest if it becomes parasitized (de Mársico & Reboreda 2008).

### **Physiological adaptations of egg-laying**

Since they are all obligate brood parasites, all species of the *Molothrus* genus have had to develop physiological adaptations to support successful brood parasitism, especially around egg-laying events. One adaptation, presumably present in all cowbirds but researched in brown-headed and shiny cowbirds, is high fecundity of females (Jackson & Roby 1992; Kattan 1993). In the study conducted by Jackson & Roby in 1992, female yearling brown-headed cowbirds laid an average of 0.56 eggs per day during the breeding season, with some individuals coming close to laying one egg daily. They seemed to also display egg clutch patterns of indeterminate layers, meaning that egg production did not cease upon a laid egg's removal. Considering that the studied cowbirds were yearlings, and yearlings begin laying later in the breeding season than adults, full-fledged adult female cowbirds likely lay at even higher rates than what was found in Jackson & Roby's 1992 study. In 1993, Kattan estimated that shiny cowbirds have an annual fecundity of about 120 eggs, both due to an average laying rate of 0.66 eggs per day and laying for a total of six months throughout the breeding season (the long breeding season coming from the shiny cowbird's tropical habitat). Female shiny cowbirds do not seem to have any morphological specializations of their reproductive tract to support this high fecundity, indicating that other physiological factors must be responsible for the sheerly high annual numbers of eggs (Rueda-Cediel et al. 2008). This presumably is also true for the brown-headed cowbird since it is also a broad generalist obligate parasite like the shiny cowbird, but no similar studies to Rueda-Cediel et al. have been conducted on the brown-headed cowbird's reproductive tract to confirm this.

Eggshells of cowbird eggs, too, have adapted to the brood-parasitic nature of cowbirds. The eggshells of brown-headed, shiny, and bronzed cowbirds are thicker than those of the cowbirds' common host species and are 30% thicker than expected for their egg size (López et al. 2018; Mermoz & Ornelas 2004; Spaw & Rohwer 1987). Thick eggshells have also been ob-

served in giant cowbirds and screaming cowbirds (Fraga 2011; Mermoz & Ornelas 2004). However, the eggshell thickness of screaming cowbird eggs is similar to that of its main host, the grayish baywing, so that specific instance of eggshell thickness may be due to an evolutionary arms race between host and parasite (Mermoz & Ornelas 2004). The presence of thick eggshells gives the cowbird eggs a greater chance for survival and for harming host eggs, especially since both brown-headed and shiny cowbirds (and presumably other cowbirds) lay their eggs from an elevated position (Ellison et al. 2019).

“Dumping” parasitism has been observed in shiny, bronzed, giant, and screaming cowbirds, in which numerous cowbird eggs are laid in abandoned host nests (Fraga 2011; Friedmann 1976; Friedmann 1963; de Mársico & Reboresda 2008). This may be an attempt by cowbirds to find any nest that has a remote chance of raising an egg, even if that chance is close to zero, or it may be an “emergency” dumping done by cowbirds because their preferred nest that they had selected for parasitism the previous day is no longer available. This “dumping” phenomenon has not yet been observed in brown-headed cowbirds, who supposedly do not have as much trouble with wasting eggs due to their high number of potential host species. Parasitism rates by brown-headed cowbirds stay relatively consistent throughout the breeding season, despite the fluctuating availability of host nests (Strausberger 1998). This also holds true for the number of cowbird eggs found per nest, suggesting that females either have a behavioral adaptation (such as eating their own eggs) when unable to find suitable nests, or there is some other adaptation. This behavioral adaptation may be the brown-headed cowbird’s equivalent of “dumping” parasitism: though “dumper” nests have not been observed in brown-headed cowbirds, brown-headed cowbirds do have a high number of unsuitable host species whose nests they lay eggs in (Lowther 2019). This behavior in brown-headed cowbirds can be seen as an equivalent to egg-dumping in other cow-

bird species and therefore could be the brown-headed cowbird's behavioral adaptation for dealing with its own excess eggs. [As a note, limiting calcium intake in brown-headed cowbirds slows egg production, while removing all imitation host nests in captive conditions does not (Holford & Roby 1993). The captive brown-headed cowbirds, when unable to find suitable nests, instead laid their eggs along the ground, in food cups, and in water containers in their aviary (Holford & Roby 1993)]. Another brown-headed version of the "dumper" phenomenon may be a single female parasitizing the same nest twice or more. In a study conducted by Rivers et al. in 2012 in an area with high cowbird populations, nests that were parasitized multiple times by brown-headed cowbirds had a high rate of full cowbird siblings within a given nest. In a given multiply-parasitized nest, about 40.4% of cowbird nestmates were full siblings (Rivers et al. 2012). When unable to find a new suitable nest due to high rates of other cowbirds parasitizing other nests, individual female brown-headed cowbirds seem to elect to lay in nests they have already parasitized. Giant cowbirds may parasitize the same nest again as well, up to about 40% of the time in Fleischer & Smith's 1992 study; this was also true of bronzed cowbirds in Ellison et al.'s 2006 study, where multiply parasitized nests were parasitized by the same individual about 12% of the time. In both of the aforementioned studies, however, the effect of population density on this behavior was not researched. No conclusion can therefore be inferred about the related screaming and shiny cowbird species' behavior when it comes to an individual bird choosing whether or not to parasitize a given nest multiple times. In summary, the high fecundity of cowbirds is not fully adaptive for their brood parasitic behavior: sometimes, birds are unable to find suitable nests, and they must find ways to cope with excess eggs.

### **Scouting behavior and nest preferences**

#### ***Scouting behavior and nest choice***

Pre-laying scouting behavior, recorded in brown-headed, shiny, bronzed, and screaming cowbirds and potentially existing in giant cowbirds, is marked by individual cowbirds visiting potential host nests—without laying an egg during that visit—before returning to that nest to lay an egg at a later time, usually the next day. The nest visitation is presumably so the cowbird can judge whether the given nest is suitable. Two main hypotheses for brood parasite nest choice have been proposed: the “shotgun” strategy, wherein brood parasites forego host discrimination in favor of producing a high number of eggs and simply laying eggs in whichever nests they can find; and any discriminatory strategy, in which brood parasites take in any number and kind of environmental information and synthesize it to choose what they think is the best nest for their offspring (White et al. 2007).

Brown-headed cowbirds have been shown to have preferences for nests, as observed by Hauber in a 2001 field study. In a population of Eastern Phoebe nests, brown-headed cowbirds parasitized nests that were built underneath eaves more often than nests built underneath bridges; eave nests were statistically much sturdier than bridge nests and therefore more likely to successfully raise a cowbird chick (Hauber 2001). Nests that were first nesting attempts of the season on the part of the Eastern Phoebe parents were also more likely to be parasitized by cowbirds, suggesting that cowbirds were keeping track of individual parent pairs, the skillset of those parents, and, by extension, the potential parental quality of those parent pairs (Hauber 2001).

White et al. has also extensively studied the nest preferences of female brown-headed cowbirds, doing so in captive aviaries; this has allowed for single-variable manipulations of nest preferences and memory capabilities to be studied, albeit in simulated environments. In 2007, White et al. showed that female brown-headed cowbirds are able to compare the contents of different nests to choose the most suitable nest to lay in. Females generally preferred to select nests

containing more eggs, containing eggs slightly smaller than their own, and containing no other cowbird eggs (White et al. 2007). Juveniles were the exception to this rule; though they still preferred nests with more eggs and eggs that were smaller than their own, juveniles heavily preferred to lay in nests which already contained a cowbird egg, suggesting that the naïvety of juvenile females led them to rely on the judgment of experienced, older adults (White et al. 2007). Furthermore, the cowbirds did not differentiate between large numbers of eggs: they spent the same amount of time observing a nest containing three eggs as a nest containing six eggs. In a later 2009 study, White et al. found that female brown-headed cowbirds were able to observe and track the relative number of eggs within a host nest. They preferred nests that were still increasing in number over those that had gone stagnant, therefore maximizing their chances of laying in a nest that hasn't yet begun brooding; they were able to tell the difference between a nest that increased by two eggs over three days (starting with one egg) and one that increased by three eggs over three days (starting with three eggs; White et al. 2009). Since cowbird eggs would likely not hatch if laid after a host had begun brooding, due to the incubation period of brown-headed cowbirds and their hosts being similar, there is strong pressure for female brown-headed cowbirds to attempt to lay their eggs before the host has started incubation (White et al. 2009). A third study by White et al. in 2017 found that female brown-headed cowbirds who have no prior information on a given group of nests will socially conform: they selected nests that they observed other females observing. This extended further: females who were more likely to remember prior nest conditions, and have knowledge about current nest conditions, were less likely to socially conform in both nest prospecting and egg laying behaviors (White et al. 2017). Socially conforming females were also more likely to remove previously existing cowbird eggs from their target nest (White et al. 2017).

Nest scouting behavior conducted by parasitic cowbirds has been extensively studied in brown-headed cowbirds, especially by White et al., but it has also been studied in other cowbirds. Female shiny cowbirds seem to follow the “shotgun” strategy when parasitizing nests, at least to some extent and when parasitizing house wrens (Kattan 1997). In the 1997 field study by Kattan, about half of laying events occurred in non-ideal nests, and females did not seem to be avoiding multiple parasitism. House wrens, however, did not resist parasitism, so the shiny cowbirds were perhaps able to afford utilizing the “shotgun” strategy due to the lack of defense mechanisms on the house wren’s part; shiny cowbirds may exhibit other parasitism strategies when faced with different host species (Kattan 1997). Furthermore, shiny cowbirds and screaming cowbirds both displayed nest scouting behavior prior to laying events in a study conducted by Scardamaglia et al. in 2016 involving radio tagging individuals. Screaming cowbirds also showed post-laying scouting behavior and sometimes re-parasitized the same nest (Scardamaglia et al. 2016). Bronzed cowbirds have also been observed to scout out nests before parasitizing the nest on a subsequent day (Peer & Seely 1999). Giant cowbirds presumably also display nest scouting behavior, but the species is largely under-researched, and so no data has currently been published on the matter.

### ***Scouting range and laying time***

Many cowbirds, presumably as an adaptation to their obligate brood parasitic behavior, have been documented as having much larger living ranges than other birds of comparable size. Brown-headed cowbirds have extensive, separate breeding/nest scouting grounds and feeding grounds; females and males spend time at their breeding and nest scouting grounds exclusively in the morning, while they spend their time at their feeding grounds later in the day (Rothstein et al. 1984). Screaming and shiny cowbirds also display morning ranges, and male and female

screaming cowbirds are shown to monogamously share ranges, supporting the observation that males and females scout for host nests together (Scardamaglia & Reboreda 2014). Giant and bronzed cowbirds may display this same division in breeding and feeding grounds, but the two species are tragically understudied, so future research must go into this topic for these two species.

Cowbird species have been observed to lay their eggs within host nests in the early morning, minutes before sunrise, in timespans as short as five to ten seconds. This is true for bronzed cowbirds, as found in the study conducted by Peer & Sealy in 1999. It also holds true for brown-headed, shiny, and screaming cowbirds, as explored by Ellison et al. 2019 for brown-headed and shiny cowbirds and Scardamaglia et al. in 2016 for shiny and screaming cowbirds. This is presumably the case for giant cowbirds as well, but no specific research has been conducted on the topic for this species. Laying in the morning before sunrise is a suitable adaptation for brood parasites because their hosts commonly lay their eggs after sunrise and oftentimes are not as attentive during the early morning hours, meaning cowbirds would be less likely to be attacked, especially due to the dark conditions (Peer & Sealy 1999; Ellison et al. 2019; Scardamaglia et al. 2016).

### **Hippocampal and memory adaptations**

Since the previous section showed that the *Molothrus* genus has behavioral adaptations to select for the best host nest, namely exhibiting strong spatial memory of nests over time, cowbirds must therefore exhibit some sort of neuroanatomical adaptation to account for these behavioral adaptations. The behavioral adaptations should also be able to be tested for in different environments than those involving egg-laying, since an increase in the propensity for spatial memory in one context, for example, will usually affect other spatial memory contexts. This is shown

to be the case in brown-headed, shiny, and screaming cowbirds, where all three species exhibit specialized adaptations in their hippocampi (Reboreda et al. 1996; Sherry et al. 1993). Originally discovered by Sherry et al. in 1993, female brown-headed cowbirds have larger relative hippocampi than their male counterparts and related nonparasitic species (but see Guigueno et al. 2016). Females in relative nonparasitic species were not shown to have larger relative hippocampi than males, so the specialized adaptation by the brown-headed cowbird for better spatial memory in females was clear (Sherry et al. 1993). Shiny and screaming cowbirds also have larger relative hippocampi than a close relative species, the grayish baywing (Reboreda et al. 1996). In Reboreda et al.'s 1996 study, both males and females in both cowbird species had larger relative hippocampi than grayish baywings; screaming cowbirds and grayish baywings showed no sex differences, while female shiny cowbirds possessed larger relative hippocampi than male shiny cowbirds. The lack of sexual dimorphism in screaming cowbirds makes sense when one considers the fact that both males and females in screaming cowbirds participate in nest prospecting behavior, meaning that both sexes heavily rely on spatial memory in their reproductive behaviors (Reboreda et al. 1996). Usage of the hippocampus is also associated with total hippocampal volume in cowbirds: hippocampi in aviary-housed brown-headed females (where they had no access to nests) were found to be significantly smaller than those of freshly wild-caught females, which was not found to be the case when comparing males (Day et al. 2008). Since males have not been documented to participate in nest prospecting behavior, as previously described, the lack of a difference between captive and wild-caught male hippocampi is logical (Reboreda et al. 1996; Sherry et al. 1993). Furthermore, neurogenesis of the hippocampus occurs when female brown-headed cowbirds enter breeding condition, and its neurodegeneration occurs after the breeding season ends, but without hippocampal volume fluctuating significantly be-

tween seasons (Guigueno et al. 2016). Additionally, newly generated neurons within the rostral hippocampus are shown to be utilized more in female brown-headed cowbirds than males during the breeding season (Lynch 2018). This shows that the neurogenesis that occurs within female brown-headed cowbirds is utilized more during the breeding season, meaning that the neurogenesis likely occurred specifically because of the breeding season and that the female cowbirds had to begin to remember the locations of prospective host nests.

All of this specialization within the female brown-headed cowbird hippocampus can be tested, as it was in Guigueno et al.'s 2014 study. In this study, female and male cowbirds were tested on their ability to recall the location of a food source over a period of 24 hours. Female cowbirds were shown to approach the food source more directly while also making fewer mistakes while doing so than males, a clear demonstration of their greater spatial memory due to greater hippocampal volume (Guigueno et al. 2014). Little to no research has been done, however, on potential sexual dimorphism in other species of cowbirds.

## **Discussion**

### ***Directions for further research***

As mentioned throughout this review, more research needs to be conducted on certain cowbird species in order to fully understand their behavioral ecology. This is especially true of the giant cowbird, as it has woefully been under-researched compared to its *Molothrus* peers, but it also is the case for the bronzed, screaming, shiny, and even the brown-headed cowbirds, in that order. The nest prospecting behavior of giant, bronzed, screaming, and shiny cowbirds needs to be researched in the manner conducted by White et al. in order to compare the behavior of all cowbird species with each other; hippocampal examinations should be made on the bronzed and giant cowbirds to compare them with those of the brown-headed, screaming, and shiny cowbirds;

behavioral experiments like that of Guigueno et al. 2014 should be conducted on giant, bronzed, screaming, and shiny cowbirds; average seasonal fecundity should be estimated for giant, bronzed, and screaming cowbirds; mafia-like retaliatory behavior in giant, bronzed, screaming, and shiny cowbirds should be researched; and more laboratory research should be conducted in general for giant and bronzed cowbirds.

Additionally, the potential environmental factors that may help to induce egg-laying in female cowbirds should be researched—on an individual egg or clutch level, not just seasonal. As per my own speculation, I hypothesize the action of scouting out specific nests helps to induce ovulation within the female cowbird's reproductive tract. As found with the brown-headed cowbird in Strausberger 1998, the percentage-based frequency of parasitism stayed rather consistent across the season, even though host availability varied greatly, suggesting that the availability of host nests had influence on the female cowbirds' laying behavior. Whether that was through behavioral changes, such as the female choosing to lay and eat her own egg when no viable nest was available, or environmental influence on physiology, such as ovulation not being induced due to low availability of host nests, was inconclusive, with only the first option being explored in Strausberger's discussion. Though Holford & Roby 1993 found that the lack of available nests had no effect on egg laying, the study took an all-or-nothing approach—the experiment completely removed all nests from the birds' environment. More subtle environmental cues such as the rate of growth of a nest's clutch or the parenting behaviors of a host nest would have an effect on female brown-headed cowbirds' ovulation and perhaps cowbirds in general, as per my hypothesis.

### **Summary**

The five cowbirds, all contained within the *Molothrus* genus of the *Icteridae* family of

songbirds, are all obligate brood parasites who must lay their eggs within other species' nests so they may successfully produce offspring (Rueda-Cediel et al. 2008). This ecological niche has resulted in multiple adaptations by the cowbird species, including but not limited to: thicker eggshells than related heterospecifics, egg-puncturing behavior of host eggs by cowbird parents, high fecundity of females, scouting behavior to discriminate ideal host nests from non-ideal nests, and greater hippocampal volume in cowbird parents who participate in said scouting behavior. The *Molothrus* genus of obligate brood parasites are quite varied, but their similarities and differences are what make them such valuable, fascinating, and noteworthy subjects of study within the field of behavioral ecology.

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