Letters

Comparison of eggshell porosity and estimated gas flux between the brown-headed cowbird and two common hosts

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The brown-headed cowbird *Molothrus ater* is a brood-parasite that lays eggs in nests of a wide range of host species, including the closely-related red-winged blackbird *Agelaius phoeniceus* and the dickcissel *Spiza americana*. Although cowbird eggs have accelerated development and hatch sooner than similar-sized host eggs, this development takes place within a thickened eggshell that could impede gas flux to the developing embryo. We tested the hypothesis that the accelerated development of the cowbird embryo relative to hosts is enabled by an increase in eggshell porosity that allows increased fluxes of respiratory gases to and from the developing embryo. We found cowbird eggshell thickness was significantly greater than the eggshells of these two common hosts. Although the number of pores per egg was similar among all three species, the total pore area per egg in cowbirds was significantly greater than that of either host, despite having a smaller eggshell surface area than the red-winged blackbird. Cowbird egg pore area was 1.9× larger than that of the red-winged blackbird. Cowbird eggshells had a significantly greater gas flux than those of the red-winged blackbird and the dickcissel. When conductance was normalized to published values of egg mass, cowbird eggs had a higher mass-specific conductance than red-winged blackbird or dickcissel eggs. These results are consistent with the hypothesis that the rapid development of brown-headed cowbird embryos is facilitated by increased eggshell porosity, and that changes in eggshell porosity represent an adaptation that enables cowbird eggs to hatch earlier than equivalently-sized host eggs.

The brown-headed cowbird *Molothrus ater* (hereafter cowbird) is a generalist brood parasite that lays its eggs in nests of host species, which then raise the cowbird nestlings. A frequent consequence of brood parasitism to the host is lowered reproductive success (Rothstein 1990, Lorenzana and Sealy 1999, Hauber 2003). To minimize costs, some host species have evolved defenses against cowbird parasitism, including removal of parasitic eggs (Peer et al. 2005). Cowbirds have evolved eggshell characteristics that likely help protect the eggs from damage by hosts or during rapid egg-laying events (Sealy et al. 1995). Cowbird eggshells are thicker than expected based on egg size (Spaw and Rohwer 1987, Picman 1989, 1997), and cowbird eggs are rounder when compared with those of nonparasitic icterids (Rahn et al. 1988, Picman 1989). Together, these result in a substantial increase in cowbird eggshell strength relative to non-parasitic songbirds.

Cowbird eggs, despite having a thicker eggshell, also have an incubation period (Friedmann 1927, but see Nice 1953) that is shorter than that predicted based on the size of their eggs (10–11 d; Briskie and Sealy 1990, Peer and Bollinger 2000, but see Mermoz and Ornelas 2004). This is surprising given that the thicker eggshells could potentially reduce respiration rates of embryos by decreasing the rates of gas diffusion across the eggshell and, in turn, lead to an incubation period that is longer than expected for an egg of similar size. Given these traits, the mechanisms by which cowbird eggs are able to hatch earlier remains unresolved.

A number of mechanisms have been proposed to explain the short incubation periods for cowbird eggs. Kattan (1995) found that eggs of the closely-related shiny cowbird *Molothrus bonariensis* contained a 23.8% lower energy content when compared with values predicted by their mass and hypothesized that lower egg-yolk reserves led to earlier hatching. Other proximate factors may affect the incubation period of eggs of the brood parasite. Davies and Brooke (1988) proposed that brood parasites remove host eggs to ensure that the increased clutch size from the addition of a parasitic egg does not exceed the host's ability to incubate the eggs. Peer and Bollinger (2000) similarly found that both host clutch size and egg size are important determinants of incubation success of cowbird eggs by affecting the extent of contact between the parasite egg and the host brood patch.

Another means by which cowbird eggs may hatch earlier is through accelerated development of the embryo. The rate of embryonic development is constrained by the rate of metabolic gas exchange across the eggshell

(Ar et al. 1974, Ar and Rahn 1978, 1985), and is therefore limited by the number and size of pores in the eggshell and eggshell thickness. Greater eggshell porosity (i.e. pore area divided by eggshell thickness), caused by increases in pore number, pore size or both, allows for an enhanced exchange of metabolic gases (i.e. gas flux) and water during embryological development and decreases the time to hatching (Paganelli 1980, Tullett and Deeming 1982, Vleck and Bucher 1998). Indeed, increased porosity of later-laid eggs within a clutch has explained intraclutch hatching synchrony in the Canada goose *Branta canadensis* (Clark et al. 2010), Magellanic penguin *Spheniscus magellanicus* (Boersma and Rebstock 2009), Snares penguin *Eudyptes robustus* (Massaro and Davis 2005), and yellow-eyed penguin *Megadyptes antipodes* (Massaro and Davis 2004). A similar result was found in an interspecific comparison among members of the Alcidae (Zimmermann and Hipfner 2007) indicating the important role eggshell porosity can play in embryo development and incubation length.

In this study we tested the hypothesis that the accelerated development of the cowbird embryo relative to hosts is enabled by an increase in eggshell porosity that allows increased fluxes of respiratory gases to and from the developing embryo. Direct comparison of eggshell characteristics between a brood parasite and its host has been previously reported. Hargitai et al. (2010) found that the thicker eggshell of the parasitic common cuckoo *Cuculus canorus* had a significantly higher pore density than that of its host, the great reed warbler *Acrocephalus arundinaceus*. Such pore density was thought to have compensated for the reduced gas conductance across the cuckoo eggshell which, coupled with differences in the egg content (e.g. enhanced levels of antioxidants and nutrients) and early embryonic development within the female oviduct led to an increased rate of development and size of the cuckoo hatchling. It should be noted that this comparison was conducted between distantly related species from different orders (i.e. Cuculiformes, Passeriformes) making it difficult to assign differences due to brood parasitism per se or to divergent evolutionary histories.

We compared the eggshell porosity of the brown-headed cowbird to the red-winged blackbird *Agelaius phoeniceus* a closely related, nonparasitic species (Price et al. 2009) and a more distantly related species, the dickcissel *Spiza americana*. Both the blackbird and dickcissel serve as important hosts for the cowbird throughout a large portion of its range, and both have slightly longer incubation periods than cowbirds (i.e. 11.5–13 d for the dickcissel [Temple 2002], 11–13 d for the red-winged blackbird [Yasukawa and Searcy 1995]). Specifically, we predicted that cowbird eggshells should have larger diameter pores, a greater number of pores, or both, than the host eggshells. In addition, we also predicted that cowbird eggs should exhibit a larger estimated gas flux than either host species. If the porosity of cowbird eggshells is greater than the closely related red-winged blackbird, it would suggest that enhanced eggshell porosity is an adaptation for a brood parasitic reproductive strategy rather than an eggshell character common to other icterids.

Methods

From 2006 to 2009 we collected eggs in various stages of embryonic development of the brown-headed cowbird, dickcissel, and red-winged blackbird from nests in western Illinois (McDonough County), northeastern Kansas (Riley County), and eastern Iowa (Scott County). After collection, eggs were stored at $-20°C$ in a laboratory freezer. Although freezing may cause eggshell breakage, we restricted our measurements to those eggs with no visible cracks or those with thin (i.e. hairline) fractures; all egg dimensions were within published ranges for all three species (Lowther 1993, Yasukawa and Searcy 1995, Temple 2002). Immediately after removal from the freezer and prior to porosity analysis, measurements of eggshell length and width (n = 20 eggs per species) were made using a Vernier digital caliper (± 0.02 mm). Eggshells were then physically broken into fragments, thawed for 1 min and then placed into boiling 5% NaOH for approximately 15 min to remove the inner eggshell membrane and outer cuticle. Eggshells were further fragmented during the boiling process, air-dried for 1–5 d, and then manually broken into smaller pieces for viewing with a compound microscope. We examined the outer surface of each eggshell fragment at $400\times$ magnification. For each measurement we examined 3.07 mm^2 of eggshell to count the number of pores and measure pore diameters using a calibrated ocular micrometer (± 2.5 µm). To estimate accurately the characteristics of the entire eggshell, we took 54 measurements of each eggshell (n = 18 each for apical, equatorial, and basal regions). The eggs for all species were in various stages of embryonic development, which may influence the pore diameter on the inner surface of the eggshell and eggshell thickness (Booth and Seymour 1987). However, this would have no effect on pore diameters that we measured on the outer eggshell surface. Our examination revealed that pores were generally circular in shape and for purposes of this analysis we assumed each eggshell pore was circular with a surface area (SA) calculated as SA (µm^2) = π(diameter/2)^2. All measurements of pore number and pore area for each eggshell fragment examined were made by one observer (MK). The precision of pore counts was checked by a second observer (BC), and we found no difference between individuals in the number of pore counts ($t_{106} = 0.00$, p = 1.00, n = 108 measurements). For each egg we also measured eggshell thickness (± 0.01 mm, n = 3 fragments per eggshell region, n = 9 measurements per egg) using a Starrett model 2600-1 thickness indicator. For each species we estimated egg surface area as egg volume$^{0.666} \times 4.951$, where egg volume = egg height $\times$ egg width$^2 \times 0.51$ (Hoyt 1976). The number of pores and pore area per egg were estimated by multiplying their average (mm^{-2}) by the eggshell surface area.

Gas conductance (water vapor conductance (G_{H_2O}, mg H_2O d^{-1} torr^{-1})) was calculated using the equation: $G_{H_2O} = 23.41 \times$ (total pore area per egg ÷ eggshell thickness) for each species (Ar and Rahn 1978). For estimates of gas flux, we assumed constant temperature and pressure. We used average mass values to normalize the data to egg size (brown-headed cowbird [Rahn et al. 1988]; red-winged

blackbird [Manning 1981]; and dickcissel [Gross 1968]) for each species, as the eggs were not weighed at the time of collection.

Statistical analyses

For each species, a mean value for each measured eggshell characteristic (i.e. pore number, pore diameter and eggshell thickness) from each egg was used for all statistical analyses. All statistical tests were performed using SPSS (ver. 17.0; IBM, Somers, New York). When the data were not normally distributed or the variances among groups were unequal (Shapiro–Wilks normality test, Levene test for equality of variance), the data were transformed using a Box–Cox transformation. We tested differences among species for each characteristic using a univariate ANOVA. To evaluate effect size, we calculated the η(eta)^2 effect statistic as the $SS_{between}$ divided by the SS_{total} for each statistically significant ANOVA ($p < 0.05$). When a significant difference among the three species was detected, protected pair-wise comparisons were evaluated using the REGW Q procedure (Field 2009). Our statistical program (SPSS) does not calculate exact p values for pair-wise comparisons with the REGW Q procedure, so we report p values as either < 0.05 or > 0.05. Using the estimated averages of pore number mm^{-2} (i.e. pore density) and pore area (μm^2) mm^{-2} for each species, plus calculated surface area (mm^2) values from width and length measurements, we were able to estimate the total pore area per egg. Data reported are untransformed means $\pm$ SE.

Results

Eggshell characteristics

There was a significant difference in the eggshell thickness among the three species ($F_{2,51} = 79.49$, $\eta^2 = 0.76$, $p < 0.001$; Table 1). Pair-wise comparisons revealed that cowbird eggshells were significantly thicker than eggshells of the red-winged blackbird and the dickcissel, and that red-winged blackbird eggshells were significantly thicker than those of the dickcissel.

Among species there were significant differences in pore density ($F_{2,57} = 3.90$, $\eta^2 = 0.16$, $p = 0.026$; Table 1). Pair-wise comparisons found that dickcissel eggshells had significantly lower pore density than those of the red-winged blackbird. However, pore density in cowbird eggshells was not significantly different from that in either eggshells of the red-winged blackbird or the dickcissel.

There was a significant difference in the pore area (μm^2) mm^{-2} of eggshell among the three species ($F_{2,57} = 17.12$, $\eta^2 = 0.45$, $p < 0.001$; Table 1). Pair-wise comparisons revealed that cowbird eggshells had a significantly greater pore area mm^{-2} of eggshell than both the eggshells of the red-winged blackbird and the dickcissel, although the average pore area mm^{-2} of the eggshell did not differ between the dickcissel and the red-winged blackbird. We also found a significant difference among species for the estimated total pore area per egg ($F_{2,51} = 14.13$, $\eta^2 = 0.42$, $p < 0.001$; Table 1). Despite having an egg surface area intermediate

Table 1. Comparison of cowbird and host eggshell characteristics. Superscripts of different letters indicate a statistically significant difference ($p < 0.05$).

	Mean	n	95% confidence interval
Eggshell thickness (mm)			
Cowbird	0.105[a]	14	0.101–0.109
Dickcissel	0.078[b]	20	0.075–0.081
Red-winged blackbird	0.089[c]	20	0.088–0.091
Pores mm^{-2} eggshell			
Cowbird	0.263[a,b]	20	0.206–0.319
Dickcissel	0.229[a]	20	0.168–0.289
Red-winged blackbird	0.352[b]	20	0.296–0.408
Pore area (μm^2) mm^{-2} eggshell			
Cowbird	9.531[a]	20	6.333–12.728
Dickcissel	2.328[b]	20	1.353–3.303
Red-winged blackbird	3.242[b]	20	2.449–4.035
Pore area (mm^2) egg^{-1}			
Cowbird	7446.5[a]	14	4432.8–10460.3
Dickcissel	1640.2[b]	20	921.2–2359.2
Red-winged blackbird	3948.2[c]	20	2863.1–5033.4
Porosity (pore area (μm^2) mm^{-1} thickness)			
Cowbird	70093.8[a]	14	44450.0–95731.7
Dickcissel	20799.7[b]	20	11942.8–29656.6
Red-winged blackbird	43892.7[c]	20	32614.2–51651.1

between these two hosts, cowbirds had a significantly greater pore area per egg than both red-winged blackbirds and dickcissels. The pore area per egg of red-winged blackbird eggshells was also significantly greater than that of dickcissels. When average eggshell porosity (pore area (μm^2) mm^{-1} eggshell thickness) was compared among species, we also found a significant difference ($F_{2,51} = 11.56$, $\eta^2 = 0.31$, $p < 0.001$; Table 1). Cowbird eggshells were significantly more porous than both eggshells of the red-winged blackbird and the dickcissel, and red-winged blackbird eggshells were significantly more porous than those of the dickcissel.

Estimates of gas flux across the eggshell

There was a highly significant difference among species in the estimated gas flux (mg H$_2$O d^{-1} torr^{-1}) across eggshells of the three species ($F_{2,51} = 11.53$, $\eta^2 = 0.31$, $p < 0.001$; Fig. 1A). Cowbird eggshells had a significantly greater gas flux than those of red-winged blackbirds and dickcissels and the predicted gas flux through red-winged blackbird eggshells was significantly greater than that of the dickcissel. After normalizing the estimated gas flux to egg mass from published studies (mg H$_2$O d^{-1} torr^{-1} g^{-1}), we also found a highly significant difference among species ($F_{2,51} = 12.19$, $\eta^2 = 0.32$, $p < 0.001$; Fig. 1B). Cowbird eggshells had a significantly greater mass-specific gas flux than both the red-winged blackbird and dickcissel, but there was no significant difference between eggshells of the red-winged blackbird and dickcissel.

Discussion

Although cowbird eggs were intermediate in size between that of the red-winged blackbird and the dickcissel, as
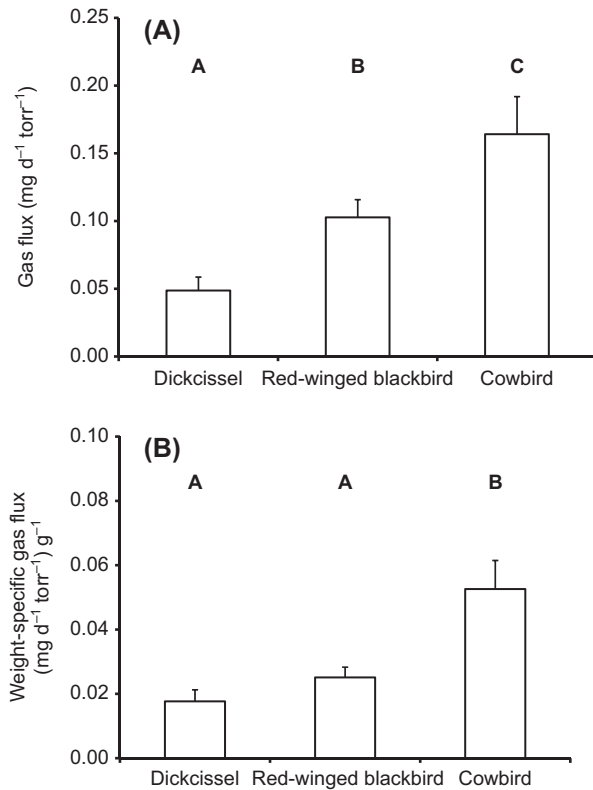
Figure 1. (A) The average estimated gas flux (mg H_2O d^{-1} $torr^{-1}$) and (B) the average estimated weight-specific gas flux ((mg H_2O d^{-1} $torr^{-1}$) g-egg $weight^{-1}$) of the eggshells of the dickcissel, red-winged blackbird and the cowbird. Each average is presented as the mean ± standard error. Values that are not statistically different ($p > 0.05$) have the same letter above their respective columns.

reported by previous authors (e.g. Picman 1989), the thickness of the cowbird eggshell was significantly greater than those of either of these two species. Despite this result, comparisons of estimated total eggshell pore area (μm^2) and porosity (μm^2 mm^{-1}) revealed that cowbird eggshells were more porous than both the closely related red-winged blackbird and the more distantly related dickcissel. These results are similar to those of Hargitai et al. (2010) who found that the parasitic common cuckoo had a thicker eggshell with a greater pore density than its distantly related host, the great reed warbler. In contrast to the cuckoo-reed warbler system, the differences in total pore area and porosity reported here were based on the larger size of cowbird eggshell pores and not the total number of pores. When compared with cowbird eggshells, the eggshells of the red-winged blackbird contained more but smaller pores whereas dickcissel eggshells contained a similar number of smaller pores.

Gas flux across the eggshell is positively correlated with egg mass (gas flux = $0.432 \times mass^{0.78}$; Ar and Rahn 1978) and the rates of gas flux across eggshells should have been highest in the red-winged blackbird, intermediate in the cowbird and lowest in the dickcissel. However, the estimated gas flux across the entire eggshell of cowbirds was significantly higher than that of both the red-winged blackbird and the dickcissel. Likewise, eggshells of cowbirds had

a significantly higher estimated mass-specific gas flux than that for eggshells of red-winged blackbirds and dickcissels.

It is noteworthy that the parasitic cowbird had a thicker eggshell and a greater mass-specific gas flux than that of the non-parasitic, but closely related, red-winged blackbird, a species that produces an egg that is $1.3\times$ larger (by mass) than the egg of the cowbird. Such differences between a brood parasitic and non-parasitic icterid suggest that these modifications in eggshell characteristics facilitate the cowbird's brood parasitic lifestyle. Mermoz and Ornelas (2004) mapped life history characters and character states for parasitic cowbirds onto a (Lanyon and Omland 1999) phylogeny of the family Icteridae. They concluded that eggshell thickness was the only character that evolved as a unique adaptation for brood parasitism. The order of the evolutionary changes in the thickness and porosity of cowbirds eggshells has received little study and there are at least two potential paths by which these changes may have occurred. First, if selection pressures initially favored an increase in development rate to enhance post-hatching survivorship of cowbird nestlings, then an increase in total pore area, which alone would reduce the structural integrity of the egg, would lead to a compensatory thickening of the eggshell. Alternatively, if increases in eggshell thickness initially evolved to protect the egg from damage because of host behavior or from rapid laying, then an increase in eggshell porosity may have arisen to compensate for reduced gas fluxes across a thicker eggshell. Measures of eggshell porosity and thickness among parasitic and non-parasitic icterid species are necessary to test these hypotheses.

The brown-headed cowbird, a generalist brood parasite, has a faster rate of embryonic development than many of its host species, despite having a considerably thicker and stronger eggshell. In two pair-wise interspecific comparisons, we found that the estimated gas flux across the eggshell is greater in cowbirds than two host species, the larger red-winged blackbird and the smaller dickcissel. Further, estimates of mass-specific gas flux are also greatest for cowbird eggs. Together, these data suggest that evolutionary changes in cowbird eggshell porosity are adaptations that enable its eggs to hatch earlier than equivalently-sized host eggs, a mechanism that has not been documented in other brood parasitic species.

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