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Shiny cowbird *Molothrus bonariensis* egg size and chick growth vary between two hosts that differ markedly in body size

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In birds, egg size affects chick growth and survival and it is an important component of reproductive success. The shiny cowbird *Molothrus bonariensis* is an extreme generalist brood parasite that uses hosts with a wide range of body masses. Survival of cowbird chicks decreases with host body mass, as competition for food with nestmates is more intense in large than in small hosts. We studied variation in shiny cowbird egg size and chick growth in two hosts that differ markedly in body size: the chalk-browed mockingbird *Mimus saturninus* (70–75 g), and the house wren *Troglodytes aedon* (12–13 g). We analyzed: 1) if females parasitizing mockingbirds lay larger eggs than those parasitizing wrens, and 2) the association between egg size and chick growth. We experimentally controlled for time of parasitism and number of host chicks and evaluated growth rate of male and female parasite chicks. Shiny cowbirds parasitizing mockingbird nests laid larger eggs than those parasitizing wren nests. Chick body mass after hatching was positively associated with egg size until chicks were five days of age, but there was no association between egg size and growth rate, or asymptotic mass. There were no sexual differences in egg size or body mass at the time of hatching, but growth rate was higher in males than in females leading to sexual dimorphism in asymptotic mass. Differences in egg size between hosts and the effect of egg size on body mass after hatching support the hypothesis that different females are specialized in the use of hosts that differ in body mass.

In birds, the reproductive value of eggs depends largely on their size (Mead et al. 1987, Anderson et al. 1997, Müller et al. 2005). Egg size is an important fitness component and it is positively associated with size of hatchlings (Williams 1994) and chick growth (Viñuela 1997) and survival (Williams 1994). Larger eggs contain more nutrients than smaller ones (Ankney and Bisset 1976, Ankney 1980, Arnold and Green 2007) and hatchlings from large eggs have more reserves than those from smaller ones (Parsons 1972, Ankney 1980). Besides, nutrient reserves positively affect nestling growth and survival in early age (Amundsen et al. 1996, Blomqvist et al. 1997, Reed et al. 1999, Styrsky et al. 1999).

Females can bestow an advantage on a particular offspring by increasing the resources (i.e. nutritional and hormonal factors) invested in the egg (Anderson et al. 1997, Cordero et al. 2000, Magrath et al. 2003). Differential resource allocation to eggs may compensate brood size hierarchy, by favouring the smallest or the most asynchronous chick (Anderson et al. 1997, Blanco et al. 2003, You et al. 2009), or the sex with higher fitness (Anderson et al. 1997, Cordero et al. 2000, Magrath et al. 2003). Thus, females would be able to invest differential resources in particular eggs to maximize their reproductive output per unit of investment (Williams 1966, Eising et al. 2001).

Obligate brood parasites, like cowbirds *Molothrus* spp. do not provide any parental care for the offspring and the reproductive effort of the female is limited to produce eggs and to search for host nests. Therefore, they offer an excellent opportunity to study maternal investment in eggs in the absence of post-laying reproductive effort. Studies of fecundity of female brown-headed cowbirds *M. ater* with molecular markers indicate that most females lay 15–20 eggs during the breeding season (Alderson et al. 1999, Hahn et al. 1999, Strausberger and Ashley 2003, Woolfenden et al. 2003). These values are considerably lower than previously published estimates (Payne 1976, Scott and Ankney 1980, 1983, Jackson and Roby 1992) and indicate that the reproductive value of eggs for cowbird females is higher than once assumed (Kattan 1997). Furthermore, egg production by parasite females may be constrained by other energetic demands and limited dietary calcium (Holford and Roby 1993, Curson and Mathews 2003). Therefore, it would be expected that female cowbirds had evolved traits that increase the survival of their eggs and chicks, maximizing female reproductive output per investment unit.

The shiny cowbird *M. bonariensis* is an extreme generalist brood parasite that uses more than 250 hosts (Ortega 1998, Lowther 2011). These hosts differ markedly in body mass, some of them much smaller than the parasite (i.e. 10 vs 45 g) and others much larger (i.e. 80 vs 45 g; Ortega 1998, Lowther and Post 1999, De Mársico et al. 2010). Survival of cowbird chicks decreases with host body mass, as competition for food with nestmates is more intense in large than in small hosts (Fiorini et al. 2009, Gloag et al. 2012). Although shiny cowbirds use many hosts at the population level (Ortega 1998, De Mársico et al. 2010), molecular evidence suggests that individual females do not lay their eggs randomly, but preferentially parasitize particular hosts or host types (Mahler et al. 2007). Such preferences may lead to divergent evolutionary histories between females that use different hosts or host types that resulted in the adjustment of their parental effort to host characteristics. In particular, females that parasitize hosts of large body mass may enhance the viability of their offspring by increasing the resources allocated in their eggs (i.e. to lay larger eggs which result in more competitive hatchlings). Accordingly, Spottiswoode et al. (2011) have shown that brood parasitic greater honeyguides *Indicator indicator* have two highly divergent mitochondrial DNA lineages that are associated with ground- and tree-nesting hosts, respectively. These authors also showed that in this parasite, eggs laid in nests of different hosts vary significantly in volume and this variation is positively correlated with variation in host body mass, indicating that a single parasitic species has evolved host-specific variation in traits highly relevant to host-parasite interactions (Spottiswoode et al. 2011).

In this study we analyze variation in egg size between shiny cowbirds that parasitize two hosts that differ markedly in body mass: the house wren *Troglodytes aedon* (hereafter wrens), a host much smaller than shiny cowbirds (12–13 vs 45–50 g) and the chalk-browed mockingbird *Mimus saturninus* (hereafter mockingbirds), a host much larger than the parasite (i.e. 70–75 g). Shiny cowbird females that parasitize these hosts showed mtDNA genetic divergence in relation to host use, suggesting the existence of genetically differentiated host races (Mahler et al. 2007). Shiny cowbird chicks face very low competition for food with host nestmates in wren nests because, in addition to their larger body mass, they normally hatch two days earlier than host chicks (Tuero et al. 2007). In contrast, competition for food is much more intense in mockingbird nests, where cowbird chicks are smaller than their nestmates and they hatch one day earlier or the same day as host chicks (Fiorini et al. 2009). Therefore, we expect that female shiny cowbirds that parasitize mockingbirds lay larger eggs than those that parasitize wrens, as size of cowbird chicks at the time of hatching is more important for intrabrood competition for food with nestmates in mockingbirds than in wrens.

Methods

Study site

The study was carried out at 'Reserva El Destino' (35°08′S, 57°23′W), near the town of Magdalena, Province of Buenos Aires, Argentina, during the breeding seasons (October–January) 2004–2005, 2005–2006 and 2006–2007. Our study site is almost flat, marshy grassland with old and second growth stands dominated by tala *Celtis tala* and coronillo *Scutia buxifolia*.

Study species

Shiny cowbirds are sexually dimorphic in plumage and body mass (females: 47 g, males: 51 g, Reboreda et al. 1996). At our study area they lay eggs from early October to late January and use wrens and mockingbirds as their main hosts (Fiorini and Reboreda 2006, Tuero et al. 2007). Because wrens nest in natural and artificial cavities (Kattan 1998), to facilitate data collection we used 100 nestboxes placed within an area of approximately 150 ha. Wrens breed from early October until mid January and they have a modal clutch size of 5 eggs (Tuero et al. 2007). Incubation starts with the laying of the penultimate egg, chicks hatch after 15 d and they leave the nest when 17 d of age (Tuero et al. 2007, Llambías 2009). At our study area, during each breeding season they have approximately 50 nesting attempts conducted by approximately 40 pairs. Sixty percent of wren nests are parasitized by shiny cowbirds with an intensity of parasitism of 1.7 eggs per parasitized nest (Tuero et al. 2007). Wren nest survival is 43% and hatching success and chick survival of shiny cowbird eggs and chicks in wren nests are 77 and 87%, respectively (Fiorini et al. 2005). Mockingbirds breed from mid-September until mid-January. They build open nests and have a modal clutch size of 4 eggs, incubation starts with the laying of the penultimate egg, chicks hatch after 14 d and they leave the nest when 12–14 d of age (Fiorini and Reboreda 2006). At our study area, each breeding season mockingbirds have approximately 80 nesting attempts conducted by 35 pairs. Seventy percent of mockingbird nests are parasitized by shiny cowbirds with an intensity of parasitism of 2.2 eggs per parasitized nest (Fiorini and Reboreda 2006, Fiorini et al. 2009). Mockingbird nest survival is 16% and hatching success and chick survival of shiny cowbird eggs and chicks in mockingbird nests are 72 and 79%, respectively (Fiorini et al. 2005).

Data collection

We followed 59, 54 and 50 nesting attempts by wrens, and 86, 90 and 77 nesting attempts by mockingbirds during the breeding seasons 2004–2005, 2005–2006 and 2006–2007, respectively. We visited wren and mockingbird nests daily until the chicks fledged or the nest failed. We collected 29 and 61 shiny cowbird eggs laid in wren and mockingbird nests respectively. We do not have information about the number of shiny cowbird females that parasitize wrens and mockingbirds at our study area but we know that there are at least 90 females (there were 90 different females trapped and ringed during 2011 breeding season, R. Gloag and R. Scardamaglia pers. comm.). Because we did not assign eggs to individual females we cannot rule out the possibility of collecting more than one egg from the same female (i.e. potential pseudoreplication). However, we consider that this probability is relatively low because we estimated each year there was approximately 90 different cowbird females at our study area and during the three years of our study we collected 29 of 94 shiny cowbird eggs laid in wren nests and 61 of 614 shiny cowbird eggs laid in mockingbird nests.

We measured length and width of each egg to the nearest 0.1 mm with a dial caliper. We calculated egg volume as

$L \times W^2 \times X$, where L and W were the length and width of the egg, and X is a species-specific constant. The value used for this constant was 5.15×10^{-4} (Nolan and Thompson 1978). To analyze differences in shiny cowbird's egg volume between hosts we pooled the data of the three breeding seasons because we did not find variation among years (ANOVA: $F_{2, 58} = 1.44$, $p = 0.24$ for mockingbirds and $F_{2, 26} = 0.20$, $p = 0.84$ for wrens). To test for sexual differences in egg size we artificially incubated eggs for 2–3 d at 37.5°C ± 1°C to ensure minimal embryonic development (Strausberger and Ashley 2001) and then frozen them. For processing, we defrosted eggs and extracted embryonic tissue.

Molecular sexing

We genetically sexed embryonic tissue taken from eggs and blood samples taken from shiny cowbird chicks by amplification of a size-different intron within the highly conserved chromo-helicase-DNA binding protein (CHD) gene located on the avian sex chromosomes (Ellegren 1996). We extracted DNA from embryonic tissue and blood samples using a standard salting-out protocol (Miller et al. 1988) and amplified the size-different intron using P2 and P8 primers (Griffiths et al. 1998). We performed PCR amplifications in 10-µl reaction volumes using 50–100 ng of DNA template, 0.5 µM forward and reverse primers, 0.25 mM each dNTP, 2.5 mM $MgCl_2$ and 0.25 u of Invitrogen Taq-Polymerase. We set annealing temperatures at 50°C and repeated for 30 cycles. We separated PCR products in 3% agarose gels stained with ethidium bromide. The presence of one band indicated males (ZZ), whereas two bands indicated females (ZW).

Experimental procedures

To study the association between egg size and chick growth, during the 2005–2006 and 2006–2007 breeding seasons we artificially parasitized wren and mockingbird nests. To produce a constant environment during parasite's development we controlled for: 1) synchronization between parasitism and host laying, and 2) number of host eggs. Because shiny cowbird females normally puncture eggs when they parasitize host nests and this leads to a reduction in host clutch size (Astié and Reboreda 2006, Peer 2006), we created experimental host clutches with the modal clutch size of parasitized nests (four eggs in wren nests and two eggs in mockingbird nests). These clutch sizes correspond to the natural competitive environment of cowbird nestlings in wren and mockingbird nests (Fiorini and Reboreda 2006, Tuero et al. 2007). To reduce clutch size we removed the last two host eggs immediately after they were laid. Because the incubation period of shiny cowbirds is two-three days shorter than that of wrens and early hatching of the cowbird chick decreases the survival of wren chicks (Tuero et al. 2007), we parasitized wren nests 3 d after the onset of incubation. This low degree of asynchrony between parasitism and the onset of incubation is similar to that observed in naturally parasitized nests of wrens and does not affect the survival or asymptotic weight of the shiny cowbird chick (Fiorini et al. 2009). On the contrary, incubation period of shiny cowbirds is one day shorter than that of mockingbirds and late hatching of shiny cowbird chicks decreases parasite survival in nests of this hosts. Therefore we parasitized mockingbird nests before the onset of incubation. Since the incubation period of cowbird eggs is 12–13 d in mockingbird and wren nests, in both hosts, cowbird chicks hatched one day before or the same day the first host chick hatched. Our experimental manipulations comply with Argentinean law.

We artificially parasitized wrens with shiny cowbird eggs collected in wren nests and mockingbirds with shiny cowbird eggs collected in mockingbird nests. We collected parasite eggs from host nests the same day the cowbird eggs were laid (i.e. they were not incubated by the host prior to the experiment). They were kept in an ambiental temperature for 24–48 h prior to translocation to the experimental nest.

We weighed chicks on average eight times during the nestling period (range 4–11 measurements) with a digital portable balance (Ohaus LS 200) to the nearest 0.1 g. We did not weight the chicks after they were 9 d of age to avoid inducing premature fledging. Although we weighed all chicks the day of hatching, the time elapsed between hatching and the first weight measurement was uncontrolled. Also, in mockingbirds' nests cowbird chicks are fed with larger food items than in wrens' nests (Tuero 2011). As a result, our estimation of body mass at hatching likely has a larger percentage error than other estimations and this error may differ between hosts. When chicks were 9 d of age we collected a small blood sample (20–30 µl) via venipuncture and stored it in lysis buffer until we performed the genetic analyses for sex determination.

Nestling growth rate

To compare the development of shiny cowbird chicks in wren and mockingbird nests we adjusted their growth curves to a logistic equation. The fitted body mass (W) reached at time t is:

$$W = A/1 + e^{-K(t-t_0)}$$

We estimated the asymptote of the growth curve (A), the constant growth rate (K), and the inflection point or age of maximum growth (t_0) of each cowbird chick. Also, we estimated weight at hatching, weight at day 5 and maximum growth rate (K_{max}, hereafter K). We calculated K_{max} as:

$$K_{max}\text{: } KA/4$$

We used K_{max} in our analysis because this growth rate is more appropriate to explain the growth variation associated with different environments (Royle et al. 1999). Besides, in passerines body size dimorphism is more strongly associated with K_{max} variation between sexes than with K variation (Richner 1991). Estimated constant growth rates did not differ between sexes ($F_{1, 38}$: 0.01, $p = 0.90$) and hosts ($F_{1, 38}$: 0.05, $p = 0.83$). Also, age of maximum growth did not differ between sexes ($F_{1, 38}$: 1.09, $p = 0.11$) and between chicks reared in mockingbird and wren nests ($F_{1, 38}$: 2.66, $p = 0.30$). We used a nonlinear model and least squares estimation minimized with the quasi-Newton option using SYSTAT software (Wilkinson et al. 1992).

Statistical analyses

To test for differences in egg size, body mass at hatching and at 5 d post-hatch and nestling growth we used two-way ANOVAs, including host and sex as fixed factors. We analyzed the relationship between egg size and body mass of chicks using a simple regression test. In this analysis, we used a subset of chicks because in some cases we did not have the corresponding measures of egg size. All analyses were made with Statistica 6.0 (StatSoft 2001). We report mean values ± SE throughout the text.

Results

Differences in egg size between hosts

Shiny cowbird eggs laid in mockingbird nests were larger than those laid in wren nests ($F_{1,\ 86} = 9.15$, $n = 90$ eggs, $p < 0.01$, Fig. 1A, B), but eggs determined as males or females did not differ in volume ($F_{1,\ 86} = 0.46$, $n = 90$ eggs, $p = 0.50$, Fig. 1A) and the interaction between host and sex was not significant ($F_{1,\ 86} = 0.03$, $n = 90$ eggs, $p = 0.85$). Also, shiny cowbird eggs laid in mockingbird nests were both longer (mockingbird: 24.28 ± 0.15; wren: 23.42 ± 0.25; $F_{1,\ 86} = 9.23$, $n = 90$ eggs, $p < 0.01$) and wider (mockingbird: 18.94 ± 0.09; wren: 18.60 ± 0.12; $F_{1,\ 86} = 3.83$, $n = 90$ eggs, $p = 0.04$) than those laid in wren nests. We did not detect sexual differences in egg length ($F_{1,\ 86} = 0.006$, $n = 90$ eggs, $p = 0.94$) or egg width ($F_{1,\ 86} = 0.38$, $n = 90$ eggs, $p = 0.53$) and the interaction between host and sex was not significant for both variables (length: $F_{1,\ 86} = 0.03$, $n = 90$ eggs, $p = 0.87$; width: $F_{1,\ 86} = 0.52$, $n = 90$ eggs, $p = 0.47$).

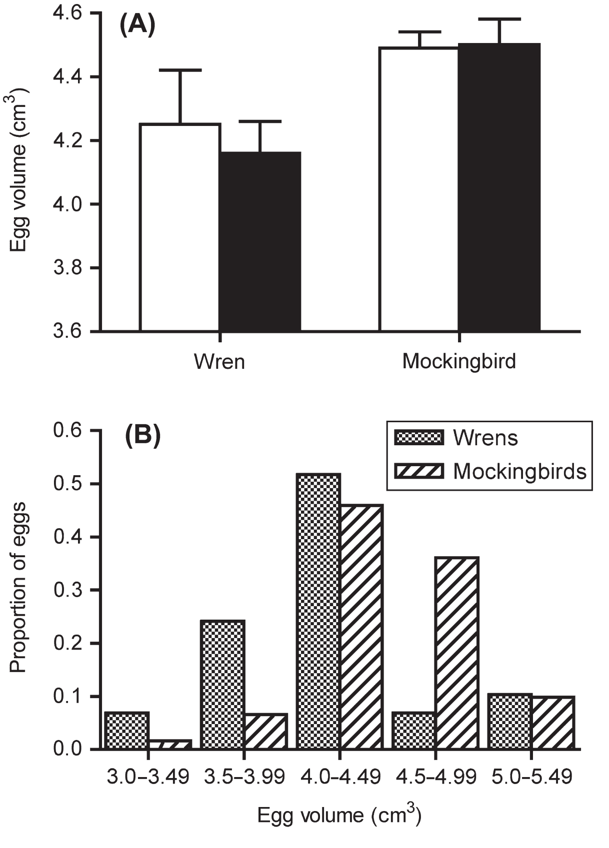

Figure 1. (A) Volume (mean ± SE) of shiny cowbird eggs laid in a large (chalk-browed mockingbird) and a small (house wren) hosts bearing females (open) or males (closed bars) embryos. Sample sizes are 32 female and 29 male shiny cowbird eggs in mockingbird nests and 12 female and 17 male shiny cowbird eggs in wren nests. (B) Frequency distribution of the egg volumes of shiny cowbird eggs laid in wren (n = 29 eggs) and mockingbird (n = 61 eggs) nests.

Egg size and chick growth

There was a positive association between weight at hatching and egg size ($R^2 = 0.41$, $p < 0.01$, $n = 17$ eggs laid in both hosts). Shiny cowbird chicks hatching from eggs laid in mockingbird nests were heavier than those hatching from eggs laid in wren nests ($F_{1,\ 38} = 6.73$, $p = 0.01$, Fig. 2A). We did not detect sexual differences in body mass at hatching ($F_{1,\ 38} = 0.20$, $p = 0.65$, Fig. 2A) and the interaction between host and sex was not significant ($F_{1,\ 38} = 1.44$, $p = 0.24$). At day 5 of age, cowbird chicks raised in mockingbird nests were still heavier than those raised in wren nests ($F_{1,\ 38} = 10.16$, $p < 0.01$, Fig. 2B). There were no sexual differences in weight at day 5 ($F_{1,\ 38} = 0.27$, $p = 0.61$, Fig. 2B) and the interaction between host and

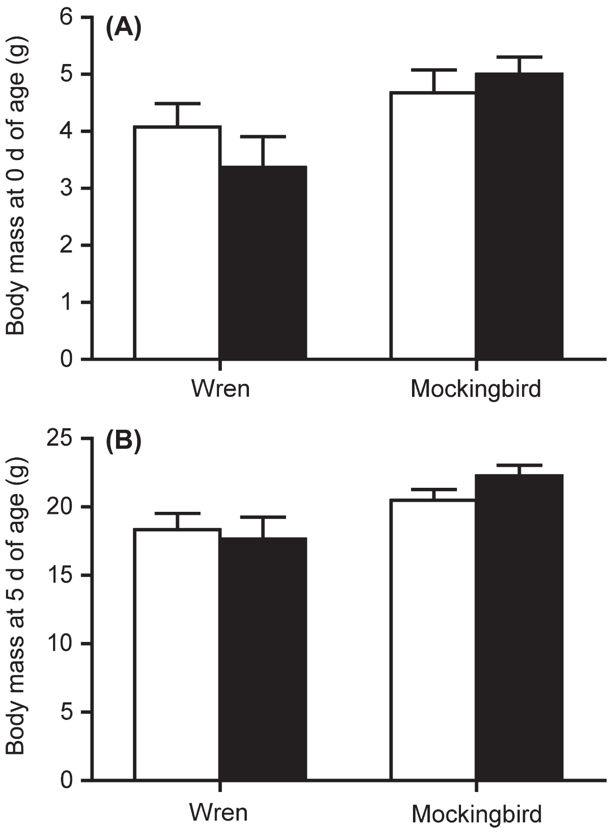

Figure 2. Body mass (mean ± SE) of female (open bars) and male (closed bars) shiny cowbird chicks in mockingbird and wren nests at: (A) time of hatching, and (B) 5 d of age. Sample sizes are 13 female and 16 male shiny cowbird chicks in mockingbird nests and 7 female and 6 male shiny cowbird chicks in wren nests.

Table 1. Relationship between egg size and chick body mass when chicks were 0–4 d old.

Age of chicks (days)	Mockingbird			Wren		
	R^2	p	n	R^2	p	n
0 d old	0.37	0.03	10	0.56	0.02	7
1 d old	0.21	0.09	10	0.56	0.02	7
2 d old	0.16	0.22	10	0.54	0.03	7
3 d old	0.06	0.48	10	0.46	0.06	7
4 d old	0.07	0.45	10	0.33	0.10	7

sex was not significant ($F_{1, 38} = 1.37$, $p = 0.25$). In mockingbird nests, chick body mass was positively associated with egg size during the first two days of age, while in wren nests body mass was positively associated with egg size during the first 3 d of age (Table 1). The percentage of chick mass explained by egg size was higher for cowbird eggs laid in wren nests than for those laid in mockingbird nests (56 vs 37%, Table 1).

Males had a higher growth rate than females ($F_{1, 1, 38} = 5.63$, $p = 0.01$, Fig. 3A) growing on average 12% faster than females. There was no effect of host on the growth rate of the parasite ($F_{1, 38} = 0.19$, $p = 0.67$, Fig. 3A) and the interaction between sex and host was not significant ($F_{1, 38} = 0.35$, $p = 0.54$). Male chicks reached a higher asymptotic weight than females (43.4 ± 1.3 g vs 38.75 ± 1.31; $F_{1, 38} = 6.30$, $p = 0.02$, Fig. 3B). Asymptotic weight of same sex chicks raised in different hosts did not differ ($F_{1, 38} = 0.45$, $p = 0.50$, Fig. 3B) and the interaction between sex and host was not significant ($F_{1, 38} = 0.11$, $p = 0.74$). Mean values of body mass when shiny cowbird chicks were 9 d of age (last measurement of body mass) were 41.2 ± 1.6 g (n = 13) and 35.9 ± 1.2 (n = 12) for males and females raised in mockingbird nests, respectively; and 38.1 ± 2.2 g (n = 5) and 35.8 ± 1.1 (n = 7) for males and females raised in wren nests, respectively. These values did not differ (Wilcoxon tests: $p > 0.06$) from those estimated using the logistic model.

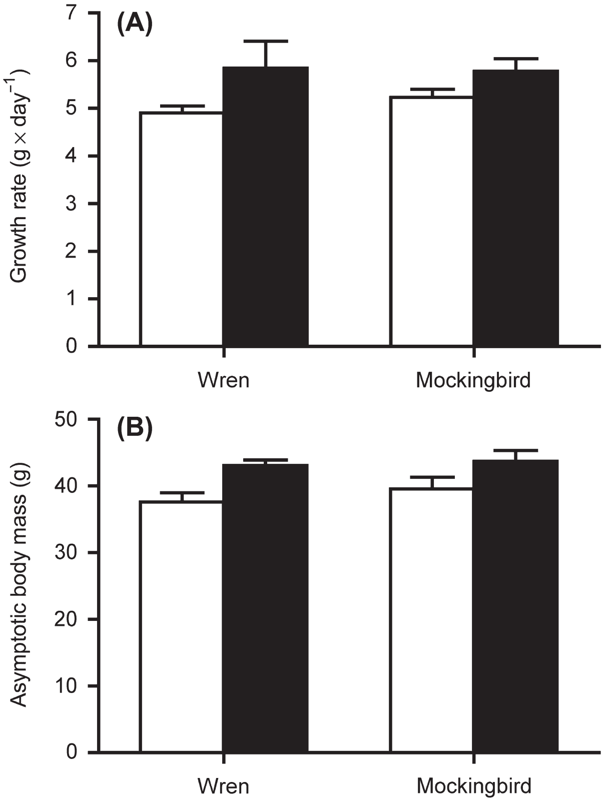

Figure 3. (A) Growth rate (mean ± SE) and (B) asymptotic weight (mean ± SE) of female (open bars) and male (closed bars) shiny cowbird chicks in mockingbird and wren nests. Sample sizes are 13 female and 16 male shiny cowbird chicks in mockingbird nests and 7 female and 6 male shiny cowbird chicks in wren nests.

Discussion

We found that shiny cowbird eggs laid by females parasitizing mockingbird nests were larger than those laid by females parasitizing wren nests. Consistent with differences in egg size, we also found that cowbird chicks in mockingbird nests had a higher body mass at hatching than those wren nests and this difference held until chicks were 5 d of age. Body mass was positively correlated with egg size until chicks were two and three days of age in mockingbird and wren nests, respectively, indicating that egg size influences cowbird growth during the first days after hatching. Egg size explained a lower percentage of the variation in cowbird's growth in mockingbird than in wren nests, suggesting that host contribution to chick growth was more important in mockingbirds. Thus, host type may have affected cowbird's growth, increasing or reducing the effect of egg size on growth.

The positive relationship between egg size and weight at hatching observed in our study is consistent with previous results by Nolan and Thompson (1978) in brown-headed cowbirds and Kleven et al. (1999) in cuckoos, who also found that egg volume was a good predictor of body mass at hatching. The size of cowbird chicks at the time of hatching is not critical to compete for food with foster siblings in wren nests because even parasite chicks hatching from small eggs are much bigger than wren chicks. Therefore, females using this host could reduce their reproductive cost by allocating fewer resources to eggs without reducing the viability of their chicks. Similarly, in superb fairy-wrens *Malurus cyaneus*, mothers with helpers lay smaller eggs of lower nutritional content that produce lighter chicks, than mothers without helpers. Helpers compensate fully for such reductions in investment and allow mothers to benefit through increased survival to the next breeding season (Russell et al. 2007). On the contrary, shiny cowbird females that use mockingbirds face the problem of their chicks competing with larger foster siblings and in this situation a larger body mass at hatching may increase the survival of the cowbird chick. Accordingly, Fiorini et al. (2009) found that hatching before host chicks (thus having a larger body mass at the time host chicks hatch) increased the survival of shiny cowbird chicks in mockingbird but not in wren nests.

Differences in egg size between hosts could be the result of divergent evolutionary histories of cowbird females that were selected for different optimal egg sizes. Accordingly, Mahler et al. (2007) found that at our study site, haplotype frequencies differ between shiny cowbirds laid in wrens and those laid in mockingbirds and suggested that individual females do not lay their eggs randomly, but preferentially parasitize particular hosts or host types. Such genetic differentiation would provide an evolutionary scenario to explain differences in egg size between females that use different hosts. An alternative adaptive explanation for our results is that individual females invest differentially in eggs depending on the host they are going to parasitize (i.e. females invest more resources in eggs when they are going to parasitize mockingbirds than when they are going to parasitize wrens). There are a couple of examples showing that individual females can adjust the size of eggs. Female mallards *Anas platyrhynchos* lay larger eggs after copulating with preferred males and smaller eggs after copulating with less preferred males (Cunningham and Russell 2000) and in superb fairy-wrens mothers lay smaller eggs when they have helpers than when they do not have helpers (Russell et al. 2007). However, we consider that this explanation is less likely because: 1) in birds, egg size appears to be a characteristic of individual females (i.e. repeatability is above 0.6 and heritability is higher than 0.5, Christians 2002), and 2) as we mention before, shiny cowbird females that parasitize these two hosts show mtDNA genetic divergence, suggesting the existence of genetically differentiated host races (Mahler et al. 2007). A non-adaptive explanation for our results is that characteristics of wren nests prevent females laying larger eggs (i.e. large females) from accessing their nests. However, female size is a weak predictor of female's ability to produce large or small eggs (Christians 2002). Besides, we found that some cowbird nestlings in wren nests fledged with a higher asymptotic body mass (47 g) than average cowbird adult females (45 g), which suggests that body size would not be a restriction for cowbird females for access to wren nests.

We did not detect differences in volume between eggs determined as males and females or sexual differences in body mass at hatching, but in both hosts males had a higher growth rate than females. This sexual difference in growth rate resulted in males fledging with higher asymptotic body mass than females (on average males were 11% heavier than females). These results show that sexual dimorphism in this species emerges early during the nestling stage. Similarly, Tonra et al. (2008) found sexual dimorphism in the growth rate of brown-headed cowbird chicks in a study where hatching synchrony between parasite and host chicks was also controlled. Interestingly, we did not detect a significant difference in the growth rate or asymptotic weight of same-sex cowbird chicks between hosts, despite the fact that cowbirds in mockingbirds must compete much more vigorously with nestmates for food than those reared in wrens. However, Gloag et al. (2012) found, under relatively similar conditions, that growth rates of body mass and tarsus length were higher for cowbirds reared in mockingbird than in wren nests. It may be that cowbirds benefit from higher provisioning rate in large hosts, which negates some of the effects of food lost to nestmates (Rivers 2007). In summary, we analyzed maternal allocation of shiny cowbird females in relation to host and sex of the offspring. Our results indicate that growth of shiny cowbird chicks in different hosts has a maternal component (i.e. egg size) and suggest that shiny cowbird females that parasitize large hosts advantage their chicks laying larger eggs than those that parasitize small hosts.

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