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DO LIFE-HISTORY TRAITS IN THE ANCESTOR OF COWBIRDS (*MOLOTHRUS* SPP.) PREDISPOSE THEM TO BECOME BROOD PARASITES?

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Resumen. – **¿Predisponen las características de historia de vida de los ancestros de los *Molothrus* a que éstos se conviertan en parásitos de cría?** – Hamilton & Orians (1965) postularon que el ancestro no parásito de los *Molothrus* habría acelerado el período de incubación y el crecimiento de sus pichones. Más tarde, al comparar los *Molothrus* con aves nidificantes, se sugirió que estas características sumadas al desarrollo de huevos pequeños con cáscara gruesa, serían verdaderas adaptaciones. Cuando estas hipótesis se probaron considerando las características del grupo donde evolucionaron los *Molothrus*: los *Quiscalus* y aliados, se encontró que la cáscara gruesa sería la única adaptación plausible. Más aún, los *Quiscalus* y aliados nidificantes mostraron el mismo patrón que los *Molothrus* (períodos de incubación cortos, pichones de crecimiento acelerado, y huevos pequeños comparados con predicciones de ecuaciones alométricas generales). En este trabajo analizamos si los huevos pequeños con períodos de incubación cortos y los pichones de crecimiento acelerado evolucionaron en el ancestro de los *Quiscalus* y aliados. Para todas las características probadas, reconstruimos las características del ancestro de los *Quiscalus* y aliados, y generamos intervalos de predicción a partir de valores de variables independientes relacionadas alométricamente con dichas características. Excepto para el desarrollo acelerado, utilizamos dos modelos de evolución de caracteres continuos incorporando los grupos externos en tres pasos. Encontramos que ni el período de incubación corto ni el desarrollo acelerado evolucionaron en el ancestro de los *Quiscalus* y aliados. En la mayoría de las reconstrucciones, el ancestro no varió el tamaño del huevo ni el peso de la hembra. Cuando sí lo hizo, aumentó ambas características. Los intervalos de predicción mostraron que dichos aumentos no implicaron un incremento más allá de lo esperado por la relación alométrica entre ambos caracteres. En consecuencia, ni el huevo pequeño, ni el intervalo de incubación corto, ni el desarrollo acelerado de los pichones, serían características que habrían predispuesto a los *Molothrus* a convertirse en parásitos de cría.

Abstract. – Hamilton & Orians (1965) stated that the non-parasitic ancestor of cowbirds accelerated its incubation period and nestling growth. Later, by comparing cowbirds with nesting birds, it was suggested that those characteristics, together with small eggs with thicker eggshell, were adaptations. When these hypotheses were tested considering the characteristics of the group in which cowbirds evolved, i.e. the "grackles and allies", it was found that only the thicker eggshell was a plausible adaptation. Moreover, nesting grackles and allies showed the same reproductive patterns as cowbirds (shorter incubation periods, faster nestling growth, and smaller eggs than those predicted by general allometric equations). In the present study, we tested whether small eggs with short incubation periods and nestlings with accelerated growth evolved in the ancestor of grackles and allies. For all the traits tested, we reconstructed ancestral states and built prediction intervals generated with independent variables that were allometrically related to them. Except for accelerated growth, we applied two evolutionary models incorporating outgroups in three steps. We found that the short incubation period and the faster nestling growth never evolved in the ancestor of grackles and allies. In most ancestor reconstructions, neither egg mass nor female body mass changed. However, when it changed, it increased both egg and female masses. The prediction intervals indicated that those increases did not imply an allometric change in size. Consequently, neither a decrease in egg mass nor an acceleration in nestling development and incubation period are considered characteristics that predisposed cowbirds to become brood parasites. *Accepted 13 October 2011.*

Key words: Cowbirds, *Molothrus*, brood parasites, adaptations, exaptations, egg mass, incubation period, nestling asymptotic body mass, allometric equation, ancestor reconstruction.

INTRODUCTION

Obligate brood parasites lay their eggs in the nests of other species. Their often unwitting hosts perform all parental care of the invasive parasitic offspring. Because brood parasites depend entirely on the host for their reproduction, it follows that they may have modified some of their life-history traits as an adaptation to this reproductive strategy (Payne 1977, Rothstein 1990). In fact, the evolutionary definition of adaptation states that it must be a feature that has been favored by natural selection for its current role (Gould & Vrba 1979 *in* Reeve & Sherman 1993). Conversely, a feature that is advantageous today but evolved earlier for another role is known as exaptation (Gould & Vrba 1979 *in* Reeve & Sherman 1993).

Obligate brood parasitism evolved independently seven times, including three times within the family Cuculidae, and once within each of the following four families or tribes: Indicatoridae, Ploceidae, Icterini, and Anatidae (Lanyon 1992, Aragón *et al.* 1999, Sorenson & Payne 2002). Therefore, it is expected that some characteristics present in the ancestors of brood parasites could have facilitated the evolution of brood parasitism. The five species of parasitic cowbirds (*Molothrus*, Icterini) lack most of the special features found in other brood parasites. Examples of this are that cowbird females do not defend the laying areas, and therefore frequency of multiple parasitism can be high (Dufty 1982, Fleischer & Smith 1992, Fraga 1998, Mermoz & Reboreda 1999), and that cowbird nestlings are not aggressive against host eggs or nestlings, and thus have to compete with them for parental care. Accordingly, among the proposed adaptations within parasitic cowbirds are the hard shell of eggs, which protects them from accidental breakage during incubation and from pecks by hosts or other cowbirds (Spaw & Rowher 1987, Rahn *et al.* 1988, Weatherhead 1991, Mermoz & Ornelas 2004), the high fecundity of females, which would be facilitated in part because they lay relatively small eggs with low energy content (Kattan 1995, Strausberger 1998), and the small and low-energy eggs, which imply comparatively short incubation periods. A short incubation period guarantees early hatching of cowbird nestlings, which, together with a rapid development, allows them to avoid competitive exclusion by host nestlings (Ortega & Cruz 1992, Kattan 1995, 1996; Strausberger 1998). To be considered plausible adaptations, the proposed traits should have evolved at the same time as parasitic behavior. However, if those traits evolved earlier, they would be rather considered as exaptations (Losos & Miles 1994). Parasitic cowbirds form a monophyletic group that evolved within one of the five Icterini clades: the "grackles and allies" (Lanyon & Omland 1999, Johnson & Lanyon 1999). Therefore, to test whether the life-history traits of parasitic cowbirds were adaptations or exaptations, we compared them with those of grackles and allies that exhibit parental care. Our analyses showed that only thicker eggshells could be considered an adaptation to parasitic behavior

(Mermoz & Ornelas 2004, Pujol & Mermoz 2006). However, we also found that grackles and allies with parental care have smaller eggs with shorter incubation periods and nestlings with larger growth rates than those predicted by general allometric equations (Mermoz & Ornelas 2004). The similar lack of adjustment of parasitic cowbirds to expected egg sizes, incubation periods, and growth rates originally led authors to propose most of their brood-parasitic putative adaptations (i.e., Kattan 1995, 1996; Strausberger 1998). Therefore, if this lack of adjustment has biological meaning, it would imply that those characteristics evolved in the ancestor of all grackles and allies. Alternatively, the lack of adjustment may result from using allometric equations developed for distantly-related species (Mermoz & Ornelas 2004). In fact, Hamilton and Orians (1965) proposed that a short incubation period and an accelerated nestling growth in ancestors of cowbirds would improve the parasite's success. If small eggs with shorter incubation periods and nestlings with accelerated growth evolved in the non-parasitic ancestor of grackles and allies, these reproductive traits could have increased the likelihood of evolution of parasitic behavior (Mermoz & Ornelas 2004).

The aim of the present work was to test whether natural selection favored small eggs with shorter incubation periods and nestlings with accelerated growth in the immediate ancestor of grackles and allies. To this end, we first identified the phylogenetic position of grackles and allies within the "New World nine-primaried oscines," and then applied two powerful comparative methods derived from Phylogenetic Independent Contrasts (PIC) to the species present in our working phylogeny with published life-history data. If small eggs with short incubation periods and nestlings with accelerated growth had evolved in the immediate ancestor of grackles and allies, such characteristics could have predisposed some species of this group to become brood parasites.

METHODS

Comparative methods rely on phylogenies and data of extant species to infer ancestral traits and the pattern and processes of character evolution (Martins & Hansen 1996). Although results obtained with comparative methods may be considered rather speculative, they turned out to be accurate when ancestors were known fossils that preserved the traits being analyzed (Polly 2001).

Phylogenetic hypothesis. To test whether parasitic cowbirds' exaptations evolved in grackles and allies, we must consider grackles and allies and the most closely related outgroup. In fact, it has been suggested that it may be useful to include species of close, intermediate, and distant relatedness (Garland & Adolph 1994). Therefore, we considered not only the sister group of grackles and allies but also all "New World nine-primaried oscines." We constructed an informal supertree (Bininda-Emonds 2004). To this end, we first built our tapestry phylogeny by combining the information of Klicka *et al.* (2000) and Yuri & Mindell (2002) (Fig. 1), and then completed it with the phylogenies of Icterini (Omland *et al.* 1999, Johnson & Lanyon 1999, Price & Lanyon 2002, Emberizini (Patten & Fugate 1998), Parulini (Lovette & Bermingham 2002), and Thraupini (Burns 1997, 1998). Nomenclature of South American species followed Remsen *et al.* (2011).

Data collection. We analyzed egg mass, length of the incubation period, nestling growth rate (K), nestling asymptotic body mass (A), and adult female body mass of species present in our working phylogeny. All data were obtained from the bibliography (Appendix 1).

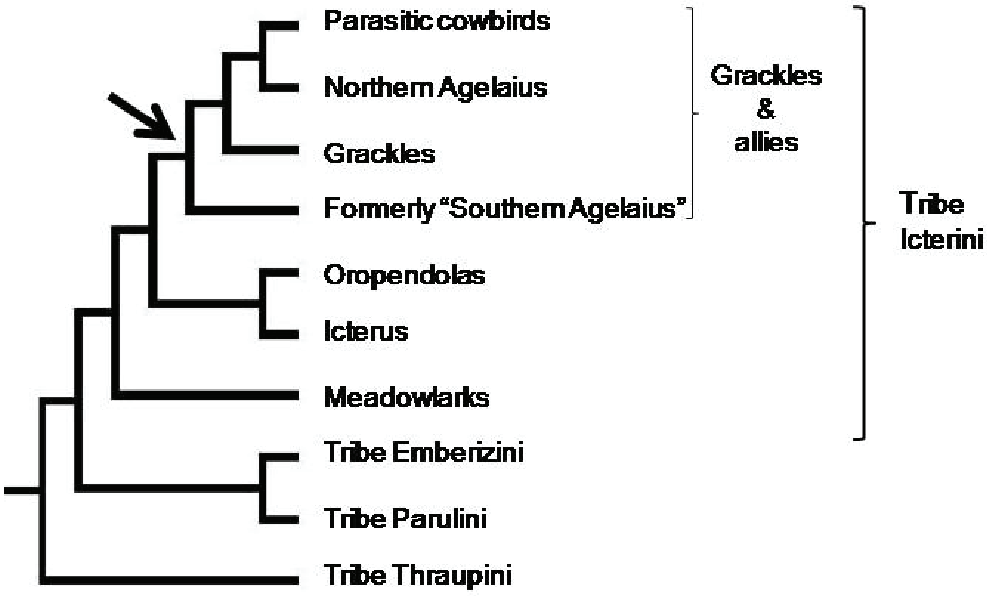

FIG. 1. General scheme of the informal supertree constructed for the analyses. Shown is the relationship of the Icterini, Emberizini, Parulini, and Thraupini within the monophyletic group of the New World nine-primaried oscines. General relationships were based on Klicka *et al.* (2000) and Yuri & Mindell (2002). The arrow indicates the ancestor whose trait values were reconstructed from two sources: grackles and allies or outgroups (see Methods: *"Reconstruction of ancestral states"*).

We applied the logarithmic transformation to all variables before the analyses.

Statistical analyses. We used two comparative methods: an extension of the Phylogenetic Independent Contrasts (PIC, Felsenstein 1985), which allows building an allometric regression line with its prediction intervals for a hypothetical species (Garland & Ives 2000), and a reconstruction of the character states of the ancestor of grackles and allies. For both methodologies we used the program PDTREE under Mesquite (Midford *et al.* 2003, Maddison & Maddison 2009), and considered two evolutionary models for continuous character evolution: Brownian Motion (BM, Felsenstein 1985) and Speciational Brownian (SB, Martins & Garland 1991). Under the BM model, changes in character states occur continuously, whereas under SB the changes occur only after speciation events. As we constructed an informal supertree for the analyses, and thus did not have any starter branch lengths to use with the BM model, we applied Nee algorithm (cited in Purvis *et al.* 1994) to estimate them. All branch lengths under the SB model are equal to one (Martins & Garland 1991).

Regression lines with prediction intervals. Traits were analyzed according to their allometric relationship. Egg mass is a direct allometric function of female body mass ($r^2 = 0.64–0.94$ for different families of Passeriformes, Rahn *et al.* 1975) and incubation period is a direct allometric function of avian egg mass (r^2 = 0.74, Rahn & Ar 1974). Conversely, regarding nestling development, there is an inverse allometric function between nestling average growth rate (K) and adult body mass (r^2 = 0.66, Starck & Ricklefs 1998). For almost all life-history traits, we generated the prediction intervals step by step, by incorporating one or various more distantly-related outgroups of our working phylogeny in each step (Garland & Adolph 1994). In a first step, we used only the Icterini; in a second step, we incorporated the Emberizini and Parulini, and in the last step, we added the Thraupini (Fig. 1). However, since we had very few data for asymptotic nestling body mass (A), we incorporated the whole phylogeny of New World nine-primaried oscines in one step. We generated 95% prediction intervals for the regression line resulting from the values of the standardized contrast. PIC prediction intervals take into account the value of the independent variable and the location of the hypothetical species with its branch length (Garland & Ives 2000). We tested whether the observed values of grackles and allies differ from the hypothetical species generated by the PIC based on other New World nine-primaried oscines. We deleted grackles and allies from the phylogenetic tree to avoid circularities (Garland & Ives 2000). If exaptations evolved in the ancestor of grackles and allies, the observed values of egg mass of grackles and allies would be smaller than those expected by the observed female body mass (Kattan 1995, Strausberger 1998). Similarly, the incubation periods of grackles and allies would be shorter than those expected by the observed egg mass (Briskie & Sealy 1990, Kattan 1996, Strausberger 1998). Finally, either the growth rate of grackles and allies' nestlings would be higher and/or nestling asymptotic body mass would be lower than expected by the observed female body mass (Ortega & Cruz 1992, Kattan 1996).

Reconstruction of ancestral states. PDTREE estimated ancestral states of traits and their confidence intervals using squared-changed parsimony (Maddison 1991). We estimated the ancestral state of the traits of grackles and allies from two sources (Fig. 1). We reconstructed them by using character states not only from grackles and allies but also from the remaining New World nine-primaried oscines (Garland & Ives 2000). Except for the analysis of nestling asymptotic mass, we reconstructed the character state of the ancestor from other New World nine-primaried oscines by incorporating outgroups in three steps (see "regression lines with prediction intervals"). We compared the trait value of the ancestral node obtained from character states of grackles and allies with that obtained from the remaining New Word nine-primaried oscines using a t-test for unequal variances with number of nodes as sample sizes (Schluter *et al.* 1997, Ruxton 2006). If exaptations had evolved in the ancestor of grackles and allies, the ancestor would have smaller eggs with a shorter incubation period when reconstructed from character states of grackles and allies than when reconstructed from other New Word nine-primaried oscines (Briskie & Sealy 1990, Kattan 1995, Strausberger 1998). Similarly, based on the observations of Kattan (1996) and Ortega & Cruz (1992), the ancestor would have nestlings with a faster growth rate and/or a lower asymptotic body mass when reconstructed from grackles and allies than when reconstructed from other New World nine-primaried oscines. Finally, we found no previous prediction for female body mass. However, we also analyzed this trait to compare the results of egg mass analyzed using allometric regression with that analyzed by ancestor reconstruction.

Test of assumptions. We verified the correct standardization of PICs by searching for the lack of association between their absolute values vs. standard deviation (Garland *et al.* 1992). The PICs of nestling asymptotic body mass (A) and growth rate (K) showed a significant regression under the BM model and both evolutionary models, respectively. Therefore, we could not test K but could test A under the speciational model (SB). We conservatively reduced the degree of freedom by one for each polytomy (Purvis & Garland 1993).

RESULTS

Regression lines with prediction intervals. Neither the results obtained under the BM model nor those obtained under the SB model changed when incorporating phylogeny in different steps. All the observed values of grackles and allies' egg masses were within the 95% prediction interval generated by female body mass (Fig. 2A). Likewise, all the observed values of incubation periods of grackles and allies were within the 95% prediction interval generated by egg mass (Fig. 2B). Finally, nestling asymptotic body mass (A) of all grackles and allies was within the 95% prediction intervals generated using the female body mass of other New World nine-primaried oscines (Fig. 2C).

Reconstruction of ancestral states. Under the BM model, results were identical after comparing each step in the ancestor reconstruction from the other New World nine-primaried oscines. Ancestral values of egg mass, incubation period, and female body mass did not differ when reconstructed using character states of grackles and allies from those reconstructed using character states of other New World nine-primaried oscines (Table 1).

Under the SB model, the values of character states of the ancestor reconstructed from grackles and allies did not differ from those reconstructed from the Icterini either in egg mass, length of incubation period, or female body mass (all *t*-tests, ns). Results obtained by reconstruction from the Icterini, Parulini, and Emberizini were indistinguishable from those obtained by reconstruction from all New World nine-primaried oscines. The incubation period of the ancestor reconstructed from other New World nine primaried oscines did not differ from that reconstructed from grackles and allies (Table 1). Likewise, nestling asymptotic body mass reconstructed from grackles and allies was indistinguishable from that reconstructed from other New World nine-primaried oscines (Table 1). However, there were statistical differences among comparisons of egg mass and female body mass (Table 1). Nevertheless, results were in the opposite direction of our predictions. The ancestor reconstructed from grackles and allies had heavier eggs (Fig. 3A) and larger female body mass (Fig. 3B) than when reconstructed from the Icterini, Parulini, and Emberizini or all New-World nine-primaried oscines.

DISCUSSION

Natural selection did not favor an accelerated development in the ancestor of grackles and allies' nestlings by lowering the asymptotic body mass. Results were similar using both methodologies. In addition, with both methodologies and evolutionary models, we found that a short incubation period did not evolve in this ancestor. However, mass results using both methodologies and different evolutionary models sometimes differed, particularly when considering more distantly related outgroups. The reconstruction of the ancestral state of egg mass either did not differ, (Brownian Motion) or increased (speciational model) in grackles and their allies compared to their relatives. If there was a change in egg mass, it occurred in the opposite direction of our predictions. However, considering the allometric relationship between traits, the observed values of egg mass were always within the prediction intervals generated by

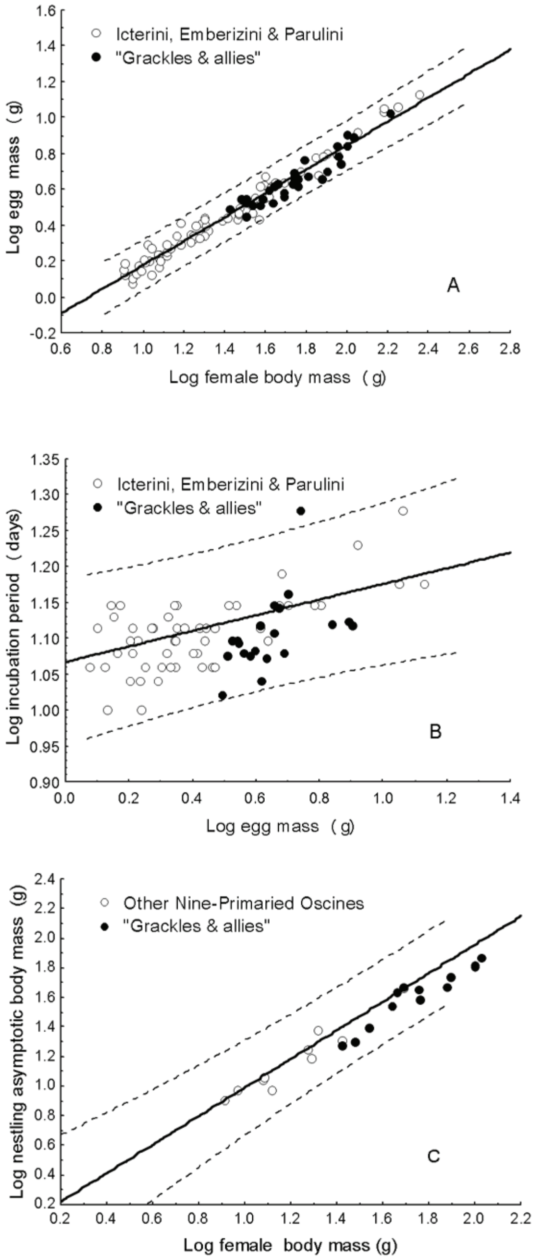

FIG. 2. Regression lines with prediction intervals generated under Speciational Brownian evolutionary model. Dashed lines indicate the 95% prediction intervals for the hypothetical grackles and allies. Black circles indicate the observed values of grackles and allies, white circles indicate observed values of other oscines. A: egg mass as a function of female body mass. B: incubation period as a function of egg mass. C: nestling asymptotic body mass as a function of female body mass.

TABLE 1. Statistical comparison of egg mass, female body mass, and incubation period of the ancestor of grackles and allies reconstructed from grackles and allies with those reconstructed from the outgroup. Tabulated statistics correspond to t-tests for independent samples with unequal variance. [1] Outgroup: Icterini, Emberizini, and Parulini; [2] outgroup: all New World nine-primaried oscines; * not tested due to assumptions not being met.

	Evolutionary model			
	Brownian Motion		Speciational Brownian	
Egg mass (g)[1]	$t_{87} = 1.34$	ns	$t_{70} = 2.03$	$P < 0.05$
Incubation period (days)[1]	$t_{44} = 0.26$	ns	$t_{54} = 0.25$	ns
Nestling asymptotic body mass (g)[2]	–*	–	$t_{19} = 0.32$	ns
Female body mass (g)[1]	$t_{67} = 1.98$	ns	$t_{77} = 2.27$	$P < 0.05$

other New World nine-primaried oscines, taking into account the observed values of female body mass. The direction of change in egg (Fig. 3A) and female body mass (Fig. 3B) was the same under the speciational model. Therefore, this increase did not imply an evolutionary change in the egg mass of grackles and allies relative to adult body mass in respect to other Nine-primaried oscines (Fig. 2A). Hence, with both the Brownian and speciational models, results of ancestor reconstruction were biologically consistent with the corresponding prediction intervals. Consequently, the lack of adjustment of life-history traits of both parasitic and non-parasitic grackles and allies to general allo-metric equations is an artifact of including distantly related species when generating such equations (Mermoz & Ornelas 2004).

Brood parasitism apparently evolved independently seven times within birds (Krüger 2007). Therefore, it would be expected to find characteristics common to some of them that could play a role as adaptations, or that, if evolving in an ancestor, could have favored their independent evolution. A likely candidate is small eggs, an adaptation within parasitic cuckoos (Krüger & Davies 2002, 2004), which might have also facilitated the evolution of brood parasitism in parasitic cowbirds (Mermoz & Ornelas 2004). Another candidate is small females, a potential exaptation within parasitic cuckoos (Krüger *et al.* 2007). However, these characteristics were not adaptations to brood parasitism in cowbirds (Mermoz & Ornelas 2004, Pujol & Mermoz 2006), and our analyses demonstrated that none of them evolved in the immediate ancestor of grackles and allies. This apparent lack of common adaptations or exaptations in brood parasites may change if more groups that evolved parasitism independently are tested by using comparative analyses.

Although we failed to find a trait that may predispose grackles and allies to become brood parasites, it is still possible that these species present other characteristics that favored the evolution of brood parasitism. Since our methodology assumptions were not met, we could not test whether accelerated growth rate (K) of nestlings evolved in the immediate ancestor of grackles and allies (Ortega & Cruz 1992, Kattan 1996). In addition, other traits have been proposed as adaptations to brood parasitism in cowbirds, which, due to the lack of comparative data, have not yet been analyzed. Some of these traits are: larger development of spatial memory (Clayton *et al.* 1997), high fecundity (Scott & Ankney 1983, Kattan 1995), and early and rapid egg laying of parasitic females (Sealy *et*

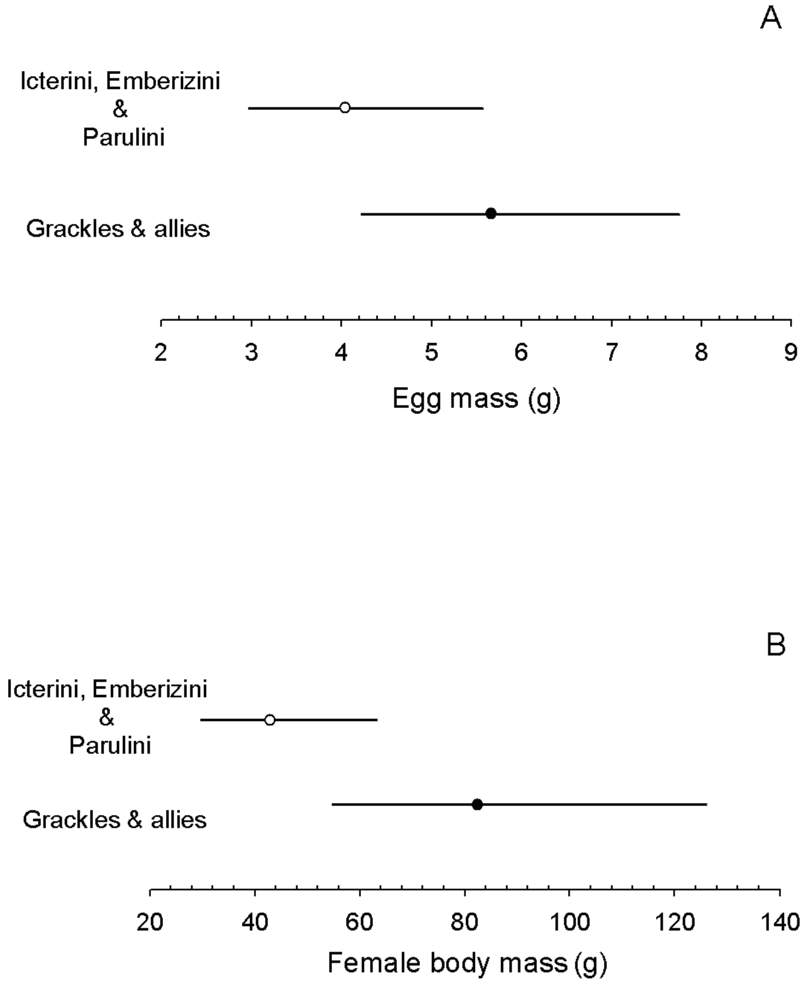

FIG. 3. Reconstructed values under Speciational Brownian evolutionary model for the ancestor of grackles and allies with 95% confidence intervals. Circles are means and lines encompass the confidence interval. A: egg mass (g) and B: female body mass (g).

al. 1995, McMaster *et al.* 2004). Consequently, they are still untested adaptations or exaptations to brood parasitism within parasitic cowbirds.

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APPENDIX 1: Life-history traits of the New World nine-primaried oscines used in the study. FM = adult female body mass (g), IP = incubation period (days), EM = egg mass (g), K = growth rate (days^{-1}), A = nestling asymptotic body mass (g). Grackles and allies data were obtained from a review by Mermoz & Ornelas (2004). For other species, most FM data were obtained from Dunning (1993) and Conway & Martin (2000), whereas EM data were obtained from Schönwetter (1984). For other data, see the reference list below: 1 - Jaramillo & Burke (1999); 2 - Kaufman (1996); 3 - Remes & Martin (2002); 4 - Isler & Isler (1987); 5 - Kilpatrick (2002); 6 - Bacich & Harrison (1997); 7 - Bent (1996–2011); 8 - Ehrlich *et al.* (1988).

APPENDIX 1. Continuation.

	FM (g)	IP (days)	EM (g)	K	A	References
Grackles and allies						
Agelasticus cyanopus	32		3.35		24.7	
Agelaius humeralis	34.4		3.25		19	
Agelaius icterocephalus	26.6	10.5	3.10		30.4	
Agelaius phoeniceus	41.5	12.1	3.95	0.583		
Chrysomus ruficapillus	32		3.50		20	
Agelasticus thilius	30	12.4	3.51	0.6		
Agelaius tricolor	49.2	11.9	3.82			
Xanthopsar flavus	38.4	12.5	3.49		46.7	
Amblyramphus holosericeus	75.5	14	4.53	0.417		
Curaeus curaeus	90		6.88			
Dives dives	90.8		6.09			
Euphagus carolinus	55.2		4.62		44.7	
Euphagus cyanocephalus	57.1	12.8	4.55	0.479		
Gnorimopsar chopi	79.5	14.5	5.02			
Gymnomystax mexicanus	93	19	5.51		34.9	
Agelaiodes badius	43.7	13.1	4.1	0.485		Fraga & Di Giacomo (2004)
Pseudoleistes guirahuro	81.9		4.65		54.5	
Pseudoleistes virescens	78.5	13.9	4.7	0.5		
Quiscalus lugubris	54.8	12	4.9		65.6	
Quiscalus major	100	13.1	8	0.393	73.5	
Quiscalus mexicanus	107	13.3	7.8	0.454		
Quiscalus niger	61.7		5.81		64.1	
Quiscalus quiscula	100	13.2	6.9	0.499		
Oreopsar bolivianus			5.27			Schönwetter (1984)
Lampropsar tanagrinus			3.14			Schönwetter (1984)
Xanthopsar flavus	43	12.5	3.35		38	
Molothrus aeneus	57.4	11	4.15	0.472	35.2	
Molothrus ater	37.6	11.9	3.22	0.508	43.5	
Molothrus bonariensis	45.6	11.8	4.3	0.581	47.1	
Molothrus rufoaxillaris	48.9	12	3.64	0.503		
Molothrus oryzivorus	162		10.59			
Tribe Icterini						
Icterus auratus	32.1		3.35			
Icterus bonana	35					
Icterus cayanensis	39		4.17			
Icterus chrysater	53.6					
Icterus chrysocephalus	41.2					
Icterus cucullatus	24.3	13	2.65			1
Icterus dominicensis	29.6		3.12			
Icterus galbula	34.15*	13	2.95			2
Icterus graducauda	42.2		4.08			
Icterus gularis	59.1	14	5			1
Icterus icterus	72.2	15.5	4.8			1
Icterus laudabilis	35					

APPENDIX 1. Continuation.

	FM (g)	IP (days)	EM (g)	K	A	References
Icterus leucopteryx	39.5		3.56			
Icterus mesomelas	39.9	14	4.7			1
Icterus nigrogularis	40.2		3.63			
Icterus oberi	35					
Icterus parisorum	37.4	14	3.45			1
Icterus pectoralis	44.5		4.35			
Icterus pustulatus	37.7	13	4.1			1
Icterus spurius	19.6	13	2.23			1
Icterus wagleri	42.4		4.1			
Amblycercus holosericeus	56.4		4.61			
Cacicus melanicterus	69.7		5.95			
Cacicus solitarius	80		6.25			
Psarocolius montezuma	225	15	13.5			1
Psarocolius atrovirens	152		10.8			
Psarocolius decumanus	152.1	15	11.2			1
Psarocolius oseryi	99.8					
Psarocolius wagleri	113	17	8.3			1
Psarocolius angustifrons	177	19	11.5			1
Dolichonyx oryzivorus	37.1*	12.5		0.511		1, 3
Sturnella militaris	35.5		3.55			
Sturnella bellicosa		14				1
Sturnella magna	76*	14	6.05			1
Sturnella neglecta	89.4	14.5		0.469		1, 3
Xanthocephalus xanthocephalus	49.15	12.5	4.35	0.49	46.1	1, 3, 5
Tribe Emberizini						
Aimophila botterii	19.9		2.75	0.489		3
Aimophila carpalis	15.3		1.95	0.555		3
Aimophila ruficeps	18.1		2.52			
Aimophila quinquestriata	18.8	12.5				2
Ammodramus bairdii	17.5	11.5	2.21	0.41		8
Ammodramus henslowii	13.1	11	1.96	0.71	9.4	2, 5
Ammodramus savannarum	17	11.5	2.01	0.462		3
Amphispiza belli	19.1	14	2.19	0.492		3
Amphispiza bilineata	13.5	13	1.86			
Junco hyemalis	20.8	11.5	2.13	0.52	17.8	
Junco phaeonotus	20.5	15	2.38	0.457		2, 3
Melospiza georgiana	17	12.5	2.22			6
Melospiza melodia	20.75	13	2.36	0.48	23.8	3, 5, 6
Melospiza lincolnii	17.5	13.5	2.1	0.574		3, 6
Oriturus superciliosus	41.5		3.65			
Passerculus sandwichensis	26	12		0.519		3, 9
Chondestes grammacus	29	11.5	2.69			2
Passerella iliaca	32.3	13				6
Pooecetes gramineus	20.4	12	2.52	0.612		2, 3
Spizella arborea	20	12.5	2.21	0.543		2, 3

APPENDIX 1. Continuation.

	FM (g)	IP (days)	EM (g)	K	A	References
Spizella atrogularis	11.9	13	1.63			2
Spizella pallida	12	12	1.46	0.532		2, 3
Spizella passerina	12.15	12.5	1.6	0.56	11.4	2, 3, 5
Spizella pusilla	11.75	11	1.71	0.656		2, 3
Torreornis inexpectata	26.7					
Xenospiza baileyi	17.4					
Zonotrichia albicollis	26	13	2.77	0.492		3, 6
Zonotrichia atricapilla	29.4	11.5	2.94	0.636		2, 3
Zonotrichia capensis	20		2.7			
Zonotrichia leucophrys	29.4	11.5	2.9	0.564		3, 6
Zonotrichia querula	33.7	14	3.26	0.541		2, 3
Tribe Parulini						
Basileuterus culicivorus	10.5		1.95			
Basileuterus flaveolus	14.5		2.2			
Basileuterus rufifrons	10.9	13	1.88			
Cardellina rubrifrons	9.8	14	1.39			2
Catharopeza bishopi	17.2					
Dendroica petechia	9.3	10	1.35	0.579	9.5	2, 5, 7
Dendroica pinus	11.9	10	1.73			2
Dendroica striata	13	11.5	1.78	0.538		3
Dendroica tigrina	11		1.33			
Ergaticus ruber	8.1		1.53			
Euthlypis lachrymosa	15.2		2.59			
Geothlypis trichas	10	12	1.62	0.537		2, 3
Helmitheros vermivorus	13	12.5	1.69			2
Limnothlypis swainsonii	19	14	2.23			2
Mniotilta varia	10.6	11	1.6			2
Myioborus pictus	8	13.5	1.42	0.557		3, 6
Myioborus miniatus	9.5	14	1.48			
Oporornis formosus	13.85	12.5		0.68		3, 6
Oporornis tolmiei	10.4	12				2
Parula americana	8.8	13	1.26			2
Parula gutturalis	9.5					
Protonotaria citrea	17.4	12	2.08			6
Seiurus aurocapilla	19.4	12	2.59	0.473	15.5	3, 5
Seiurus noveboracensis	18	12.5	2.19			6
Setophaga ruticilla	8.1*	11.5	1.33	0.613		2, 3
Vermivora ruficapilla	8.9	11.5	1.19			2
Wilsonia canadensis	10.2		1.56			
Tribe Thraupini						
Anisognathus flavinuchus			2.7			
Calochaetes coccineus	46.3					
Chlorochrysa calliparaea	17					
Chlorornis riefferii	53		6.5			
Chlorothraupis carmioli	39		3.72			

APPENDIX 1. Continuation.

	FM (g)	IP (days)	EM (g)	K	A	References
Chrysothlypis chrysomelas	13					
Cissopis leveriana	76	12.5	5.66			4
Cnemoscopus rubrirostris			3.5			
Conothraupis speculigera	25					
Creurgops dentata	19					
Cyanerpes caeruleus	12	12.5	1.3			8
Cypsnagra hirundinacea	29					
Dacnis cayana	13	13	1.6			4
Diglossa lafresnayii	16					
Eucometis penicillata	27	15	3.58			4
Habia rubica	31	13.5	4			4
Hemispingus atropileus	22					
Hemithraupis flavicollis	13					
Lamprospiza melanoleuca	34					
Lanio versicolor	17					
Mitrospingus cassinii	40.4		4.01			
Nemosia pileata	16		1.95			
Nephelornis oneilli	14.9					
Nesospingus speculiferus			4.65			
Phaenicophilus palmarum	27.2	10				4
Piranga bidentata	34.7		3.82			
Piranga flava	38	13	3.85			8
Piranga leucoptera			3.24			
Piranga ludoviciana	28.1	13	3.37			2
Piranga olivacea	28.5	13	3.31	0.431		2, 3
Piranga rubriceps	29			0.704		3
Piranga rubra	28.2	11.5	3.5			2
Piranga roseogularis	24					
Pyrrhocoma ruficeps	15					
Ramphocelus bresilius	32.9	13	3.75			4
Ramphocelus carbo	28	12	3.3			4
Ramphocelus nigrogularis	31		2.6			
Ramphocelus passerinii	32	12.5	3.6			4
Ramphocelus sanguinolentus	41		3			
Schistochlamys melanopis	33		2.95			
Sericossypha albocristata	114					
Spindalis zena	21.1		3.34			
Tachyphonus surinamus	19		3.6			
Tangara gyrola	21	13.5	1.78			4
Tersina viridis	29	15	2.92			4
Thraupis bonariensis	36		3.9			