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ECOLOGICAL CORRELATES AND SEX DIFFERENCES IN EARLY DEVELOPMENT OF A GENERALIST BROOD PARASITE

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ABSTRACT.—Parents influence the phenotype of their offspring by determining the environment in which early development occurs. The many factors that affect growth in avian brood parasites provide an excellent context in which to examine how ecological variables and sex differences influence plasticity of early development. We used a model-selection approach to determine the most important variable(s) for explaining patterns in growth rate of the Brown-headed Cowbird (*Molothrus ater*). Using published growth-rate estimates across various host species, we found that the age-adjusted size of Brown-headed Cowbird chicks increases with increasing hatching synchrony between host and parasite chicks. We also quantified Brown-headed Cowbird growth rates in nests of Song Sparrows (*Melospiza melodia*) and Yellow Warblers (*Dendroica petechia*), two common host species at Mono Lake, California, to examine the role of variation in hatching synchrony in broods within host species. Statistical models to explain variation in Brown-headed Cowbird chicks' growth rates were constructed from ecological variables (host species, brood size, multiple parasitism, hatching synchrony between parasite and host chicks) and chick sex. The best model included only sex and there was a 99% chance that this was the best model, given the data set and models compared. Male Brown-headed Cowbird gained an average of 0.7 g day^{-1} more than females and weighed 13% more at the same age. The only significant ecological variable, host–parasite hatching synchrony, was found to be sex-dependent, with males more likely than females to hatch earlier than their nest mates. We discuss the possible mechanisms underlying this sex effect and the importance of determining sex when studying nestling growth and competition. *Received 9 December 2006, accepted 9 May 2007.*

Key words: brood parasitism, Brown-headed Cowbird, development, hatching asynchrony, *Molothrus ater*, nestling growth, sexual size-dimorphism.

Correlatos Ecológicos y Diferencias de Sexo en el Desarrollo Temprano de un Parásito de Nidada Generalista

RESUMEN.—Los padres influencian el fenotipo de sus crías al determinar el ambiente en donde ocurre el desarrollo temprano de sus crías. Los múltiples factores que afectan el crecimiento de los parásitos de nidadas de aves brindan un contexto excelente para examinar como las variables ecológicas y las diferencias de sexo influencian la plasticidad del desarrollo temprano. Empleamos un enfoque de selección de modelo para determinar la o las variable/s más importante/s que explican los patrones en la tasa de crecimiento de *Molothrus ater*. Usando estimados de las tasas de crecimiento publicados para varias especies hospederas, encontramos que el tamaño ajustado por edad de los pichones de *M. ater* aumenta con una mayor sincronía de eclosión entre los pichones hospederos y parásitos. También cuantificamos las tasas de crecimiento de *M. ater* en nidos de *Melospiza melodía* y *Dendroica petechia*, dos especies hospederas comunes en el Lago Mono, California, para examinar el papel de la variación de la sincronía de eclosión en las nidadas de especies hospederas. Los modelos estadísticos para explicar la variación en las tasas de crecimiento de los pichones de *M. ater* fueron construidos a partir de variables ecológicas (especie hospedera, tamaño de la nidada, parasitismo múltiple, sincronía de eclosión entre pichones parásitos y hospederos) y del sexo del pichón. El mejor modelo incluyó sólo el sexo y hubo una probabilidad del 99% de que éste fuera el mejor modelo, dados los datos y los modelos comparados. Los machos de *M. ater* engordaron un promedio de 0.7 g día^{-1} más que las hembras y pesaron un 13% más a la misma edad. La única variable ecológica significativa, la sincronía en eclosión entre hospedero y parásito, fue sexo-dependiente, presentando los machos una mayor probabilidad que las hembras de eclosionar más temprano que sus compañeros de nido. Analizamos los posibles mecanismos que causan este efecto del sexo y la importancia de determinar el sexo cuando se estudia el crecimiento y la competencia entre los pichones.

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IN MOST SPECIES, parents have a critical influence on the ontogeny of their offspring in choosing the latter's early environment. In birds, for instance, nest site, clutch size, predator defense, or variation in maternally deposited egg constituents (e.g., macronutrients, hormones, and other metabolites) are adjusted by parents to maximize the survival and competitive ability of their young (Deeming 2002). Nestlings of brood-parasitic birds typically develop under a more diverse set of social and ecological conditions than those of nonparasitic species, because they are raised in nests of hosts with varying parental ability (Soler et al. 1995, Davies et al. 2003) and, in the case of generalists, among multiple host species (Hauber 2003b, Rivers 2007). Although studies of nonparasitic altricial birds have found that growth is generally limited by intraspecific variation in quality and delivery of food (Starck and Ricklefs 1998), studies of nestling growth in brood parasites have focused on a variety of potential factors that vary interspecifically among host species (Kleven et al. 1999, Burhans et al. 2000, Mermoz and Fernandez 2003, Grim 2006). These variables include host body size (Kilpatrick 2002), competition with other parasite chicks in the nest (Trine 2000), and the number and size of host nestlings (Hatch 1983, Mermoz and Reboreda 2003, Kilner et al. 2004, Hauber and Moskát 2008). In addition, age differences and changes in brood composition caused by hatching asynchronously with the eggs of the host could potentially influence development and fledging success of parasite chicks (Lorenzana and Sealy 1999, Hauber 2003a). The influence of physiological differences associated with sex on brood-parasite growth rates has received mixed support (Weatherhead 1989, Kilner et al. 2004 vs. Scott and Lemon 1996, K. Ellison and S. G. Sealy unpubl. data). Although brood parasites may exhibit unusual plasticity in their growth as an adaptation for brood parasitism (Kleven et al. 1999, Kilpatrick 2002, Kilner et al. 2004), the extensive variation in the early environment under which brood-parasitic young develop provides an excellent system in which to examine factors contributing to the plasticity and consequences of nestling growth.

Hatching (a)synchrony between brood-parasite and host young (hereafter "hatching synchrony") (Kattan 1995, Hauber 2003a) has received relatively little attention in the empirical literature in relation to parasite growth and survival (Kilner 2003). Parasite eggs can be laid at different stages during host laying and incubation, resulting in age differences between host and parasitic young. In addition, adaptations resulting in shorter incubation periods of brood-parasite eggs promote early hatching and, thus, age discrepancies between parasite and host; theoretically, this results in a competitive advantage for the parasite in acquiring resources (Kattan 1995, Davies 2000, Sealy et al. 2002). Although a negative relationship between growth and hatching order is seen in nonparasitic species (e.g., Albrect 2000, Badyaev et al. 2002), to our knowledge such a relationship is yet to be demonstrated for a brood parasite. There are two possible effects that hatching synchrony can have on offspring growth. Hauber (2003a) found that early hatching by a single Brown-headed Cowbird (*Molothrus ater*) chick resulted in decreased hatching and fledging success of host young. As a result, and given the positive relationship found by Kilner et al. (2004) between growth of Brown-headed Cowbirds and presence of host young, it is possible that early hatching could indirectly result in diminished growth for the parasite because of reduction in brood size. Alternatively, early hatching by Brown-headed Cowbird chicks could optimize the competitive advantage that older chicks have over nest mates (Kilner et al. 2004) owing to size (Dearborn et al. 1998, Lichtenstein and Sealy 1998), which enables them to grow faster than in more synchronously hatched nests. We used published data to assess the directionality of covariation in the relationship between synchrony and growth rate in the Brown-headed Cowbird.

Brood parasites in the genus *Molothrus* are strongly sexually dimorphic, males being larger than females (Weatherhead 1989, Hauber et al. 1999). Growth rate is often sex-dependent in sexually size-dimorphic avian taxa (Bortolotti 1986, Anderson et al. 1993; however, see Vedder et al. 2005 for lack of a relationship). Despite prominent dimorphism of juvenile (Hill 1976, Farmer and Holmgren 2000, Ellison 2004, K. Ellison and S. G. Sealy unpubl. data) and adult Brown-headed Cowbirds (Lowther 1993), Kilner et al. (2004) did not find statistically significant sex differences in growth rate (though males grew faster; $n = 18$ total), and Weatherhead (1989) found not only that male and female Brown-headed Cowbirds grew at similar rates, but that they also had similar weights when measured at the same age ($n = 39$ total). By contrast, sex differences in the weight of age-matched chicks have been reported for both Brown-headed Cowbirds (Scott and Lemon 1996, K. Ellison and S. G. Sealy unpubl. data) and Bronzed Cowbirds (*M. aeneus*; K. Ellison and S. G. Sealy unpubl. data). We set out to examine the covariation of sex differences in parasite growth rate and hatching synchrony between parasites and hosts.

Given the multitude of factors that could influence the growth, fledging success, and, ultimately, the fitness of a developing generalist brood parasite, it is necessary to take a holistic approach to determine which early factors have the greatest influence on development. We used an information-criterion model-selection approach to determine the best fitting and most parsimonious model, from the factors discussed above, for explaining the variation in growth of Brown-headed Cowbirds (hereafter "cowbirds") in the nests of two different-sized hosts. We tested the hypothesis that cowbird growth was positively associated with the number of nest mates, absence of other cowbirds, and hatching synchrony. After discovering some interdependencies between factors, we performed a *post-hoc* analysis to explore the relationship between cowbird sex and hatching synchrony.

METHODS

Growth Rate Comparison across Host Species

To test the hypothesis that cowbird growth rate and size increase with increasing hatching synchrony between cowbirds and different host species, we compiled logistic growth constants (K days^{-1}) and mean size (mass at 8 days old) values for cowbird chicks in a variety of host species from Kilpatrick (2002), and incubation times for each host from Hauber (2003a), Kilner (2003), and others (see Appendix for full list of sources). We calculated the difference between mean cowbird incubation time (10.5 days; Hauber 2003a) and host incubation time as a rough estimate of cowbird–host hatching synchrony. If a range was given for host incubation time, the midpoint value was used.

We used nonlinear regression to compare synchrony with growth rate and size because we found, in both cases, that a

quadratic line provided the best fit. To normalize residuals, we square-root transformed both growth rate and size. Data for host species-level comparisons are plotted below; independent contrast scores, following Hauber (2003b), were used to check that statistical relationships remained consistent when accounting for phylogenetic relatedness of hosts (data not shown). We included host body size as a potential confounding variable in preliminary models but did not include it in the final analysis because it showed no significant contribution to explaining variation in the data ($F = 0.041$, df = 1 and 15, $P = 0.842$).

Field Study

Study site.—We conducted this portion of the study in riparian corridors of three natural tributaries and one anthropogenic watercourse that flow into Mono Lake (38°1′N, 119°3′W): Lee Vining, Mill, Rush, and Wilson creeks, respectively, located on the east slope of the Sierra Nevada, Mono County, California. Study plots on these streams were 29.5, 15, 39, and 15 ha, respectively, and encompassed 2–3 km of each stream.

Field procedures.—During the 2005 breeding season, Song Sparrow (*Melospiza melodia*) and Yellow Warbler (*Dendroica petechia*) nests were located and monitored on the study plots using standard methods (Martin and Geupel 1993, Ralph et al. 1993). Each nest was revisited every one to four days to determine outcome and contents. Nests were visited every one or two days starting four days before the predicted hatch date to ensure accurate determination of hatching sequence. We ascertained hatching synchrony through either observed hatching sequence or observed age differences between the first-hatched parasite and host chicks, determined by morphological features of the nestlings (e.g., feather emergence, eye development, size) (Baicich and Harrison 1997). The features used for aging were corroborated by extensive observations of known-age nestlings from the study site (S. Heath and C. Tonra pers. obs., PRBO Conservation Science unpubl. data). We considered a cowbird "synchronous" if it hatched on the same day as the first host nestling, "early" if it hatched one or more days before the host, and "late" if it hatched one or more days after the host. Our analysis included parasitized nests in which at least one cowbird and one host hatched. In all but two nests included in the sample, host young survived to fledging.

We weighed cowbird nestlings to the nearest 0.1 g using an electronic balance on day two and day six, where hatching day was day zero. We recorded the time at which the nestling was weighed on day two and the time difference between then and when the nestling was weighed on day six to calculate a growth rate (g h^{-1}). This period is within the linear phase of growth for cowbirds and, therefore, two weight measurements are sufficient to determine growth rate (Dearborn et al. 1998, Burhans et al. 2000). On day six, in nests with multiple cowbird young, we marked nestlings on the tarsus with colored string to identify each individual.

Nestling sexing.—To determine the sex of nestling cowbirds, we collected blood from all nestlings after they were weighed on day six. A sample of 15–50 μL of blood was collected via puncture of the brachial vein and transferred to a lysis buffer. To determine sex, standard molecular sexing techniques (Griffiths et al. 1998) were used in a commercial facility (Alan Wilson Centre for Molecular Evolution, Massey University, Albany, New Zealand), with known-sex adult cowbirds from the study site and Lance-tailed Manakins (*Chiroxiphia lanceolata*; DuVal 2005) used as controls (C. Tonra and M. Hauber unpubl. data).

2004 data.—We included data from the 2004 breeding season in *post-hoc* analyses. Nests were monitored in the same fashion as those in 2005, with the exception of synchrony estimation. We determined synchrony-group membership for each cowbird nestling after completion of the field season using field notes that described age differences between cowbird and host young. Field technicians always recorded observations of differences in age and development; however, they did not visit the nest more often around hatching (as was done in 2005), because, synchrony determination was not yet an objective of the study. As a result, it is possible that the 2004 estimates of synchrony are less precise than those from 2005. We did not measure cowbird growth in 2004; however, we determined sex as in 2005.

Statistical analysis.—We used generalized linear models (GLM) with the dependent variable g h^{-1} in an information-theoretic model-selection approach (Burnham and Anderson 2002) to determine the best model for explaining variation in growth rate. To verify that the data satisfied the assumptions for GLM, we used omnibus normality of residuals and modified Levene equal-variance tests. We generated 47 *a-priori* models using plausible additive and multiplicative combinations of the variables: cowbird sex, host species, host clutch size, number of nest mates (1, 2, or $\geq$3), presence–absence of another cowbird egg, presence–absence of another cowbird nestling, and synchrony (early, synchronous, or late) and included plot as a potential confounding variable. We executed models using the PROC MIXED command with no random effect variable in SAS, version 9.1 (SAS Institute, Cary , North Carolina) and ranked them by Akaike's Information Criterion corrected for sample size (AIC_c) and corrected Akaike weights (w_i). Running PROC MIXED without a random effect treats the model as a standard GLM but has the advantage of reporting a −2 log likelihood from which AIC_c can be calculated.

The results of the growth-rate analysis led us to further examine the relationship between cowbird sex and synchrony. We used logistic regression to determine whether synchrony is statistically associated with the sex of cowbird chicks. When coding the variable synchrony, we used "synchronous" as the reference value and included hatch date as a potential covariate. To determine goodness of fit, we generated a receiver operator characteristic (ROC) curve and calculated the area under the curve (AUC; Zweig and Campbell 1993, Fielding and Bell 1997). We used SPSS, version 11.5 (SPSS, Chicago, Illinois) for this analysis.

When modeling sex and synchrony for both 2004 and 2005 combined, we discovered an interaction between year and the predictive power of synchrony. As a result, we performed this analysis separately for 2004 and 2005. We included eight additional nestlings from 2005 that lacked growth rate measurements in the regression for that year.

RESULTS

Growth Rate Comparison across Host Species

Cowbird chicks were heaviest at eight days of age following hatching ($r^2 = 0.566$, $P = 0.001$, $n = 19$; Fig. 1A and Appendix)

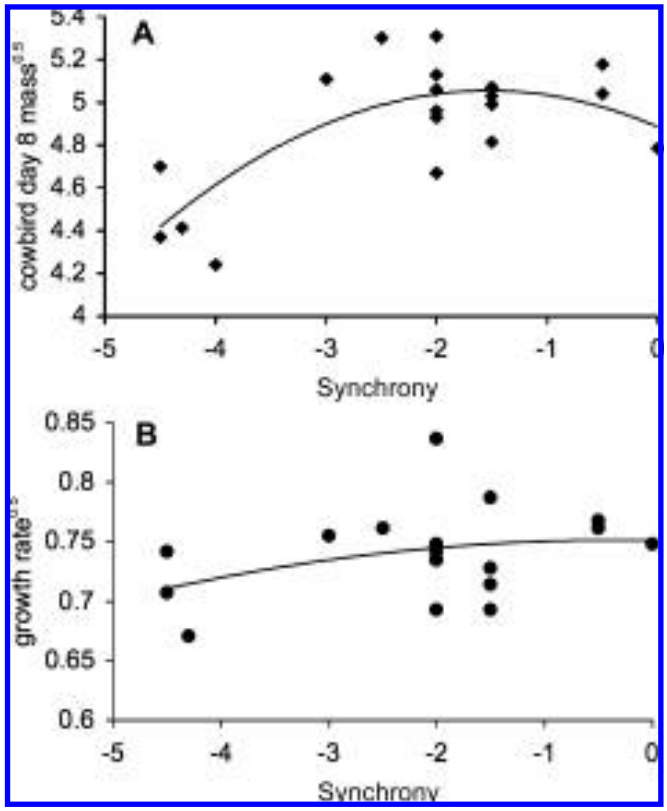

FIG. 1. Variation in (A) cowbird mass on day eight (g) and (B) logistic growth constant (K with units of days^{-1}) (values for each were square-root transformed to normalize residuals) in relation to cowbird hatch synchrony between host species. See Appendix for data sources.

when reared by hosts with mean incubation times one to two days shorter than the mean cowbird incubation time. By contrast, cowbird growth rates were not significantly related to hatching synchrony between parasite and host young, across species ($r^2 = 0.129$, $P = 0.355$, $n = 18$; Fig. 1B, Appendix).

Field Study

We included 33 nestlings from 2005 in the analysis of nestling growth (15 from Song Sparrow nests; 18 from Yellow Warbler). The proportion of females was 0.60 and 0.50 in Song Sparrow and Yellow Warbler nests, respectively, which did not differ statistically from parity (binomial test: Song Sparrow $P = 0.607$, Yellow Warbler $P = 1$) or between host taxa ($\chi^2 = 0.33$, df = 1, $P = 0.56$, $n = 33$). The best GLM to explain variation in growth rate included only the variable sex (Table 1). Based on the corrected Akaike weights, there was a 99% chance that this was the best model given the data used and the models compared. This model was 99× better than the next best model and explained 53% of the variation in growth rate. Male cowbird nestlings gained an average of 0.7 g day^{-1} more than females (males: mean growth rate (± SE) = 0.17 ± 0.003 g h^{-1}; females: mean growth rate = 0.14 ± 0.003 g h^{-1}; $F = 35.06$, df = 1 and 31, $P < 0.001$). There was no change to the relationship after adding nestlings excluded from the model selection analysis because of host hatching failure ($F = 51.47$, df = 1 and 37, $P < 0.001$). Male cowbirds were also significantly heavier than females on day six ($t = 3.96$, df = 31, $P < 0.001$).

TABLE 1. Model-selection results for generalized linear models explaining the variation in cowbird growth rate (g h^{-1}) in Mono County, California, in 2005; the top 10 models are presented.

Model[a]	k	AIC_c	ΔAIC_c	w_i
Sex	2	−170.20	0.00	0.994
Cowbirdegg + sex	3	−159.07	11.13	0.004
Sex + host	3	−158.97	11.23	0.004
Sex + sync	3	−157.27	12.93	0.002
Sync	2	−154.70	15.50	0.000
Sex + host + sex*host	4	−150.27	19.93	0.000
Cowbirdyng	2	−150.20	20.00	0.000
Cowbirdegg	2	−150.20	20.00	0.000
Host	2	−150.10	20.10	0.000
Cowbirdegg + sex + cowbirdegg*sex	4	−149.87	20.33	0.000

[a]Models are ranked by descending corrected Akaike weights (w_i); k is the number of parameters, AIC_c is Akaike's Information Criterion corrected for sample size, and ΔAIC_c is the change in AIC_c from the best model. Cowbirdegg = presence–absence of another cowbird egg, cowbirdyng = p/a of another cowbird nestling, host = Song Sparrow vs. Yellow Warbler, sync = early vs. synchronous vs. late. Additive models are indicated by +, and multiplicative models by *.

The only one of the top five models that did not include sex included only the variable synchrony, which was a highly significant predictor of growth rate when alone ($F = 7.42$, df = 2 and 30, $P = 0.002$) but not when included in a model with sex ($F = 0.766$, df = 5 and 27, $P = 0.475$). Males grew faster than females within all synchrony categories; however, the difference was significant only for early ($t = 4.67$, df = 9, $P = 0.001$) and synchronous nests ($t = 2.32$, df = 15, $P = 0.03$). By contrast, there was no significant difference in growth rate between synchrony groups within either sex (female: $F = 0.01$, df = 2 and 15, $P = 0.99$, male: $F = 2.57$, df = 2 and 12, $P = 0.475$). No other variables had significant coefficients for explaining the variation in growth rate.

Sex dependence.—The logistic-regression model of sex (2005 data set) that included synchrony and hatch date as predictor variables was a 25% improvement over chance (AUC = 0.75). Synchrony was the only significant variable, and it was significant only for the difference between early and synchronous nests (Table 2A). Early-hatching cowbirds were significantly more likely to be male, whereas synchronously hatching cowbirds were more likely to be female (Fig. 2A).

In 2004, the proportion of females was 0.47 and 0.63 in Song Sparrow ($n = 17$) and Yellow Warbler ($n = 19$) nests, respectively, which did not differ statistically from parity (binomial test: Song Sparrow $P = 1$, Yellow Warbler $P = 0.35$) or between host taxa ($\chi^2 = 0.94$, df = 1, $P = 0.33$, $n = 36$). Neither variable in the 2004 logistic-regression model was significant, though hatch date was nearly significant ($P = 0.059$), with males tending to hatch earlier in the season than females (Table 2B). The overall model was only a slight improvement over chance (AUC = 0.66; Table 2B). The relationship between sex and synchrony did not follow the pattern observed in 2005 (Fig. 2B).

TABLE 2. Estimates of parameter coefficients (β) and 95% confidence intervals (CI) for logistic-regression models predicting cowbird sex in (A) 2005 and (B) 2004 in Mono County, California.

Variable	β	SE	Wald χ^2	df	P	95% CI
(A) 2005						
Constant	−5.705	5.020	1.292	1	0.256	−15.544 to 4.133
Synchrony (overall)			10.132	2	0.006	
Synchrony = early	−3.076	0.980	9.852	1	0.002	−4.996 to −1.155
Synchrony = late	−1.559	0.956	2.659	1	0.103	−3.433 to 0.315
Hatch date	0.038	0.028	1.812	1	0.178	−0.017 to 0.094
(B) 2004						
Constant	−11.280	6.030	3.499	1	0.061	−23.099 to 0.539
Synchrony (overall)			0.441	2	0.802	
Synchrony = early	0.433	1.149	0.142	1	0.706	−1.819 to 2.685
Synchrony = late	0.546	0.903	0.366	1	0.545	−1.223 to 2.315
Hatch date	0.064	0.034	3.561	1	0.059	−0.002 to 0.130

Note: Synchrony was a categorical variable, with "early" representing cowbird nestlings that hatched one or more days before host young, "late" representing those that hatched one or more days after, and "synchronous" representing those that hatched on the same day. The latter was used as the reference value.

DISCUSSION

The comparative analysis showed that the extent of hatching synchrony between brood-parasitic Brown-headed Cowbirds and their hosts covaries with the growth rate and mass of the parasite nestlings in broods of the different host species. By contrast, our field observations demonstrated that sex of the parasite nestling alone was the most important variable that contributed to measurable variation in cowbird growth rates. Sex of the nestling as a covariate of cowbird growth outperformed all ecological variables that we quantified and included in the model-selection protocol. Male cowbirds grew faster than females, independent of any environmental factor measured. Furthermore, the only ecological variable that had a significant correlation with growth rate was hatching synchrony, and this relationship was dependent on sex. Therefore, we found no support for the hypothesized effects of number of nest mates, presence of other cowbirds, or hatching synchrony on cowbird growth. Our results highlight the importance of determining sex when examining early development and nestling competition in sexually size-dimorphic species (Kasumovic et al. 2002). Thus, although we demonstrated in our growth-rate comparison that synchrony is correlated with at least the size of cowbird nestlings across host species, we cannot rule out the possibility that this correlation is a result of cowbird sex not being controlled in the source studies.

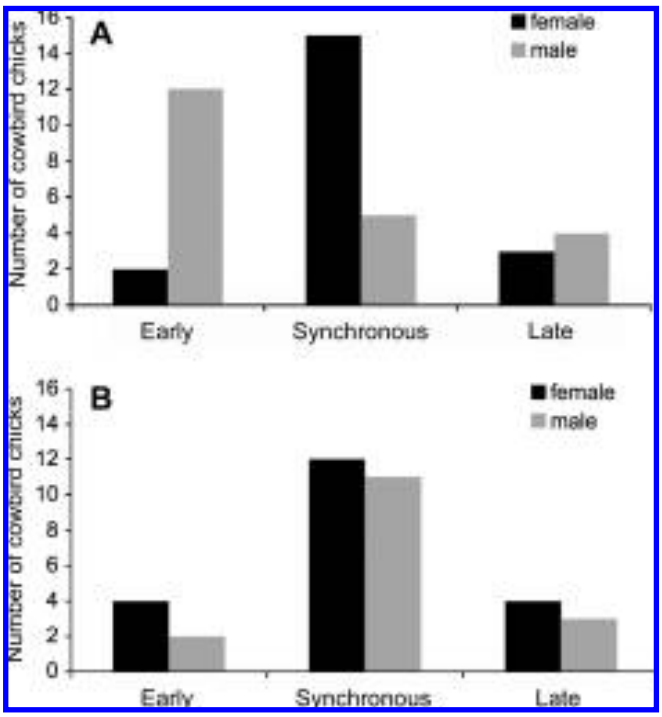

FIG. 2. Number of male and female cowbirds in each hatching synchrony category in (A) 2005 and (B) 2004 in Mono County, California.

We found that males were, on average, 13% heavier than females of the same age. Our findings support patterns of sex dimorphism in cowbird chicks (Scott and Lemon 1996, K. Ellison and S. G. Sealy unpubl. data) and are in contrast to those of other studies that did not document a significant difference in growth between the sexes in this species (Weatherhead 1989, Kilner et al. 2004). Kilner et al. (2004) found that male cowbirds grew faster than females in Eastern Phoebe (*Sayornis phoebe*) nests, but not significantly so. However, the lack of a detectable difference could have been because of small sample sizes or because the study was experimental and designed to minimize the effects of sex on growth and, thus, may not be comparable to the observations of naturally parasitized nests presented here. Similarly, Weatherhead (1989) found no sex difference in either growth rate or the mass of male vs. female nestlings of the same age. It is possible that unmeasured ecological factors may affect the relationship between sex and growth, such that under certain conditions there is no observable difference. For instance, Zanette et al. (2005) found that the size of a female Song Sparrow chick was significantly reduced when she shared the nest with both a cowbird chick and a male Song Sparrow chick, presumably because she could not sufficiently compete with both to obtain adequate resources. It is unlikely that

the sex composition of host broods was biased in our data set as compared with the other data sets, because we found no sex-ratio bias of parasite chicks from parity in either host species' nests, and Kilner et al. (2004) used equal numbers of male and female chicks in their study. It is possible, therefore, that female cowbird chicks have reduced competitive ability when sharing the nest with larger host chicks (i.e., males), which is perhaps associated with sex differences in the intensity and efficiency of begging displays of cowbird young (Hauber and Ramsey 2003).

Consistent with Kasumovic et al. (2002), we found no evidence of a sex-ratio bias of cowbird chicks between or within host species. We found evidence of a bias in sex ratio among synchrony categories of chicks in 2005, males being more likely to hatch before host chicks and females more likely to hatch on the same day as host chicks. These relationships were not observed in 2004, and although this could indicate that the 2005 relationship is anomalous, we believe that this discordance was instead attributable to the methodological differences, and resulting decrease in precision, in estimating hatching synchrony in 2004. For example, synchrony estimation was not yet an objective of the study in 2004 and, therefore, field biologists may have been less discerning in their estimation of age differences. Nests were visited every four days around hatching in 2004 (as opposed to every one or two days in 2005); therefore, in many cases, synchrony estimates were made when the chicks were up to four days old. By day four, developmental differences could have resulted from differential food-acquisition abilities rather than hatching order (Lichtenstein and Sealy 1998, Zanette et al. 2005). However, the nearly significant relationship between hatch date and sex in 2004, with males hatching earlier in the season, could indicate that male eggs were laid earlier in the host laying cycle (i.e., in an oviposition sequence that would promote asynchronous hatching).

There are three main possibile explanations for why male cowbirds hatch earlier than females: (1) male embryos may develop faster than female embryos, owing to a sex bias in egg provisioning (e.g., Blanco et al. 2003); (2) differences in profitability of the sexes may lead to different selective pressures on hatching order between the sexes (e.g., Trivers and Willard 1973, Albrect 2000, Badyaev et al. 2002); and (3) there may be a sex bias in the timing of laying by female cowbirds. Although we do not know which mechanism is more likely to apply to cowbirds, the present study is the first to imply a sex bias in timing of laying in a brood-parasitic species. If male cowbirds have an advantage when hatching early in host nests, there may be selection for females to time male eggs such that they hatch before host young. It is unclear how female cowbirds could ensure that male eggs hatch early, given that (unlike nonparasitic species) they do not lay all the eggs in the same nest and do not control initiation of incubation. A sex bias in either manipulation of size and energy content of eggs (Kattan 1995) or synchronization of parasitism with host laying via a female cowbird's observations of adult hosts (Woolfenden et al. 2004, Fiorini and Reboreda 2006) are possible mechanisms. Ultimately, however, because of the correlative nature of the data in the present study and the lack of primary sex-ratio determination (only tertiary sex ratio at six days of age), the relationship between hatching synchrony and sex could be attributable to differential costs of competing with synchronously hatched host young for male versus female cowbirds (because of significant growth differences between sexes).

Interestingly, the lack of a relationship between number of nest mates and cowbird growth in the field study contrasts with the negative relationship found in Dickcissel (*Spiza americana*) hosts (Hatch 1983) and the positive relationship found in Eastern Phoebe (Kilner et al. 2004). In a comparative survey, Kilner (2003) also demonstrated that cowbird chicks survive best when in nests of intermediate-sized hosts with one or two nest mates. These contrasting results suggest a complex relationship between host species and brood size in terms of cowbird development, such as an interactive effect between host size or host clutch size and number of nest mates.

Along with other recent studies (Badyaev et al. 2002, Zanette et al. 2005), our results demonstrate the importance of determining sex-specific patterns of growth before drawing conclusions about ecological relationships when examining aspects of nestling competition and development. These studies have encompassed species with varying magnitudes of sexual dimorphism. Had sex not been measured in the present study, our results would have lent support to our hypothesis, erroneously leading us to conclude that hatching synchrony was the best variable explaining growth rate.

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Literature Cited

Albrecht, D. J. 2000. Sex ratio manipulation within broods of House Wrens, *Troglodytes aedon*. Animal Behaviour 59:1227–1234.

Anderson, D. J., J. Reeve, J. E. Martinez Gomez, W. W. Weathers, S. Hutson, H. V. Cunningham, and D. M. Bird. 1993. Sexual size dimorphism and food requirements of nestling birds. Canadian Journal of Zoology 71:2541–2545.

Badyaev, A. V., G. E. Hill, M. L. Beck, A. A. Dervan, R. A. Duckworth, K. J. McGraw, P. M. Nolan, and L. A. Whittingham. 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. Science 295:316–318.

Baicich P. J., and C. J. O. Harrison. 1997. A Guide to the Nests, Eggs, and Nestlings of North American Birds, 2nd ed. Academic Press, New York.

Bemis, C., and J. D. Rising. 1999. Western Wood-Pewee (*Contopus sordidulus*). *In* The Birds of North America, no. 451 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Bevier, L. R., A. F. Poole, and W. Moskoff. 2004. Veery (*Catharus fuscescens*). *In* The Birds of North America Online (A. Poole and F. Gill, Eds.). Cornell Laboratory of Ornithology, Ithaca, New York. Available at bna.birds.cornell.edu/BNA/account/Veery/.

Blanco, G., J. Martínez-Padilla, J. A. Dávila, D. Serrano, and J. Viñuela. 2003. First evidence of sex differences in the duration of avian embryonic period: Consequences for sibling competition in sexually dimorphic birds. Behavioral Ecology 14:702–706.

Bortolotti, G. R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. American Naturalist 127:495–507.

Burhans, D. E., F. R. Thompson III, and J. Faaborg. 2000. Costs of parasitism incurred by two songbird species and their quality as cowbird hosts. Condor 102:364–373.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

Davies, N. B. 2000. Cuckoos, Cowbirds and Other Cheats. T & A D Poyser, London.

Davies, N. B., S. H. M. Butchart, T. A. Burke, N. Chaline, and I. R. K. Stewart. 2003. Reed Warblers guard against cuckoos and cuckoldry. Animal Behaviour 65:285–295.

Dearborn, D. C., A. D. Anders, F. R. Thompson III, and J. Faaborg. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100:326–334.

Deeming, D. C., Ed. 2002. Avian Incubation: Behaviour, Environment, and Evolution. Oxford University Press, Oxford, United Kingdom.

DuVal, E. H. 2005. Age-based plumage changes in the Lance-tailed Manakin: A two-year delay in plumage maturation. Condor 107:915–920.

Ellison, K. 2004. Host use by sympatric cowbirds (*Molothrus aeneus* and *M. ater*). Ph.D. dissertation, University of Manitoba, Winnipeg.

Farmer, C., and M. A. Holmgren. 2000. Sexual dichromatism in the plumage of juvenile Brown-headed Cowbirds. Journal of Field Ornithology 71:429–436.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Fiorini, V. D., and J. C. Reboreda. 2006. Cues used by Shiny Cowbirds (*Molothrus bonariensis*) to locate and parasitise Chalk-browed Mockingbird (*Mimus saturninus*) nests. Behavioral Ecology and Sociobiology 60:379–385.

Greene, E., V. R. Muehter, and W. Davidson. 1996. Lazuli Bunting (*Passerina amoena*). *In* The Birds of North America, no. 232 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Grim, T. 2006. Cuckoo growth performance in parasitized and unused hosts: Not only host size matters. Behavioral Ecology and Sociobiology 60:716–723.

Hatch, S. A. 1983. Nestling growth relationships of Brown-headed Cowbirds and Dickcissels. Wilson Bulletin 95:669–671.

Hauber, M. E. 2003a. Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. Behavioral Ecology 14:227–235.

Hauber, M. E. 2003b. Lower begging responsiveness of host versus parasitic Brown-headed Cowbird (*Molothrus ater*) nestlings is related to species identity but not to early social experience. Journal of Comparative Psychology 117:24–30.

Hauber, M. E., N. S. Clayton, A. Kacelnik, J. C. Reboreda, and T. J. DeVoogd. 1999. Sexual dimorphism and species differences in HVC volumes of cowbirds. Behavioral Neuroscience 113:1095–1099.

Hauber, M. E., and C. K. Ramsey. 2003. Honesty in host–parasite communication signals: The case for begging by fledgling Brown-headed Cowbirds *Molothrus ater*. Journal of Avian Biology 34:339–344.

Hauber, M. E., and C. Moskát. 2008. Shared parental care is costly for nestlings of Common Cuckoos and their Great Reed Warbler hosts. Behavioral Ecology 19:79–86.

Herkert, J. R., P. D. Vickery, and D. E. Kroodsma. 2002. Henslow's Sparrow (*Ammodramus henslowii*). *In* The Birds of North America, no. 672 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Hill, R. A. 1976. Sex ratio determination of immature Brown-headed Cowbirds. Bird-Banding 47:112–114.

Kasumovic, M. M., H. L. Gibbs, B. E. Woolfenden, S. G. Sealy, and H. Nakamura. 2002. Primary sex-ratio variation in two brood parasitic birds: Brown-headed Cowbird (*Molothrus ater*) and Common Cuckoo (*Cuculus canorus*). Auk 119:561–566.

Kattan G. H. 1995. Mechanisms of short incubation period in brood-parasitic cowbirds. Auk 112:335–342.

Kilner R. M. 2003. How selfish is a cowbird nestling? Animal Behaviour 66:569–576.

Kilner, R. M., J. R. Madden, and M. E. Hauber. 2004. Brood parasitic cowbird nestlings use host young to procure resources. Science 305:877–879.

Kilpatrick, A. M. 2002. Variation in growth of Brown-headed Cowbird (*Molothrus ater*) nestlings and energetic impacts on their host parents. Canadian Journal of Zoology 80:145–153.

Kleven, O., A. Moksnes, E. Røskaft, and M. Honza. 1999. Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. Behavioral Ecology and Sociobiology 47:41–46.

Lichtenstein, G., and S. G. Sealy. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic Brown-headed Cowbird chicks in Yellow Warbler nests. Proceedings of the Royal Society of London, Series B 265:249–254.

Lorenzana, J. C., and S. G. Sealy. 1999. A meta-analysis of the impact of parasitism by the Brown-headed Cowbird

on its hosts. Pages 241–253 *in* Research and Management of the Brown-headed Cowbird in Western Landscapes (M. L. Morrison, L. S. Hall, S. K. Robinson, S. I. Rothstein, D. C. Hahn, and T. D. Rich, Eds.). Studies in Avian Biology, no. 18.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* The Birds of North America, no. 47 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: Methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

Mermoz, M. E., and G. J. Fernández. 2003. Breeding success of a specialist brood parasite, the Screaming Cowbird, parasitizing an alternative host. Condor 105:63–72.

Mermoz, M. E., and J. C. Reboreda. 2003. Reproductive success of Shiny Cowbird (*Molothrus bonariensis*) parasitizing the larger Brown-and-yellow Marshbird (*Pseudoleistes virescens*) in Argentina. Auk 120:1128–1139.

Peer, B. D., and E. K. Bollinger. 1997. Common Grackle (*Quiscalus quiscula*). *In* The Birds of North America, no. 271 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993 . Handbook of Field Methods for Monitoring Landbirds. U.S. Department of Agriculture, Forest Service, General Technical Report PSW-GTR 144.

Rivers, J. W. 2007. Nest mate size, but not short-term need, influences begging behavior of a generalist brood parasite. Behavioral Ecology 18:222–230.

Robertson, R. J., B. J. Stutchbury, and R. R. Cohen. 1992. Tree Swallow (*Tachycineta bicolor*). *In* The Birds of North America, no. 11 (A. Poole, P. Stettenheim, and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Scott, D. M., and R. E. Lemon. 1996. Differential reproductive success of Brown-headed Cowbirds with Northern Cardinals and three other hosts. Condor 98:259–271.

Sealy, S. G., D. G. McMaster, and B. D. Peer. 2002. Tactics of obligate brood parasites to secure adequate incubators. Pages 254–269 *in* Avian Incubation: Behaviour, Environment, and Evolution (D. C. Deeming, Ed.). Oxford University Press, Oxford, United Kingdom.

Soler, J. J., M. Soler, A. P. Møller, and J. G. Martínez. 1995. Does Great Spotted Cuckoo choose Magpie hosts according to their parenting ability? Behavioral Ecology and Sociobiology 36:201–206.

Starck, J. M., and R. E. Ricklefs, Eds. 1998. Avian Growth and Development: Evolution within the Altricial–Precocial Spectrum. Oxford University Press, New York.

Trine, C. L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting success. Pages 135–144 *in* Ecology and Management of Cowbirds and Their Hosts: Studies in the Conservation of North American Passerine Birds (J. N. M. Smith, T. L. Cook, S. I. Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Twedt, D. J., and R. D. Crawford. 1995. Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). *In* The Birds of North America, no. 192 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Vedder, O., A. L. Dekker, G. H. Visser, and C. Dijkstra. 2005. Sex-specific energy requirements in nestlings of an extremely sexually size dimorphic bird, the European Sparrowhawk (*Accipiter nisus*). Behavioral Ecology and Sociobiology 58:429–436.

Weatherhead, P. J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358–366.

Woolfenden, B. E., H. L. Gibbs, C. M. McLaren, and S. G. Sealy. 2004. Community-level patterns of parasitism: Use of three common hosts by a brood parasitic bird, the Brown-headed Cowbird. Écoscience 11:238–248.

Zanette, L., E. MacDougall-Shakleton, M. Clinchy, and J. N. M. Smith. 2005. Brown-headed Cowbirds skew host offspring sex ratios. Ecology 86:815–820.

Zweig, M. H., and G. Campbell. 1993. Receiver operating characteristic (ROC) plots: A fundamental evaluation tool in clinical medicine. Clinical Medicine 39:561–577.

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APPENDIX. Data used for regression analysis examining the relationship between synchrony and cowbird growth.

Host species	Host incubation period (days)	Synchrony	K (days^{-1})	Mass on day 8 (g)	n
Western Wood-Pewee (*Contopus sordidulus*)[a]	14.8	−4.3	0.45	19.5	5
Tree Swallow (*Tachycineta bicolor*)[b]	14.5	−4	—	18	2
Veery (*Catharus fuscescens*)[c]	12	−1.5	0.62	25.3	2
Blue-gray Gnatcatcher (*Polioptila caerulea*)	15	−4.5	0.5	19.1	10
Plumbeous Vireo (*Vireo plumbeus*)	15	−4.5	0.55	22.1	43
Red-eyed Vireo (*V. olivaceus*)	12.5	−2	0.54	28.2	4
Yellow Warbler (*Dendroica petechia*)	11	−0.5	0.59	25.4	12
Ovenbird (*Seiurus aurocapilla*)	12.5	−2	0.7	26.3	3
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)[d]	12.5	−2	0.48	21.8	11
Red-winged Blackbird (*Agelaius phoeniceus*)	11	−0.5	0.58	26.8	23
Common Grackle (*Quiscalus quiscula*)[e]	13.5	−3	0.57	26.1	15
Northern Cardinal (*Cardinalis cardinalis*)	12	−1.5	0.48	25.7	3
Indigo Bunting (*Passerina cyanea*)	12.5	−2	0.56	24.6	15
Lazuli Bunting (*P. amoena*)[f]	12	−1.5	0.53	23.2	8
Dickcissel (*Spiza americana*)	12	−1.5	0.51	24.9	15
Henslow's Sparrow (*Ammodramus henslowii*)[g]	10.5	0	0.56	22.9	2
Dark-eyed Junco (*Junco hyemalis*)	12.5	−2	0.55	24.3	13
Chipping Sparrow (*Spizella passerina*)	12.5	−2	0.54	25.6	2
Song Sparrow (*Melospiza melodia*)	13	−2.5	0.58	28.1	4

Note: All growth measurements were taken from Kilpatrick (2002). Synchrony was calculated as the difference between mean cowbird incubation time (10.5 days; Hauber 2003b) and mean host incubation time. K (days^{-1}) is the logistic growth constant, and n is the number of cowbird nestlings measured. All host incubation times are from Hauber (2003a) and Kilner (2003), except for species names that are followed by superscript letters.

[a]Bemis and Rising 1999. This host did not fledge cowbird young.

[b]Robertson et al. 1992.

[c]Bevier et al. 2004.

[d]Twedt and Crawford 1995.

[e]Peer and Bolinger 1997.

[f]Greene et al. 1996.

[g]Herkert et al. 2002.