

Developmental asynchrony and host species identity predict variability in nestling growth of an obligate brood parasite: a test of the “growth-tuning” hypothesis

S.K. Winnicki, B.M. Strausberger, N.D. Antonson, D.E. Burhans, J. Lock, A.M. Kilpatrick, and M.E. Hauber

Abstract: Generalist obligate brood parasites are excellent models for studies of developmental plasticity, as they experience a range of social and environmental variation when raised by one of their many hosts. Parasitic Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)) exhibit host-specific growth rates, yet Cowbird growth rates are not predicted by hosts' incubation or brooding periods. We tested the novel “growth-tuning” hypothesis which predicts that total asynchrony between Cowbirds' and hosts' nesting periods results in faster parasitic growth in nests where host young fledge earlier than Cowbirds. We tested this prediction using previously published and newly added nestling mass data across diverse host species. Total nesting period asynchrony (summed across incubation and brooding stages) predicted Cowbird growth; 8-day-old Cowbirds were heavier in host nests with relatively shorter nesting periods. We further explored the drivers of variation in growth using mass measurements of Cowbirds in Song Sparrow (*Melospiza melodia* (A. Wilson, 1810)) and Red-winged Blackbird (*Agelaius phoeniceus* (Linnaeus, 1766)) nests. Our top models included host species (Cowbirds grew faster in Sparrow nests), numbers of nestmates (slowest when raised alone), and sex (males grew faster). These results confirm that multiple social and environmental factors predict directional patterns of developmental plasticity in avian generalist brood parasites.

Key words: brood parasitism, growth, offspring, development, Brown-headed Cowbird, *Molothrus ater*, Red-winged Blackbird, *Agelaius phoeniceus*, Song Sparrow, *Melospiza melodia*.

Résumé : Les parasites de nids obligatoires généralistes constituent d'excellents modèles pour l'étude de la plasticité développementale, puisqu'ils présentent un éventail de variations sociales et environnementales quand ils sont élevés par une de leurs nombreuses espèces hôtes. Si les vachers à tête brune (*Molothrus ater* (Boddaert, 1783)), une espèce parasite, présentent des taux de croissance dépendant de l'hôte, la durée des périodes d'incubation ou de soin des oisillons des hôtes ne prédit toutefois pas ces taux. Nous avons testé l'hypothèse de la « modulation de la croissance », qui prédit qu'une asynchronie totale entre les périodes de nidification des vachers et de leurs hôtes se traduit par une croissance plus rapide des parasites dans les nids où les jeunes des hôtes s'envolent plus tôt que les vachers. Nous avons mis cette prédiction à l'épreuve en utilisant des données nouvelles et déjà publiées sur la masse d'oiseaux niais de différentes espèces hôtes. L'asynchronie totale des périodes de nidification (sommées des périodes d'incubation et de soin des oisillons) prédit la croissance des vachers; les vachers de 8 jours sont plus lourds dans les nids d'hôtes caractérisés par des périodes de nidification relativement plus courtes. Nous avons en outre exploré les facteurs de variation de la croissance en utilisant des mesures de la masse de vachers dans des nids de bruants chanteurs (*Melospiza melodia* (A. Wilson, 1810)) et de carouges à épaulettes (*Agelaius phoeniceus* (Linnaeus, 1766)). Nos meilleurs modèles incluent l'espèce hôte (les vachers croissent plus vite dans les nids de bruants), le nombre d'oisillons dans le nid (les oisillons solitaires croissent le plus lentement) et le sexe (les mâles croissent plus rapidement). Ces résultats confirment que de multiples facteurs sociaux et environnementaux expliquent les variations de la plasticité développementale chez les oiseaux parasites de nids généralistes. [Traduit par la Rédaction]

Mots-clés : parasitisme de nids, croissance, progéniture, développement, vacher à tête brune, *Molothrus ater*, carouge à épaulettes, *Agelaius phoeniceus*, bruant chanteur, *Melospiza melodia*.

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S.K. Winnicki and M.E. Hauber. Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, 515 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA; Program in Ecology, Evolution, and Conservation, University of Illinois at Urbana-Champaign, 278 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA.

B.M. Strausberger. Pritzker Laboratory for Molecular Systematics and Evolution, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605, USA.

N.D. Antonson. Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, 515 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA.

D.E. Burhans. Division of Biological Sciences, University of Missouri, 110 Tucker Hall, Columbia, MO 65211, USA.

J. Lock. School of Biological Sciences, University of Auckland, 7 Symonds Street, Auckland 1010, New Zealand.

A.M. Kilpatrick. Department of Ecology and Evolutionary Biology, University of California at Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA.

Corresponding author: S.K. Winnicki (email: sarahkw2@illinois.edu).

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Introduction

Animals develop and grow at different rates (McCarty 2001; Dmitriew 2011), with often critical impacts on survival and fitness (Mousseau and Fox 1998). These developmental differences can be caused by inputs from inherited (West-Eberhard 1989; McCarty 2001) and (or) environmental variations (Hoffmann and Merilä 1999). Assessing the interactive roles of genetic and environmental effects in wild populations can be challenging (Schew and Ricklefs 1998; Snell-Rood 2012). Birds are excellent models to measure and compare developmental variation, as they develop outside the maternal body and vary as much as 40-fold in post-hatch growth rates (Gil et al. 2008; Chaby 2016).

Altricial nestlings, which require extended parental provisions and develop in a focal nest, often compete with their siblings for food. Nestling competition can, therefore, be a powerful social driver of variation in growth rates (Kilner and Johnstone 1997; Wright and Leonard 2002). In turn, nestling growth can be strongly related to fitness, as dependent young that receive less food have slower growth rates (Soma 2006), are less likely to fledge (Schwagmeyer and Mock 2008), and are recruited into breeding populations at lower rates compared with nestlings with heavier fledging mass (Both et al. 1999; Schwagmeyer and Mock 2008). Moreover, competition can be exacerbated by asynchrony in the timing of hatching, favoring earlier hatched and larger chicks within each nest (Magrath 1989; Royle et al. 1999; Hauber 2003a). Hatching asynchrony and the size and number of competing nestlings can, therefore, impact the growth rates of individual altricial birds (Hauber 2003a; Tonra et al. 2008).

Whereas hatching asynchrony can impact competition, it may not be the only social and environmental driver of growth and development variation. Altricial nestlings also rely on their parents for food after they leave the nest (Clutton-Brock 1991; Jones and Ward 2020); thus, leaving the nest at the same time as their siblings may be crucial for nestlings that need continued access to parental provisioning. Accordingly, nestlings should minimize the asynchrony in the time that they take to leave the nest relative to the rest of the brood: this can be approximated by the total duration between laying and fledging (i.e., summing incubation and nestling stages), or the total “nesting period”.

Intraspecific variation in growth and development is often constrained by the similar nest microhabitats and social milieu shared by conspecifics (Starck et al. 1995). This is not the case for generalist obligate brood parasitic birds, which lay their eggs in the nests of diverse host species and are, therefore, exposed to diverse early growth and social milieu in a variety of host nests (Kleven et al. 1999; Kilpatrick 2002; Kilner 2003; Kilner et al. 2004; Remeš 2006). Generalist brood parasites are, therefore, an excellent system with which to assess social and environmental impacts on nestling growth specifically, and developmental plasticity in general.

Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783); hereafter Cowbirds), an obligate generalist brood parasite native to North America, parasitize hundreds of host species and, subsequently, experience extreme social and environmental variation during development (Lowther 2020). Cowbird nestling growth is known to vary with brood size; Cowbirds may grow faster in smaller broods (Hatch 1983; Kilner 2003; but see Remeš 2010) and may receive most parental provisions in medium-sized broods (Kilner et al. 2004). Cowbirds often parasitize nests multiple times (Lowther 2020); they then typically act as a more competitive nestmate than their hosts and could, therefore, negatively impact the growth of each other (Hauber 2003b; Rivers and Peer 2016; but see Rivers et al. 2013). Cowbird nestling growth rates are also known to vary with the identity of the host species (Kilpatrick 2002; Remeš 2010). Cowbird chicks can successfully outcompete and eliminate some or all of the offspring of smaller hosts (Dearborn and Lichtenstein 2002; Hauber 2003a; Kilner 2003)

but may also benefit from being raised by large enough hosts for sufficient provisioning; subsequently, Cowbird chick growth and survival are most favored in hosts of intermediate sizes (Lorenzana and Sealy 2001; Kilner 2003; Kilner et al. 2004; but see Kilpatrick 2002). However, size is not the only way host species biology varies; mean incubation and brooding length of hosts can also vary both from each other and from that of the average Cowbird.

Brood parasites may need to match their developmental times to the hosts' to ensure that they are cared for; parasitic Common Cuckoos (*Cuculus canorus* Linnaeus, 1758) fledge later than their hosts, so must “tune” their development, including incubation and begging displays, to procure parental care well after the regular developmental period of their hosts' dependent young (Davies 2011). In turn, Brown-headed Cowbirds parasitize hundreds of species, experiencing a wide range of host development times to which they would need to tune their growth. For example, the average Field Sparrow (*Spizella pusilla* (A. Wilson, 1810)) hosts hatch at the same time as Cowbirds but fledge ~2.5 days before the average Cowbird, yielding a +2.5 day total nesting period difference (Carey et al. 2020). Host parents may not continue to feed parasites in the nest after the host offspring have fledged, resulting in starvation of the Cowbird young (S.K. Winnicki, personal observation), so Cowbirds should tune their growth to fledge at the same time or earlier than hosts. At the other extreme, in the nests of Eastern Phoebes (*Sayornis phoebe* (Latham, 1790)), this parasite hatches ~5 days before the hosts and fledges ~6 days before the other chicks, causing a -11 day total nesting period difference between Cowbird and Phoebe chicks (Hauber 2003a). Rapid growth is therefore not necessary and could even be detrimental (Mangel and Stamps 2001; Royle et al. 2005). Cowbirds could achieve effective “tuning” by matching their incubation time to that of the hosts, but while Cowbirds can experience hatching asynchrony relative to host nestlings, this has little impact on Cowbird growth rate across hosts (Remeš 2010; but see Tonra et al. 2008). In turn, Cowbirds could match their brooding (nestling) period to hosts', but host brooding period is only weakly negatively correlated with the parasite's logistic growth rate across hosts (Kilpatrick 2002). To reconcile these conflicting results, we test the possibility that Cowbirds might actually tune their entire developmental period to match that of the host.

We hypothesize that Cowbirds tune their entire developmental period to the developmental period of the host offspring, growing more rapidly across both the embryonic and the nestling stages when the host nesting period is shorter relative to the average Cowbirds'. As there are no published embryonic growth data for Cowbird in diverse host species' nests, we evaluated this novel “growth-tuning” hypothesis as the summation of the total nesting period (incubation and brooding), predicting that the relative differences in Cowbirds' and their hosts' total nesting periods positively correlate with parasitic growth across different host species (Fig. 1). We assessed this prediction with previously published (Kilpatrick 2002) Cowbird growth and mass data and by adding data from four additional host species and three additional populations that span the full range of natural variation in host nesting period. Critically, however, our comparative and brood manipulation approaches did not address whether Cowbirds engage in compensatory or catch-up growth during their nestling period (as defined by Hector and Nakagawa 2012).

To further explore the ways in which environmental variation can impact Cowbird growth, we also monitored parasitic young in experimentally manipulated broods of two common native host species, Red-winged Blackbird (*Agelaius phoeniceus* (Linnaeus, 1766)) and Song Sparrow (*Melospiza melodia* (A. Wilson, 1810)), in northern Illinois, USA. We predicted that Cowbird growth rate would be impacted by (i) host species identity and by (ii) sibling

Fig. 1. The “growth-tuning” hypothesis based on relative nesting period difference. When the brood parasite’s mean total nesting period (incubation and brooding stages combined) is longer than the total nesting period of host 1, we predict that Brown-headed Cowbirds (*Molothrus ater*) grow faster to avoid being left behind at fledging. When the parasite’s nesting period is shorter than host 2, we predict that Cowbirds grow slower than Cowbirds in nests of host 2.

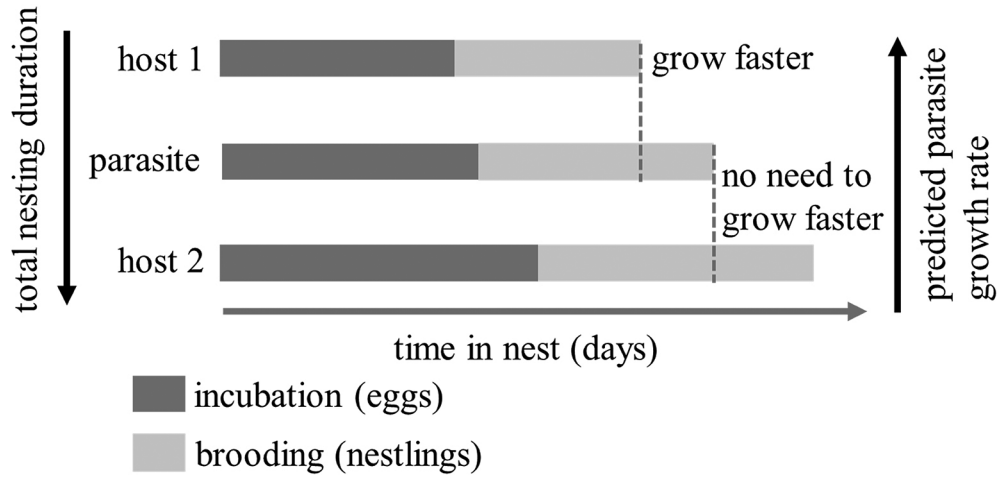
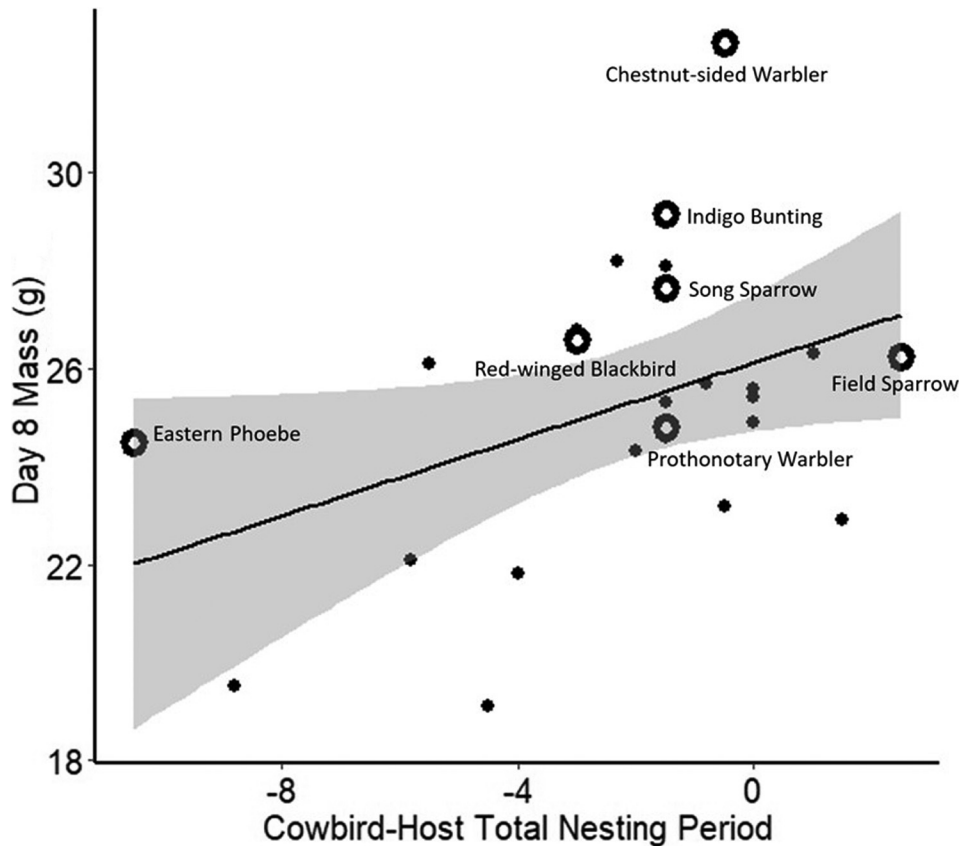


Fig. 2. The difference between Brown-headed Cowbird (*Molothrus ater*) and host species’ mean total nesting period positively predicts the day 8 mass (g) of Cowbird nestlings. Lower difference values indicate hosts whose eggs and nestlings spend more time in the nest than the mean Cowbird egg and nestling. Solid black circles indicate data from Kilpatrick (2002), whereas open circles indicate new data points. Labels indicate the identity of the host species. The relationship is significant with $(t_{[20]} = 2.084, P = 0.050)$ and without $(t_{[16]} = 2.335, P = 0.033)$ the addition of the new data. The solid line is the mean of the slope and the shaded area is its 95% confidence interval.



competition, with slower growth with more nestmates and slower growth when those nestmates are highly competitive Cowbirds. Finally, Cowbirds are sexually dimorphic in size (adult males are larger than adult females; Lowther 2020) and

growth during their nestling and fledgling periods may or may not vary with nestling sex (e.g., no: Weatherhead 1989; yes: Hauber and Ramsey 2003; Tonra et al. 2008), so we also included sex in our analyses of parasitic nestling growth.

Materials and methods

Cross-species data set

We compiled host-specific Cowbird mass data on day 8 post hatch from Kilpatrick (2002); as day 8 mass covaries positively with the K metric of growth rate ($\rho = 0.534$, $P = 0.023$) in that data set. We also sourced and added day 8 mass for Cowbirds growing in the nests of an additional four host species: Eastern Phoebes (Kilner et al. 2004); Chestnut-sided Warblers (*Setophaga pensylvanica* (Linnaeus, 1766); Friedmann 1929); Field Sparrows (Burhans et al. 2000); and Prothonotary Warblers (*Protonotaria citrea* (Boddaert, 1783); N.D. Antonson, unpublished data). These species expanded the data set so that it now spans the full range of host-specific environmental variation that Cowbirds may experience; Eastern Phoebes' mean nesting period is 11 days longer than Cowbirds' mean nesting period, whereas Field Sparrows' mean nesting period is 2.5 days shorter (Hauber 2003a; Carey et al. 2020).

We also included Cowbird day 8 masses from our own field collection in Song Sparrow and Red-winged Blackbird nests (see Field methods below) and from a published source of Indigo Bunting (*Passerina cyanea* (Linnaeus, 1766); Burhans et al. 2000) nests. Because these three species were already included in the Kilpatrick (2002) data set, we included species identity as a random effect in our models (see Statistical methods below). For the Field Sparrow and Indigo Bunting nests, Cowbird growth data were available only up to day 5 and 7, respectively (Burhans et al. 2000); therefore, we estimated day 8 masses by calculating a daily growth rate between days 3 and 5 and then projecting it by assuming a linear growth between days 4 and 8 for these Cowbird chicks (e.g., Lowther 2020).

We obtained mean host species' nesting period duration data (incubation period plus latency from hatching to fledging) from the Birds of the World species accounts. We subtracted the nesting period duration of host species from the mean total nesting period of Cowbirds (Lowther 2020) to calculate a metric of total nesting period asynchrony between Cowbirds and hosts. Interspecific analyses, even if they are sourced for the same parasite but from diverse host species, should include phylogenetic corrections for data sets with $N = 25$ to generate sufficient statistical power (stimulated $\beta > 0.8$) (Blomberg et al. 2003), which we did not meet ($N = 22$ host species). Therefore, we treated each host species' Cowbird growth data point independently.

Host species for fieldwork

Song Sparrows and Red-winged Blackbirds are two common and sympatric Cowbird host species capable of raising their own young alongside the parasitic Cowbird nestlings (Hauber 2003a). Brown-headed Cowbird adults (female 32–38 g, male 40–49 g; Lowther 2020) are larger than Song Sparrows (adult mass 24–28 g; Arcese et al. 2020) and smaller than Red-winged Blackbirds (female 43 g, male 60–70 g; Yasukawa and Searcy 2020). Sparrows have a shorter nesting (incubation plus brooding) period duration (mean 23 days) relative to Blackbirds (mean 24.5 days), but both are longer in duration than the mean nesting period duration of Cowbirds (mean 21.5 days; Lowther 2020). We studied the dynamics of nestling Cowbird growth in the nests of Song Sparrows ($N = 28$) and the Red-winged Blackbirds ($N = 14$) during the first 9 days post hatching.

Field data collection

From 2001 through 2008, we conducted brood manipulation experiments at host nests located at The Morton Arboretum in northeastern Illinois, USA. We placed Cowbirds randomly between nests to reflect natural rates of multiple parasitism and to separate the impacts of nestling competition from any potential impacts of host-specific maternal programming. The research protocols here were approved by the Illinois Department of Natural Resources (NH15.5892) and followed guidelines of the Animal Behavior Society for the ethical treatment of animals in research and the

Table 1. Models of Brown-headed Cowbird (*Molothrus ater*) mass gain over time in the nests of Red-winged Blackbirds (*Agelaius phoeniceus*) and Song Sparrows (*Melospiza melodia*), ranked by AIC_c values.

	df	logLik	AIC_c	ΔAIC_c	Weight
Day + TotalNG + Host + Sex	8	-21.256	59.9	0	0.271
Day + Host + Sex	7	-22.535	60.2	0.23	0.241
Day + Host	6	-24.501	61.8	1.88	0.106
Day + TotalNG	6	-24.544	61.9	1.97	0.101
Day + PropBHCO + Host + Sex	8	-22.411	62.2	2.31	0.085
Day + Sex	6	-25.077	63	3.03	0.059
Day \times Sex	7	-24.265	63.6	3.69	0.043
Day \times TotalNG	7	-24.358	63.8	3.88	0.039
Day \times Host	7	-24.366	63.8	3.89	0.039
Day	5	-27.924	66.4	6.49	0.011
Day + PropBHCO	6	-27.9	68.6	8.68	0.004
Day \times PropBHCO	7	-27.894	70.9	10.95	0.001

Note: df, degrees of freedom; logLik, log likelihood; AIC_c , Akaike's information criterion values adjusted for small sample size; ΔAIC_c , difference in AIC_c values from the top model; weight, model weight; TotalNG, total number of nestlings in the brood (Cowbird and host); PropBHCO, proportion of Cowbirds in the nest relative to host nestlings. Shaded models have $\Delta AIC_c < 2.0$.

guidelines and principles of the Canadian Council on Animal Care (CCAC). Within 16 h of the nestlings' hatching, we manipulated broods by placing one or two just-hatched Cowbirds and one or two host nestlings of equal age into previously monitored Red-winged Blackbird and Song Sparrow nests. We uniquely marked all hatchlings using non-toxic food coloring. We measured the mass of Cowbird hatchlings and re-marked them before 1300, typically every other day (range 1–8 days), until large enough to retain unique leg bands. We measured mass every other day when possible and the final body mass measurements on days 8 or 9 after hatching (to reduce forced fledging since the minimum fledging age is 8 days post hatching; Lowther 2020). The nestlings that disappeared from nests were assumed to have died and were excluded from analyses. Chick mass was obtained using a digital balance to the nearest 1 mg (Acculab Model #PP-150B; Acculab, East Brunswick, New Jersey, USA).

Molecular assignment of 141 Cowbird chick sex

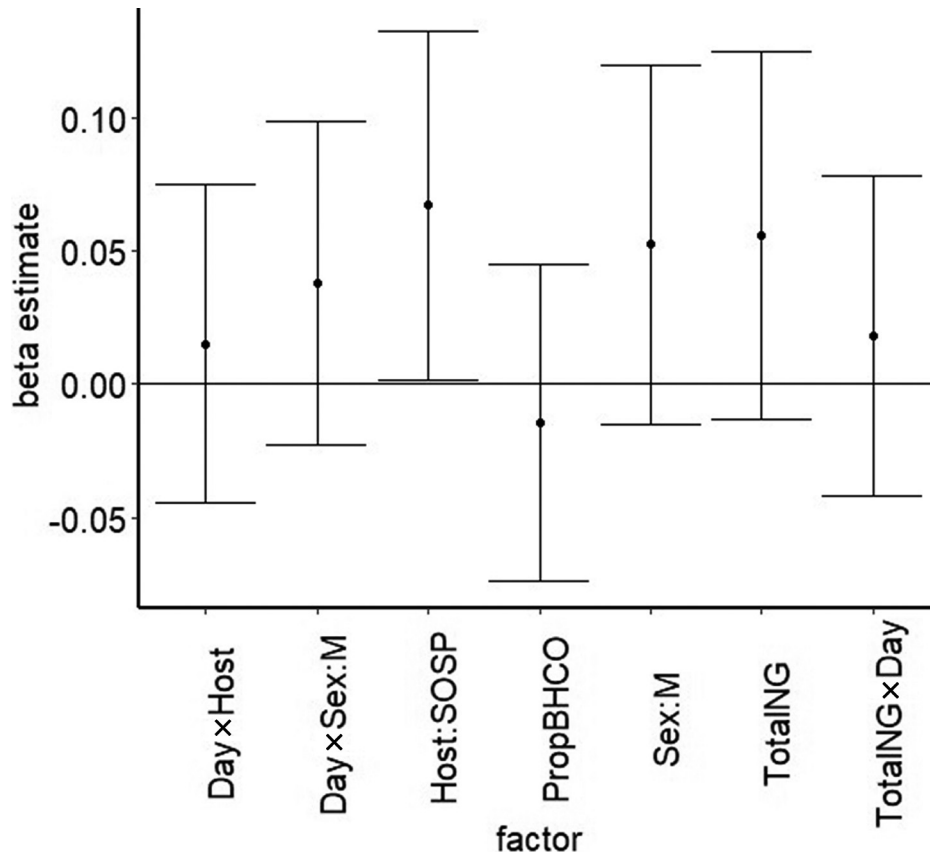
We determined the sex of Cowbird chicks using avian molecular markers to amplify an intron of the *CHD1* gene on the sex chromosomes of birds (Griffiths et al. 1998). When the *CHD-W* sex-linked gene is present, the amplified introns vary in length resulting in differently sized PCR products (Griffiths et al. 1998). We used PCR primers P8 and P2 (Griffiths et al. 1998), which are among the most commonly used primer pairs for sex identification in avian species. PCR amplification consisted of 35 cycles with a 48 °C annealing temperature. We separated products on 3% agarose gels and stained them with ethidium bromide. We considered individuals with one and two bands to be male and female, respectively.

Statistical methods

For the day 8 mass data, we used linear mixed-effects models in the R (version 3.6.3; R Core Team 2013) package "nlme" (version 3.1-145; Pinheiro et al. 2020) to test the predicted relationship between the nesting period asynchrony and the host species specific Cowbird growth rates, holding species identity as a random effect to account for repeated species measurements. We estimated variance in the model using package "performance" (version 0.4.8; Lüdtke et al. 2020).

To analyze the novel Cowbird growth rate data from the two Illinois host species, we generated linear mixed-effect models of Cowbird log mass gain over age (in days) since hatch, holding individual nestling and nest ID as random effects. We created a list of candidate models with additive and interactive

Fig. 3. Beta estimates from the mean of models of Brown-headed Cowbird (*Molothrus ater*) nestling log mass over time carrying the top 95% of the model weight. This excludes the beta estimate for Day (i.e., nesting age), which was greater than 0. Bars indicate 95% confidence intervals. SOSP, Song Sparrow (*Melospiza melodia*); PropBHCO, proportion of Cowbirds in the nest relative to host nestlings; TotalNG, total number of nestlings in the brood (Cowbird and host).



combinations of host species identity, total number of nestlings (hosts and Cowbird), sex of the Cowbird nestling, and proportion of Cowbirds to total nestlings. We used Akaike's information criterion adjusted for small sample size (AIC_c) (Anderson and Burnham 2002) to select models $\Delta AIC_c < 2$ in the R package "MuMIn" (version 1.43.15; Barton and Barton 2019). We averaged models that contributed to the top 95% of model weights to calculate beta estimates and confidence intervals for each factor. We graphed results of the top model(s) with the R package "ggplot2" (version 3.3.0; Wickham 2016).

Results

Our analysis of the host-specific Cowbird mass data revealed a positive relationship between parasitic chick growth and the Cowbird–host nesting period differences; when hosts had longer total nesting periods relative to Cowbirds, the parasites were lighter on day 8 (Kilpatrick 2002) (with data alone: $t_{[16]} = 2.335$, $P = 0.033$, adjusted $R^2 = 0.183$; with additional data added: $t_{[20]} = 2.084$, $P = 0.050$, Nakagawa's marginal $R^2 = 0.264$; Fig. 2). The pattern was not explained by the adult mass of the host species ($t_{[16]} = -0.158$, $P = 0.877$, adjusted $R^2 = -0.061$; see also Kilpatrick 2002).

Using our Cowbird chick growth rate patterns from two sympatric hosts, the top AIC_c models indicated that parasite mass gain over time was related to the total number of nestlings in the nest (host and Cowbird combined), the host species identity, and the sex of the Cowbird chick (Table 1). The proportion of Cowbird chicks among the nestmates was not a factor in the top models. However, the estimates of the confidence intervals of the

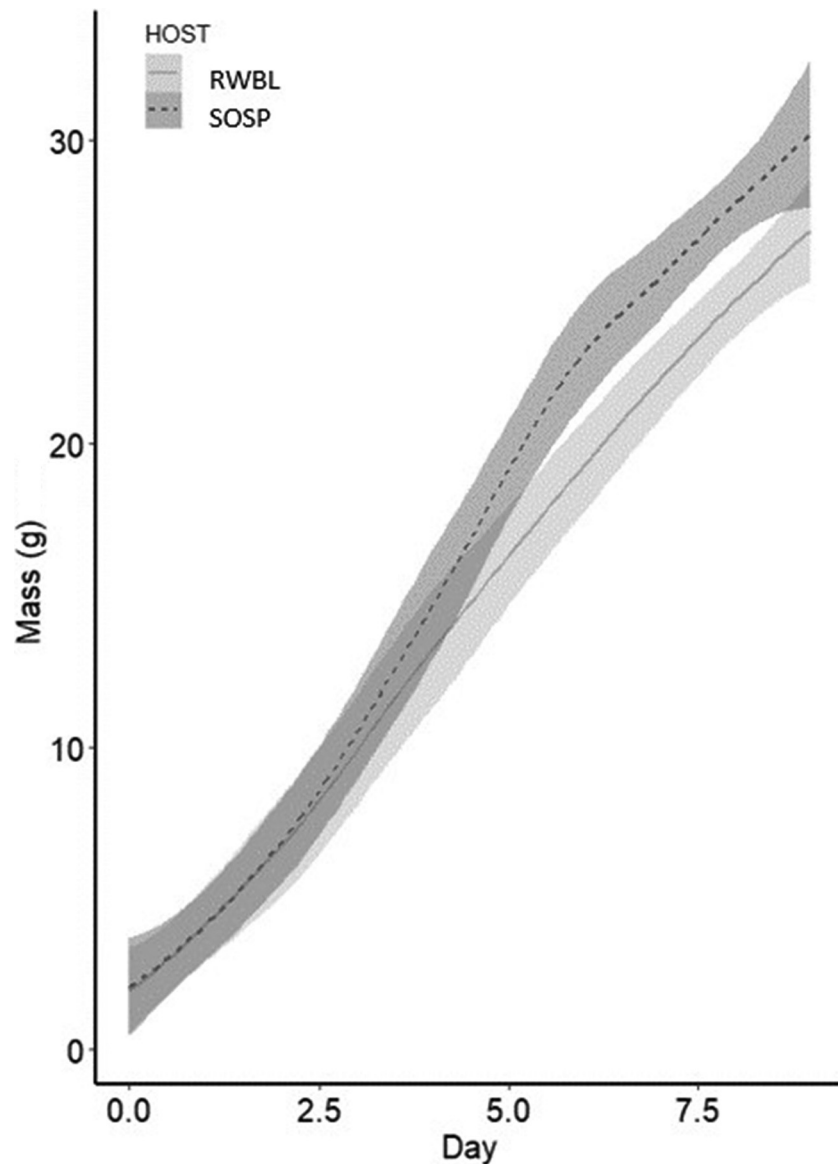
coefficient for most factors overlapped zero, with the exception of host species identity (Fig. 3).

Cowbird chicks gained mass faster in the nests of Song Sparrows and reached a higher mass at fledging relative to Cowbirds in Red-winged Blackbird nests (Fig. 4). Male and female Cowbird nestlings gained mass at approximately the same rate in the first 7 days of development, after which female Cowbird mass gain slowed and the nestlings reached a lower fledging mass relative to male Cowbirds. Cowbird nestlings in nests by themselves gained mass more slowly than nestlings in nests with two or four total nestlings. Again, even though these relationships and interaction terms were included in our top ($\Delta AIC_c < 2$) model(s), the model-averaged confidence intervals of the coefficient estimates for each of these predictors overlapped with zero (Fig. 3).

Discussion

Our analysis of interspecific data revealed that parasitic Cowbird nestlings reached greater masses on day 8 in nests of hosts with relatively shorter nesting (incubation plus brooding) periods. These results support the directional predictions of the novel "growth-tuning" hypothesis. Still, the model only explains a quarter of the variance in Cowbird day 8 mass, suggesting that additional unaccounted factors contribute to host-specific variation in Cowbird growth. In turn, in our focal two-host species data set, nestling sex resulted in higher male than female mass gain trajectories past the seventh day following hatching. Competition with nestmates, but not proportion of Cowbirds in the nest, was also included in the top model sets (Table 1). However, other than host species identity, none of the other factors had a

Fig. 4. Brown-headed Cowbird (*Molothrus ater*) nestlings gained mass (g) faster in Song Sparrow (*Melospiza melodia* (SOSP); broken line) nests than in Red-winged Blackbird (*Agelaius phoeniceus* (RWBL); solid line) nests. The shaded areas are the standard error estimates.



significant difference on growth rates of Cowbirds in our field sample.

These results suggest that Cowbird nestlings grow faster in nests of hosts that have a nesting period (Fig. 1) shorter than the mean total nesting period of the Cowbird offspring. Critically, the observed pattern of host versus Cowbird asynchrony applies to the total nesting period. It is not merely the outcome of the hosts' incubation (Tonra et al. 2008; Remeš 2010) or the nestling (Kilpatrick 2002) periods' duration alone which impacts Cowbird growth, but rather the summation of the two periods that appears to matter most. This could be consistent with a pattern that the Cowbirds' faster growth is not only the result of host provisioning effort or other behaviors during brooding alone, but rather also potentially coevolved pre-hatch mechanisms that promote faster growth in both the embryonic and the nestling stages in Cowbirds in the nests of hosts with shorter nestling incubation periods. However, there is no published evidence that maternal programming by female Cowbirds, for example through consistently different parasitic egg sizes and (or) yolk-hormone

allocations in eggs laid into different host species' nests, covaries reliably with those hosts' own traits (Mills 1987; Merrill et al. 2017). Future work should address embryonic growth rate differences in Cowbird eggs across different host species' nests and measure hatching asynchrony, fledging asynchrony, and total nesting period differences directly in diverse host species' nests parasitized by Cowbirds, rather than modeling differences between hosts and parasites using generic, published species-level mean values of life history stage durations.

Our new field data also revealed that Cowbirds grew faster in Song Sparrow nests relative to Red-winged Blackbird nests. Although two-species comparisons provide weak evidence for comparative patterns, this directional difference is predicted by our "growth-tuning" hypothesis (Fig. 1); Sparrows have shorter nesting periods relative to Blackbirds, so Cowbirds in Sparrow nests should grow faster to fledge at the same time as the Sparrow offspring. However, Blackbirds are also larger than, and are at least as competitive (Rivers et al. 2013), as Cowbirds, whereas Sparrows are an intermediate-sized Cowbird host, and host-

parasite size asymmetry had been previously associated with differences in Cowbird growth and survival in host nests (Kilner 2003; Kilner et al. 2004). Nevertheless, because host species identity and host-specific nesting period duration are conflated with each other in this host pairwise analysis, we cannot discriminate between the specific mechanism(s) impacting Cowbird growth rates in our field data. In contrast, in the multi-host correlations, adult host body size was not a predictor of Cowbird growth rate patterns, implying that nesting period difference is a stronger factor than host size to predict Cowbird chick growth rates.

Both nestling sex and the total number of nestlings (hosts and parasite) in a brood appeared as factors in the best-supported models with effect sizes nearing that of host ID, but the confidence intervals of coefficients overlapped zero, suggesting high uncertainty in the measurements. Cowbird males can grow faster than Cowbird females (Tonra et al. 2008; this study) and reach a higher mass near or at fledging (Hauber and Ramsey 2003; this study), but the difference in our growth rate data was only present at the end of development, after approximately 7 days. This result could explain why nestling sex impacted Cowbird growth in some (Tonra et al. 2008) but not in other (Weatherhead 1989) previous studies.

Cowbird nestlings provide a research opportunity to assess the impact of a broad range of environmental variation not observed in the nesting biologies of single host species. Our study revealed the complex impacts of multiple metrics of environmental variation on Cowbird mass gain, supporting previous studies showing the effects of host identity, chick sex, and competition with siblings on altricial nestling growth. In addition, we recommend that future work on nestling competition in altricial birds assess not only hatching asynchrony but also the combination of hatching and fledging asynchronies (i.e., “nesting period differences”), as this summed metric may also affect intraspecific growth variation in other species. Our sample size restricts us from comparing statistical models with interactions between these factors; therefore, future studies should assess the ways these environmental factors interact to influence growth rate. Quantifying diverse environmental drivers of offspring growth and variation can also allow us to identify and to test the adaptive developmentally plastic responses to changing environments.

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