

Explaining postnatal growth plasticity in a generalist brood parasite

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Received: 9 June 2009 / Revised: 27 November 2009 / Accepted: 30 November 2009 / Published online: 19 December 2009
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Abstract Selection of a particular host has clear consequences for the performance of avian brood parasites. Experimental studies showed that growth rate and fledging mass of brood parasites varied between host species independently of the original host species. Finding correlates of this phenotypic plasticity in growth is important for assessing adaptiveness and potential fitness consequences of host choice. Here, I analyzed the effects of several host characteristics on growth rate and fledging mass of the young of brown-headed cowbird (*Molothrus ater*), a generalist, non-evicting brood parasite. Cowbird chicks grew better in fast-developing host species and reached higher fledging mass in large hosts with fast postnatal development. A potential proximate mechanism linking fast growth and high fledging mass of cowbird with fast host development is superior food supply in fast-developing foster species. So far, we know very little about the consequences of the great plasticity in cowbird growth for later performance of the adult parasite. Thus, cowbird species could become interesting model systems for investigating the role of plasticity and optimization in the evolution of growth rate in birds.

Keywords Brood parasitism · *Molothrus* · Cuckoo · Growth · Plasticity

Electronic supplementary material The online version of this article (doi:10.1007/s00114-009-0635-5) contains supplementary material, which is available to authorized users.

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Introduction

Avian brood parasitism is an excellent model for investigating coevolutionary interactions between species. Multiple adaptations were revealed on the side of both parasites and hosts (Davies 2000). Whereas hosts are selected to avoid parasitism, one of the key components of the success of the parasite is to choose a suitable host (Krüger 2007).

Selection of a particular host species has clear consequences for the fitness of the brood parasite. In the first line of defense, hosts differ in the level of aggression near the nest (Røskaft et al. 2002). Similarly, hosts differ in their ability to eject parasitic eggs (Peer and Sealy 2004) and to desert the parasitized nest (Hosoi and Rothstein 2000). Further, hatching and fledging success of the parasite differ strongly among host species in both cuckoo (Kleven et al. 2004) and cowbird (Kilner 2003). Even if the parasitic chick successfully fledges, it might do so in different body mass and condition with important fitness consequences (Gebhardt-Henrich and Richner 1998). Brood parasite's growth rate and fledging mass differed strongly among 10 hosts of common cuckoo (*Cuculus canorus*; Kleven et al. 1999; Grim 2006; Grim et al. 2009) and 20 hosts of brown-headed cowbird (*Molothrus ater*; Kilpatrick 2002). Consequently, the challenge is to find ecological and life-history characteristics of host species that explain different growth performance of parasites in their nests.

Studies done so far used host body size (Kleven et al. 1999; 2004; Kilpatrick 2002; Grim 2006) or hatching synchrony between parasite and host (Kilner 2003; Tonra et al. 2008) as predictors of the performance of parasitic chicks. However, other host traits might be decisive for parasite's performance, and all potentially important traits should be studied simultaneously to weigh their relative

importance. Here, I assessed potential influence of multiple host traits on the growth and fledging mass of the nestlings of brown-headed cowbird, a generalist, non-evicting brood parasite. I studied host body mass, hatching synchrony between host and cowbird, host postnatal developmental rate, number of host young reared alongside with the cowbird young, and the length of historical co-occurrence between host and cowbird (Kilpatrick 2002; Kilner 2003; Remeš 2006; Tonra et al. 2008), and statistically separated their independent effects.

Materials and methods

To test alternative hypotheses about factors decisive for growth and development of cowbird young, I modeled effects of multiple explanatory variables on cowbird growth rate and fledging mass. Based on previous research, I included host body mass (Kilpatrick 2002), hatching synchrony between cowbird and host (Kilner 2003; Tonra et al. 2008), and the number of host young raised together with the cowbird chick (Kilner et al. 2004). I included two other host characteristics. First, length of the historical co-occurrence of cowbird with a host might have led to coevolutionary interactions affecting suitability of a particular host (Hosoi and Rothstein 2000; Hauber 2003; Kilner et al. 2004; Remeš 2006). Second, fast host development might indicate superior parenting abilities (Saether 1994) and thus affect cowbird chick growth. I also included quadratic effects of the following four factors: host body mass (Rivers 2007), number of host young raised together with the cowbird chick (Kilner 2003; Kilner et al. 2004), development rate, and hatching synchrony (Tonra et al. 2008).

I assembled data for this study from published sources. I took data for cowbird growth rate (day^{-1}), cowbird mass at 8 days of age (as a proxy for fledging mass, g), host growth rate (day^{-1}), and host nestling period (days) from Kilpatrick (2002). Growth rate was quantified as constant K of the logistic growth model (see Remeš and Martin 2002; Remeš 2007). I took host adult body mass (g) from Dunning (1993). Host species vary in the average number of own young that is raised with the parasitic chick, with potential consequences for cowbird growth (Kilner et al. 2004). I took this number from Trine et al. (1998), Lorenzana and Sealy (1999), Kilner et al. (2004), and the BBIRD database (2005). I calculated the difference between mean cowbird incubation time (10.5 days; Hauber 2003) and host incubation time (days; from Tonra et al. 2008) as a rough estimate of cowbird-host hatching synchrony (Hauber 2003; Tonra et al. 2008). I based the categorization of hosts into those with long vs. short co-occurrence with cowbird on habitat association (Hosoi and Rothstein 2000).

Forest species were considered to have had short co-occurrence, whereas hosts from other habitats were considered to have had long co-occurrence. I took this information from Hosoi and Rothstein (2000), Peer and Sealy (2004), and Remeš (2006). The dataset is presented in Electronic supplementary material (Appendix S1).

Host growth rate and nestling period length were highly correlated, Pearson's $r = -0.54$ ($P = 0.014$, $N = 20$). When these two variables were combined together by a principal components analysis, the first component explained 77.1% of variability. Component loadings were 0.88 for growth rate and -0.88 for nestling period. Thus, high values of this new composite variable (“development rate”) indicated fast growth and short nestling period. Nestling period duration and host body mass were \log_{10} transformed in all the analyses. In all models, I checked residuals for any deviations from normality, equal variance, and linearity. First, I present results of univariate analyses of individual factors. Second, I fit multivariate models of cowbird growth and fledging mass. Subsequently, I removed nonsignificant factors (at $\alpha = 0.05$) from multivariate models starting with the least significant one until I ended with the minimum adequate model (Grafen and Hails 2002). To ensure that the results of this procedure were not biased, I also built the final model by forward addition of individual factors. I ended up with the same models as in the backward elimination procedure. Significance level was set at $\alpha = 0.05$. β statistics are standardized regression coefficients. All statistical analyses were done in JMP 7.0.1 software (SAS Institute Inc., Cary, USA).

Results

Growth rate of the cowbird chick varied from 0.3 to 0.7 day^{-1} (mean \pm SD = 0.536 ± 0.080 day^{-1} , $N = 19$) and fledging mass from 14.8 to 28.2 g (23.6 ± 3.52 g, $N = 20$). Cowbird growth rate and fledging mass were highly correlated ($r = 0.76$, $P < 0.001$, $N = 19$). Thus, in certain hosts, cowbird chicks reached high fledging mass and fast growth, whereas the opposite was true in other hosts. I aimed to find out correlates of this variation.

In univariate analyses, cowbird growth rate correlated positively only with host development rate (Table 1, Fig. 1a). Cowbird fledging mass increased nonlinearly with host development rate and linearly with hatching synchrony (Table 1, Fig. 1b). In multivariate analyses, both backward elimination and forward building of multivariate models revealed only positive linear effect of host development rate on cowbird growth rate (Table 1, Fig. 1a). In the multivariate analysis of cowbird fledging mass, both backward and forward procedures revealed the same final model including positive linear effect of host body mass

Table 1 Univariate relationships of cowbird growth rate and fledging mass (mass at 8 days of age) to several host traits

Predictor	Cowbird growth rate					Cowbird fledging mass				
	<i>F</i>	<i>P</i>	<i>DF</i>	β	<i>R</i> ²	<i>F</i>	<i>P</i>	<i>DF</i>	β	<i>R</i> ²
Host body mass (log)	0.01	0.940	1, 17	0.02	<0.001	1.32	0.265	1, 18	0.26	0.069
Hatching synchrony	2.26	0.151	1, 17	0.34	0.117	7.96	0.011	1, 18	0.55	0.307
Host development rate	9.66	0.006	1, 17	0.60	0.362	9.78	0.006	1, 18	0.59	0.352
No. of host young	0.32	0.581	1, 16	0.14	0.019	2.69	0.120	1, 16	0.38	0.144
Historical co-occurrence	0.85	0.369	1, 17	0.22	0.048	0.65	0.430	1, 18	-0.19	0.035
Hatching synchrony ^a	0.02	0.902	2, 16		0.118	1.94	0.181	2, 17		0.378
Host body mass (log) ^a	<0.01	1.000	2, 16		<0.001	0.12	0.733	2, 17		0.075
Host development rate ^a	0.81	0.381	2, 16		0.393	5.42	0.033	2, 17		0.509
No. of host young ^a	1.03	0.325	2, 15		0.083	3.11	0.098	2, 15		0.291

Statistically significant values are in bold

^aQuadratic effect

($F_{1,16}=5.78$, $P=0.029$) and quadratic, nonlinear effect of host development rate ($F_{2,16}=6.19$, $P=0.024$; whole model: $F_{3,16}=9.44$, $P=0.001$, $R^2=0.64$; Fig. 1b).

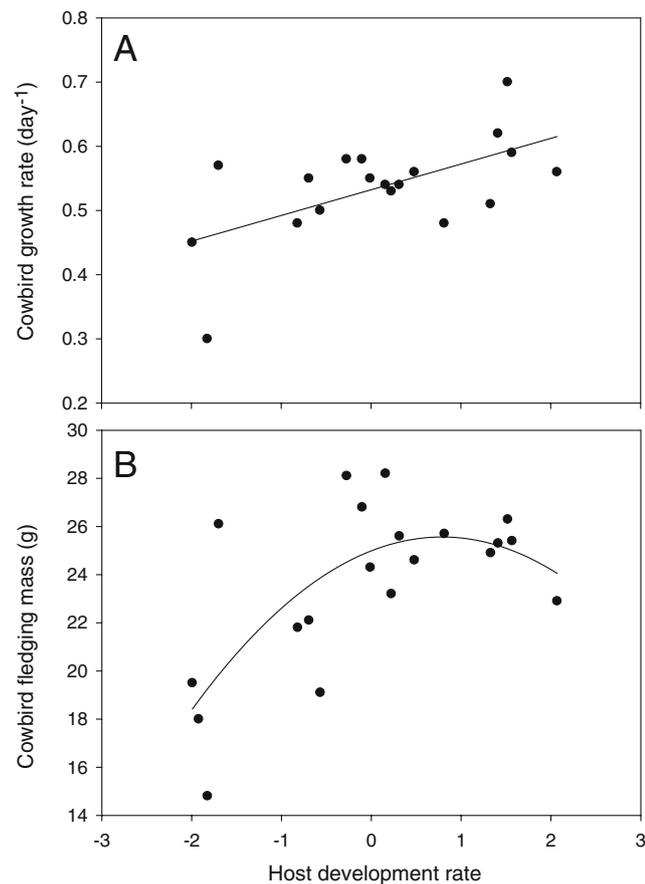


Fig. 1 Relationships of **a** growth rate and **b** fledging mass of the cowbird chick to host development rate, characterized as the first component of PCA on host growth rate and nestling period length (see “Results”)

Discussion

Brown-headed cowbird chicks grew better in fast-developing host species and reached higher fledging mass in large hosts with fast postnatal development. All these relationships were independent of multiple other host traits tested simultaneously.

A potential proximate mechanism linking fast cowbird growth and high fledging mass with fast host development rate is parental food supply. Fast growth and short nestling periods require more energy and, consequently, more food delivered by parents (Weathers 1996). Accordingly, bird species with young developing fast bring more food to the nest than slowly developing species (Saether 1994). This high food supply might lead to high cowbird growth rate, because bird growth is plastic in response to food supply (Martin 1987; Schew and Ricklefs 1998). At the same time, it seems that cowbird fledging mass reached an asymptote in relation to host development rate, and it was depressed only in slowly developing hosts (Fig. 1b). Positive effect of host body mass on cowbird fledging mass demonstrated here is also at least partly consistent with the role of food supply. Cowbird chick receives the smallest amount of food in the nests of small hosts, although available evidence suggests that it receives the largest amount of food from middle-sized hosts instead of the largest ones (Rivers 2007).

Host postnatal development and body mass (see also Wiley 1986) emerged from this multivariate analysis as the main determinants of cowbird growth. Neither cowbird-host hatching synchrony (Tonra et al. 2008) nor the number of host young reared with the cowbird in the nest (Kilner et al. 2004; but see Tonra et al. 2008), revealed as significant in previous studies, were important in this broader analysis. However, cowbird-host synchrony was correlated with host

postnatal development rate ($r=0.76$, $P<0.001$, $N=20$) and that is probably why synchrony was significant in univariate analyses of cowbird fledging mass (Table 1) and in Tonra et al. (2008), who did not control for host postnatal development rate. Further, since sex ratio of cowbird young does not differ among host species (Kasumovic et al. 2002; Tonra et al. 2008), it is not likely that the sex of cowbird young (Tonra et al. 2008) have biased results presented here. Taken together, the best predictors of cowbird growth emerging from comparisons of available data across host species seem to be host development rate and body mass. Only experiments on a large number of host species (see Rivers 2007) will show how robust these effects are and whether they are causal or not.

Generally, growth of the young cowbird in various hosts proved to be surprisingly plastic, varying from 0.3 to 0.7 day⁻¹. This within-species variation even matched variation among host species analyzed here, where growth rate varied from 0.4 to 0.7 day⁻¹ ($N=20$ species; body mass from 6 to 114 g). Similarly, in North American songbirds similar in size to cowbird (35–50 g), growth rate varied from 0.3 to 0.6 day⁻¹ among species ($N=20$ species; Remeš 2006, 2007). Such great within-species plasticity in young cowbirds, comparable in magnitude to among-species variability, might have strong consequences for adult performance (Schew and Ricklefs 1998; Metcalfe and Monaghan 2001; Remeš 2007). Similarly, cowbird fledging mass varied twofold among different host species (from 14.8 to 28.2 g) again with potentially important fitness consequences (Gebhardt-Henrich and Richner 1998). Cowbird species, together with cuckoos (Grim 2006; Hauber and Moskát 2008; Grim et al. 2009), could thus become interesting model systems for investigating the role of plasticity, constraints, and optimization in the evolution of growth rate in birds (Remeš 2006).

Acknowledgements This study was supported by grants from Czech Science Foundation (206/05/P581) and Czech Ministry of Education (MSM6198959212). I am obliged to B. Matysioková and anonymous reviewers for very helpful comments on the manuscript. This work would not be possible without dedicated work of many field ornithologists who collected the original data.

References

- BBIRD database (2005) <http://www.umt.edu/bbird/> (accessed 10 October 2005)
- Davies NB (2000) Cuckoos, cowbirds and other cheats. Poyser, London
- Dunning JB (1993) CRC handbook of avian body masses. CRC, Boca Raton
- Gebhardt-Henrich S, Richner H (1998) Causes of growth variation and its consequences for fitness. In: Starck JM, Ricklefs RE (eds) Avian growth and development. Oxford Univ Press, Oxford, pp 324–339
- Grafen A, Hails R (2002) Modern statistics for the life sciences. Oxford Univ Press, Oxford
- Grim T (2006) Cuckoo growth performance in parasitized and unused hosts: not only host size matters. Behav Ecol Sociobiol 60:716–723
- Grim T, Rutila J, Cassey P, Hauber ME (2009) Experimentally constrained virulence is costly for common cuckoo chicks. Ethology 115:14–22
- Hauber ME (2003) Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. Behav Ecol 14:227–235
- Hauber ME, Moskát C (2008) Shared parental care is costly for nestlings of common cuckoos and their great reed warbler hosts. Behav Ecol 19:79–86
- Hosoi SA, Rothstein SI (2000) Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. Anim Behav 59:823–840
- Kasumovic MM, Gibbs HL, Woolfenden BE, Sealy SG, Nakamura H (2002) Primary sex-ratio variation in two brood parasitic birds: Brown-headed Cowbird (*Molothrus ater*) and Common Cuckoo (*Cuculus canorus*). Auk 119:561–566
- Kilner RM (2003) How selfish is a cowbird nestling? Anim Behav 66:569–576
- Kilner RM, Madden JR, Hauber ME (2004) Brood parasitic cowbird nestlings use host young to procure resources. Science 305:877–879
- Kilpatrick AM (2002) Variation in growth of Brown-headed Cowbird (*Molothrus ater*) nestlings and energetic impacts on their host parents. Can J Zool 80:145–153
- Kleven O, Moksnes A, Røskaft E, Honza M (1999) Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. Behav Ecol Sociobiol 47:41–46
- Kleven O, Moksnes A, Røskaft E, Rudolfsen G, Stokke BG, Honza M (2004) Breeding success of common cuckoos *Cuculus canorus* parasitising four sympatric species of *Acrocephalus* warblers. J Avian Biol 35:394–398
- Krüger O (2007) Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. Philos Trans R Soc Lond B 362:1873–1886
- Lorenzana JC, Sealy SG (1999) A meta-analysis of the impact of parasitism by the Brown-headed Cowbird on its hosts. Stud Avian Biol 18:241–253
- Martin TE (1987) Food as a limit on breeding birds, a life-history perspective. Annu Rev Ecol Syst 18:453–487
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends Ecol Evol 16:254–260
- Peer BD, Sealy SG (2004) Correlates of egg rejection in hosts of the Brown-headed Cowbird. Condor 106:580–599
- Remeš V (2006) Growth strategies of passerine birds are related to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*). Evolution 60:1692–1700
- Remeš V (2007) Avian growth and development rates and age-specific mortality: the roles of nest predation and adult mortality. J Evol Biol 20:320–325
- Remeš V, Martin TE (2002) Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518
- Rivers JW (2007) Nestmate size, but not short-term need, influences the begging behavior of a generalist brood parasite. Behav Ecol 18:222–230
- Røskaft E, Moksnes A, Stokke BG, Bičík V, Moskát C (2002) Aggression to dummy cuckoos by potential European cuckoo hosts. Behaviour 139:613–628
- Saether BE (1994) Food provisioning in relation to reproductive strategy in altricial birds – a comparison of 2 hypotheses. Evolution 48:1397–1406

- Schew WA, Ricklefs RE (1998) Developmental plasticity. In: Starck JM, Ricklefs RE (eds) Avian growth and development. Oxford Univ Press, Oxford, pp 288–304
- Tonra CM, Hauber ME, Heath SK, Johnson MD (2008) Ecological correlates and sex differences in early development of a generalist brood parasite. *Auk* 125:205–213
- Trine CL, Robinson WD, Robinson SK (1998) Consequences of brown-headed cowbird brood parasitism for host population dynamics. In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts: studies in coevolution. Oxford Univ Press, Oxford, pp 273–295
- Weathers WW (1996) Energetics of postnatal growth. In: Carey C (ed) Avian energetics and nutritional ecology. Chapman & Hall, New York, pp 461–496
- Wiley JW (1986) Growth of Shiny Cowbird and host chicks. *Wilson Bull* 98:126–131