

GROWTH STRATEGIES OF PASSERINE BIRDS ARE RELATED TO BROOD PARASITISM BY THE BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*)

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Abstract.—Sibling competition was proposed as an important selective agent in the evolution of growth and development. Brood parasitism by the brown-headed cowbird (*Molothrus ater*) intensifies sibling competition in the nests of its hosts by increasing host chick mortality and exposing them to a genetically unrelated nestmate. Intranest sibling competition for resources supplied by parents is size dependent. Thus, it should select for high development rates and short nestling periods, which would alleviate negative impacts of brood parasitic chicks on host young. I tested these predictions on 134 North American passerines by comparative analyses. After controlling for covariates and phylogeny, I showed that high parasitism rate was associated with higher nestling growth rate, lower mass at fledging, and shorter nestling periods. These effects were most pronounced in species in which sibling competition is most intense (i.e., weighing over about 30 g). When species were categorized as nonhosts versus old hosts (parasitized for thousands of years) versus new hosts (parasitized the last 100–200 years), there was a clear effect of this parasitism category on growth strategies. Nestling growth rate was the most evolutionarily flexible trait, followed by mass at fledging and nestling period duration. Adjustments during incubation (incubation period length, egg volume) were less pronounced and generally disappeared after controlling for phylogeny. I show that sibling competition caused by brood parasites can have strong effects on the evolution of host growth strategies and that the evolution of developmental traits can take place very rapidly. Human alteration of habitats causing spread of brood parasites to new areas thus cascades into affecting the evolution of life-history traits in host species.

Key words.—Brood parasitism, comparative analysis, development, growth, habitat change, sibling competition.

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One of the major challenges in evolutionary biology is to explain interspecific phenotypic variation. Growth is an integral part of a species' life history; thus, knowing the factors responsible for its evolutionary diversification is a key issue. Many factors were hypothesized to be responsible for driving the evolution of growth and development rates (review in Starck and Ricklefs 1998; Remeš and Martin 2002). However, despite substantial research attention, we still have an incomplete knowledge of the factors critical in shaping the evolution of growth.

One of the factors with strong potential to drive the evolution of juvenile growth is sibling competition. Strong sibling competition over limited resources should lead to elevated growth rates, provided rapid growth ensures monopolization of the resources (Werschkul and Jackson 1979; Ricklefs 1982). Despite the clear logic of this theoretical concept, empirical studies have generated mixed results (Werschkul and Jackson 1979; Ricklefs 1982; Bortolotti 1986; Royle et al. 1999; Lloyd and Martin 2003). An emerging consensus seems to have been that juvenile growth rates are rather insensitive to sibling competition or at most that the potential relationship is unclear and obscured by confounding variables (Ricklefs 1982; Lloyd and Martin 2003; but see Royle et al. 1999). However, the role of sibling competition as a selective agent depends on the evolutionary flexibility of growth rates in response to mortality (Ricklefs 1982). An overview of growth variation in diverse taxa showed that growth rates are often tuned to prevailing environmental conditions (Arendt 1997). More importantly, Remeš and Martin (2002) showed that bird growth and development can be evolutionarily flexible in relation to juvenile mortality. Thus, it seems appropriate to rigorously re-examine the potential role of sibling competition in the evolution of growth and development rates.

The brood parasitic system of the brown-headed cowbird (*Molothrus ater*) and its avian hosts in North America is an ideal model for addressing this issue. The feasibility of this study system depends on two assumptions: (1) brood parasitism leads to stronger sibling competition in the host, and (2) elevated growth provides selective advantage to its bearer in sibling contest for resources.

First, the intensity of sibling competition is set by an interplay between the benefits of obtaining more resources and both direct and indirect costs (Godfray 1991; Mock and Parker 1997). Direct costs include, for example, the danger of luring nest predators by conspicuous begging behavior (Haskell 1994; Dearborn 1999). Indirect costs include harm to gene-sharing nestmates (intra-brood conflict) and future offspring of the parents (inter-brood conflict; Trivers 1974) incurred by nestlings monopolizing food brought by parents. Young of interspecific brood parasites have zero genetic relatedness to both their immediate nestmates and future offspring of the caring parents. Although selfishness of the parasitic chick is limited by positive effects of host young on its well-being (Kilner et al. 2004), cowbird young can afford more unequal monopolization of resources without bearing indirect costs (i.e., costs to their inclusive fitness; Hamilton 1964). This lower indirect cost leads to the escalation of sibling competition (more precisely, nestmate competition) between cowbird and host young and may cascade to affect the evolution of begging display (e.g., more vigorous begging by brood parasites and hosts; Briskie et al. 1994; Dearborn 1998, 1999), and host growth rates (Royle et al. 1999). If the presence of a more selfish nestmate (i.e., cowbird chick) in the nest leads to higher host young mortality (Lorenzana and Sealy 1999) and growth rate is evolutionarily sensitive to nestling mortality (Remeš and Martin 2002), this would

also lead to the evolution of more rapid growth (Ricklefs 1982).

Second, the young of brood parasites depend fully on their foster parents and thus the ability to acquire adequate resources from them. More importantly, nonevicting brood parasites (including the brown-headed cowbird) must procure these resources in the presence of competing host young (Davies 2000). The interaction of parasitic and host young in the parasitic system of the brown-headed cowbird is strongly height dependent. Who gets fed depends critically on the height to which the nestling reaches with its gape (Dearborn 1998; Lichtenstein and Sealy 1998), and young of similar-sized hosts are not out-competed by cowbird nestlings (Dearborn and Lichtenstein 2002). Thus, it seems reasonable to speculate that elevated growth rate with resulting larger body size for a given age bears a clear advantage in this system (see also Friedmann 1963; Rothstein 1975). It should be noticed that chick discrimination (preferential feeding of their own young by host parents) could invalidate this argument. However, although it is known in several hosts of related species of cowbird (Fraga 1998; Lichtenstein 2001), it has not been found in any host of the brown-headed cowbird (see Grim 2006).

Brown-headed cowbirds (body mass = 45 g, incubation period 11.5 days) successfully parasitize passerine species differing widely in adult body mass (Kilpatrick 1999). In small hosts, the cowbird chick is able to monopolize the majority of food brought by parents (see above). Consequently, the competition between other nestlings (i.e., true siblings) is very intense and every increase of the growth rate could bring a strong advantage. However, the smaller the host species, the higher the host young mortality, reaching even 100% (Lorenzana and Sealy 1999; Hauber 2003a; Kilner 2003). Thus, in small hosts, there is little selection on growth strategies because a large majority of host young experiencing the presence of the cowbird young die and do not pass on their genes into future generations. In contrast, nestlings of large species fare well even in the company of parasitic nestmates, who die within a couple of days, thus eliminating any selection pressure on growth strategies of the host's chicks (Scott and Lemon 1996). In intermediate hosts, the cowbird chick is a strong competitor, and at the same time host chicks survive to fledge. This combination of factors should bring the strongest selection on growth strategies in this size category of host species. Consequently, I predicted that the effect of the intensity of parasitism on the evolution of host growth rates would vary with host body mass, with the highest effect in the intermediate host mass, roughly equaling the mass of the cowbird.

There are also other possible adjustments of host growth strategies for coping with the young cowbird in the nest, or at least for mitigating negative effects of its presence. Host young may increase their size, and consequently their competition potential, by hatching from larger eggs for a given adult body mass, or by shortening the incubation period to gain a head start in the development. Alternatively, they may escape direct competition with the cowbird chick by leaving the nest earlier and with lower body mass. However, since cowbirds beg vigorously even after leaving the nest (Hauber and Ramsey 2003), the strength of selection for early nest

leaving will depend on the ability of the host young to compete with the cowbird young while in the nest as compared to after fledging. I also tested these hypotheses.

Recent expansion of the cowbird breeding range in North America adds both complexity and appeal to this study system. Natural breeding habitat for the brown-headed cowbird is short grass vegetation with low or scattered trees (Lowther 1993). Thus, before European settlement they were mainly restricted to the grasslands of the Great Plains. Today, cowbirds breed throughout the whole United States and southern Canada (Sauer et al. 2005). Their expansion eastwards (from about the late 1700s) and westwards (from about 1900) was enabled by transformation of woodlands to pastures and fields, which are readily adopted for breeding (Mayfield 1965; Ortega 1998). This led to the contact of the brown-headed cowbird with a number of new hosts (woodland species) with no previous experience with brood parasitism. At present, brown-headed cowbirds parasitize more than 200 passerine species (Ortega 1998; Davies 2000). New hosts (woodland species) have been exposed to parasitism for the last 100–200 years and thus differ from open-country species (either old hosts or nonhosts) in length of coevolution with the cowbird. This enables us to test not only the flexibility of avian growth and development in relation to sibling competition, but also the tempo of their evolution.

In summary, parasitic young compete directly for food with host young, cause host young mortality (the strength of which depends on host size; Lorenzana and Sealy 1999), and can afford stronger sibling conflict because of its lower indirect cost for them. Furthermore, competition for resources is size dependent. These processes should result in selection for higher growth rates of host young. Alternative developmental strategies could include a short incubation period, laying large eggs, and shortening the nestling period by fledging soon and with low body mass. I tested these predictions on a sample of 134 species of North American passerines victimized to a certain degree by the brown-headed cowbird. I predicted rapid growth, low fledging mass, short nestling and incubation periods, and large eggs with increasing parasite pressure. If the tempo of the evolution of adaptation in growth and development to brood parasitism is slow, I predicted that old hosts would differ from nonhosts, whereas new hosts would not. On the contrary, if the tempo of this evolution is rapid, I predicted that both old and new hosts would differ from nonhosts.

METHODS

Dataset

General procedures for collection and preparation of life-history data were as in Remeš and Martin (2002). After conducting an exhaustive search of databases, I added growth and life-history data for an additional 19 species (see Appendix 1 available online only at <http://dx.doi.org/10.1554/06-170.1.s1>), making the total of 134 species. I collated data on growth rate, fledging mass, incubation and nestling periods, clutch size, adult body mass, nest predation rate, foraging mode (aerial vs. nonaerial forager), and latitude of the growth study. As a measure of growth rate for subsequent analyses, I used the constant K of the logistic growth equation

fit both to the growth data truncated at the highest mass reached in the nest (K_{max}) and at 70% of adult body mass (K_{70}), according to analytical procedures developed by Remeš and Martin (2002).

For every species I searched data on percentage of nests parasitized by the brown-headed cowbird (Ortega 1998, appendix C, D; Poole and Gill 1992–2002), breeding habitat and nest site (Ehrlich et al. 1988), and rejection rate of parasitic eggs (Rothstein 1975; Peer and Sealy 2004). I took the mean parasitism rate for each species by calculating average weighed by sample size of nests (together there were 844 studies; median number of studies per species: 4; interquartile range: 1–8). For 590 studies, the years in which they were conducted were known. Of these studies, 49 were done before 1900, 112 between 1901 and 1950, and the remaining 429 studies after 1950. There was large intraspecific variation in reported parasitism rates. In species where there were at least two studies and mean larger than zero, mean coefficient of variation was 106%, and it decreased with mean parasitism rate ($r = -0.70$, $P < 0.001$, $n = 81$).

Percentage of nests parasitized by a cowbird is not an ideal measure of the real impact of parasitism on the host growth strategies. First, some parasitized clutches are deserted/buried by hosts; thus, their nestlings are not exposed to cowbird chicks. Second, the cost of parasitism at the nestling stage (i.e., percentage of nestlings dying in nests with a cowbird chick as compared to nests without it) varies widely between species (Lorenzana and Sealy 1999). I was able to collate data on percentage of nests deserted/buried for 33 species (Hosoi and Rothstein 2000) and on the cost of parasitism for 54 species (Lorenzana and Sealy 1999; Hauber 2003a; Kilner 2003). This generated data on the real impact of parasitism on the growth strategies of host nestlings (i.e., [% parasitized \times (1 – proportion deserted or buried)] \times cost of parasitism) for only 29 species, which is too few for a rigorous analysis. However, if desertion of a parasitized nest is a rapid event (Hosoi and Rothstein 2000), then the majority of nests found and reported in the literature as parasitized do not include nests later deserted/buried. Thus, the percentage of nests reported as parasitized may be a rather good predictor of the force of selection on hosts. Therefore, I used percentage of nests parasitized as a proxy for the exposure of host nestlings to cowbird chicks and host body mass as a proxy for the impact of parasitism on host offspring (Lorenzana and Sealy 1999; see above).

Based on the information on parasitism rate I also categorized every species as either a host or a nonhost. Species with parasitism below 2% were categorized as nonhosts and other species as hosts, with three exceptions. *Carduelis tristis* and *Bombycilla cedrorum* were treated as nonhosts despite their parasitism rate of about 4%, because they feed their young with food unsuitable for cowbird chicks. *Toxostoma rufum*, in spite of its 4.5% parasitism rate, is a rejecter species (rejection of cowbird eggs $> 96\%$; Rothstein 1975) and was also categorized as nonhost. For reasons explained in the introduction, I also categorized every host species as either an old or a new host. This categorization was based on breeding habitat, because that reveals long-term exposure to cowbird parasitism (for justification, see Hosoi and Rothstein 2000). Forest hosts were categorized as new hosts whereas

hosts breeding in edge, shrub, marsh, and open habitats were categorized as old hosts. Data are summarized in Appendix 2 available online only at <http://dx.doi.org/10.1554/06-170.1.s2> (for other life-history data for these species, see Remeš and Martin 2002). There was no difference in nest predation rate among habitats ($F_{4,124} = 1.15$, $P = 0.335$).

Among nonhost species, there are both rejecters (species ejecting cowbird eggs from their nests at rates $> 75\%$) and acceptors (species rejecting $< 25\%$ of parasitic eggs). Acceptors are not parasitized for other reasons (e.g., no range overlap with cowbird, cavity nesting etc.). Species are either rejecters or acceptors with almost no intermediates (Rothstein 1975, 1992). Also in my sample of nonhosts for which I was able to collate data on rejection of natural parasitic eggs, species fell either above 87% (rejecters, $n = 16$) or below 20% ejection (acceptors, $n = 6$). Since these two categories of nonhosts may differ in the length of their coevolutionary interaction with cowbird, I compared all analyzed traits between them. There was no difference in either trait ($F_{2,19} < 2.38$, $P > 0.140$; body mass always controlled). Thus, these two groups of nonhosts may safely be assumed to have been correctly grouped.

Analyses

Based on prior knowledge of the factors related to avian growth and development rates (Starck and Ricklefs 1998; Remeš and Martin 2002) I fitted models with growth rate (constant K of the logistic equation; day^{-1}), relative fledging mass (mass at fledging/adult body mass), nestling period duration (day), incubation period duration (day), and egg volume (cm^3) as response variables, and adult body mass (g), nest predation rate (daily rate of nest loss due to predation; day^{-1}), clutch size (no. of eggs), and foraging mode (aerial vs. nonaerial forager) as predictors. In the analysis of growth rate, I also included latitude of the particular growth study (degrees north). To this baseline model, I added a variable expressing either the level or the length of cowbird parasitism. It was either parasitism rate (% of nests parasitized) or parasitism status (nonhost vs. new host vs. old host). To minimize the number of statistical tests, I tested interaction of these parasitism variables only with adult body mass (see above), nest predation, and the quadratic effect of parasitism rate and nest predation (to detect possible nonadditive effects of mortality factors). I selected final models based on backward elimination of nonsignificant variables (at $\alpha = 0.05$). In all models, I checked plots of residuals for any deviations from normality of error, linearity of effects, and homogeneity of variance (Grafen and Hails 2002). Variables were appropriately transformed, if necessary.

In all analyses, species were treated as datapoints. Common descent of species may cause problems in the analysis of interspecific data. Species are historically related, which causes nonindependence of varying strength among datapoints. This violates assumptions of standard statistical techniques (Harvey and Pagel 1991). To overcome this problem, I applied the phylogenetic regression of Grafen (1989). This method is based on generalized least squares and adjusts the statistical analysis for nonindependence among species. This method is very flexible and enables fitting of standard sta-

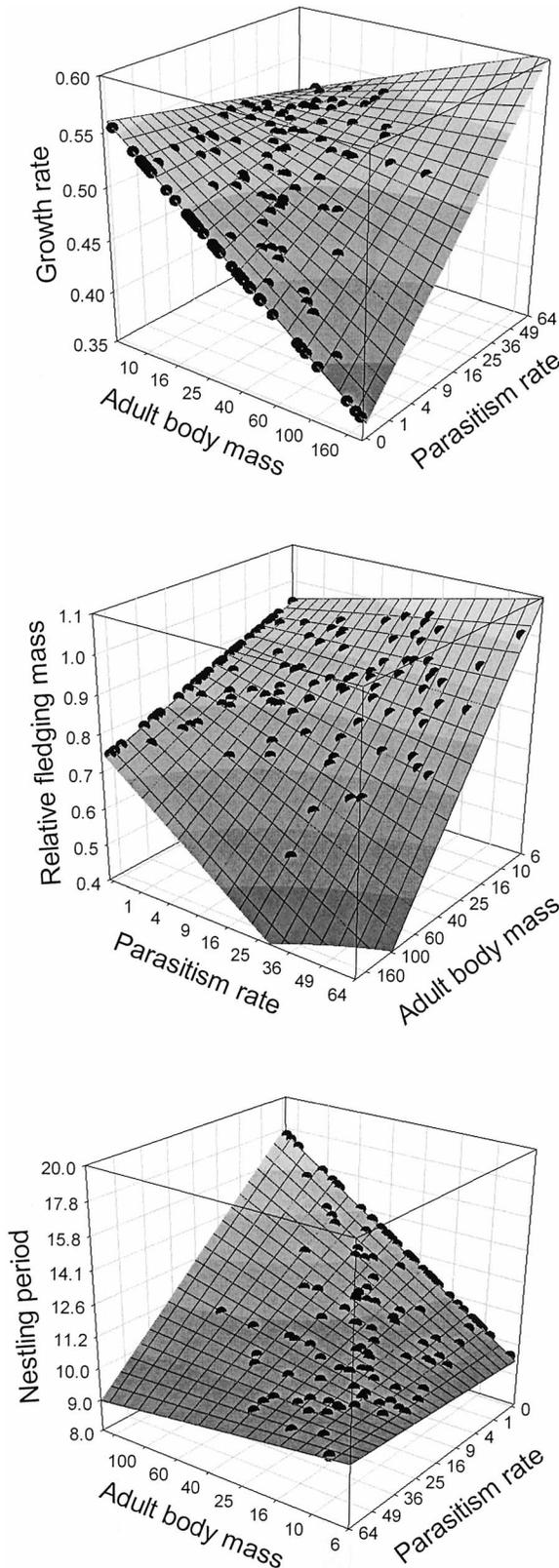


FIG. 1. Relationship between growth rate (K_{max} , day⁻¹; top), relative fledging mass (mass at fledging/adult mass; middle), and nestling period (day; bottom), and adult host body mass (g) and parasitism rate (%). Shown are predicted relationships for average values of continuous variables controlled for in the analyses

tistical models, including interactions and categorical predictors. I used the PHYREG macro for SAS written by A. Grafen (Grafen 2005). I tested significance of either parasitism rate or parasitism category (or their interaction with a factor, if necessary) against other covariates that were selected as significant in the raw species data analyses.

I assembled a working phylogeny of the studied species based on Sibley and Ahlquist (1990), Martin and Clobert (1996); and Remeš and Martin (2002), supplemented by the most recent molecular phylogenies (see Appendix 3 available online only at <http://dx.doi.org/10.1554/06-170.1.s3>). Since the phylogeny was assembled from many sources, I had no consistent estimates of branch lengths. I adopted uniform branch lengths. However, another arbitrary branch lengths option, Grafen's (1989) branch lengths, generated qualitatively identical results.

RESULTS

Growth Rate

Growth rate (K_{max}) was positively related to parasitism rate, but this effect depended on adult body mass of the host (interaction [IN hereafter]: $F_{1,120} = 6.18, P = 0.014$; Fig. 1) and nest predation rate (IN: $F_{1,120} = 6.39, P = 0.013$). There was also a positive effect of latitude ($F_{1,120} = 7.43, P = 0.007$; whole model: $R^2 = 0.48, F_{6,120} = 18.56, P < 0.001$). Similar results were obtained when K_{70} was used as a response. Growth rate was again positively related to parasitism rate, and this effect depended on adult host body mass (IN: $F_{1,101} = 9.24, P = 0.003$). There was also a simple positive effect of nest predation rate ($F_{1,101} = 7.78, P = 0.006$) and latitude ($F_{1,101} = 16.14, P < 0.001$), and a negative effect of clutch size ($F_{1,101} = 7.39, P = 0.008$; whole model: $R^2 = 0.45, F_{6,101} = 13.60, P < 0.001$). Phylogenetically adjusted analyses generated the same results. The effect of parasitism rate on growth still depended on body mass in both K_{max} (IN: $F_{1,117} = 8.15, P = 0.005$) and K_{70} (IN: $F_{1,99} = 5.96, P = 0.020$).

Growth rate (K_{max}) differed between parasitism categories, but this effect depended on host body mass (IN: $F_{2,117} = 3.08, P = 0.050$; Fig. 2) and nest predation rate (IN: $F_{2,117} = 6.45, P = 0.002$). There was also a significant positive effect of latitude ($F_{1,117} = 6.68, P = 0.011$; whole model: $R^2 = 0.50, F_{9,117} = 13.16, P < 0.001$). Analyses of K_{70} generated similar results. There was a difference between parasitism categories, but this effect depended on host body mass (IN: $F_{2,99} = 4.83, P = 0.010$). There was also a simple positive effect of nest predation rate ($F_{1,99} = 5.69, P = 0.019$) and latitude ($F_{1,99} = 13.87, P < 0.001$), and a negative effect of clutch size ($F_{1,99} = 6.42, P = 0.013$; whole model: $R^2 = 0.46, F_{8,99} = 10.56, P < 0.001$). Again, the interaction of parasitism category and adult body mass remained significant

← reported in Results (latitude = 42°N, nest predation rate = 0.127) and aerial foragers. Black dots are observations projected on the predicted plane, which should highlight parts of the plane that are most supported by data and thus best interpretable.

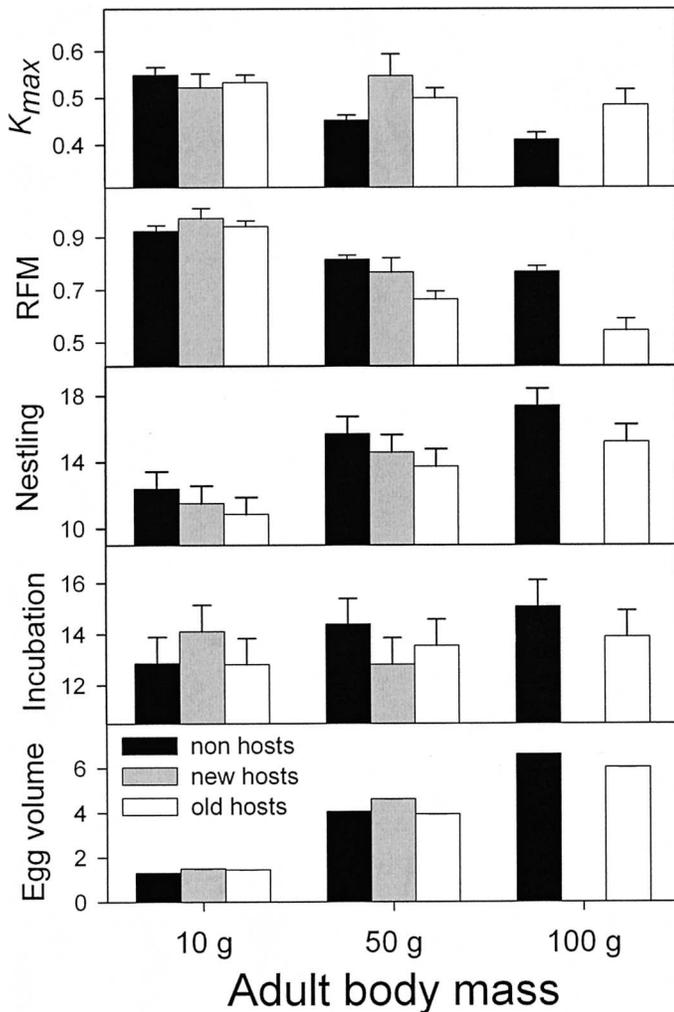


FIG. 2. Least squares means (+1 SE) of developmental characteristics (growth rate [day^{-1}], relative fledging mass, nestling period [day], incubation period [day], and egg volume [cm^3]) estimated separately for nonhosts, new hosts, and old hosts, for three host body masses. These were chosen to represent minimum body mass found among hosts (10 g), body mass close to the mass of the brown-headed cowbird (50 g), and body mass twice as large (100 g). There is no estimate for 100 g for the new hosts, because no new host was as heavy; no old host was heavier than 100 g. Least squares means were estimated from analyses reported in Results. Error bars are hardly visible for egg volume, because standard errors are too small.

even after adjusting for phylogeny in both K_{max} (IN: $F_{2,114} = 3.59$, $P = 0.031$) and K_{70} (IN: $F_{2,97} = 4.66$, $P = 0.012$).

Relative Fledging Mass

Relative fledging mass was negatively related to parasitism rate, but this effect depended on adult body mass of the host (IN: $F_{1,122} = 19.65$, $P < 0.001$; Fig. 1). There was also a negative effect of nest predation rate ($F_{1,122} = 18.59$, $P < 0.001$) and a difference between aerial foragers (least squares mean [SE] = 0.89 [0.023], $n = 20$) and nonaerial foragers (0.81 [0.009], $n = 108$; $F_{1,122} = 10.84$, $P = 0.001$; whole model: $R^2 = 0.56$, $F_{5,122} = 31.61$, $P < 0.001$). The effect of parasitism rate on relative fledging mass still depended on

host body mass in the phylogenetically adjusted analyses (IN: $F_{1,119} = 5.87$, $P = 0.017$).

Relative fledging mass differed between parasitism categories, and this effect depended on adult body mass (IN: $F_{2,120} = 7.46$, $P < 0.001$; Fig. 2). There was again a significant negative effect of nest predation ($F_{1,120} = 18.86$, $P < 0.001$) and a significant effect of foraging mode ($F_{1,120} = 9.23$, $P = 0.003$; whole model: $R^2 = 0.57$, $F_{7,120} = 22.63$, $P < 0.001$). The effect of parasitism category still interacted with host body mass in phylogenetic analyses (IN: $F_{2,117} = 3.34$, $P = 0.039$).

All the analyses of the relative fledging mass were done without the strongly outlying *Leucosticte tephrocotis* (relative fledging mass = 1.54).

Nestling Period

Length of the nestling period was negatively related to parasitism rate, but this effect depended on adult body mass (IN: $F_{1,122} = 5.85$, $P = 0.017$; Fig. 1) and nest predation rate (IN: $F_{1,122} = 12.97$, $P < 0.001$). There was also a difference between aerial foragers (least squares mean [SE] = 16.2 [1.05] days, $n = 20$) and nonaerial foragers (11.8 [1.02] days, $n = 108$; $F_{1,122} = 38.12$, $P < 0.001$; whole model: $R^2 = 0.68$, $F_{6,122} = 43.49$, $P < 0.001$). In phylogenetically adjusted analyses, the interaction of parasitism rate with host body mass became slightly nonsignificant (IN: $F_{1,119} = 2.79$, $P = 0.097$), whereas the interaction with nest predation remained significant (IN: $F_{1,119} = 8.33$, $P = 0.005$). When the interaction of parasitism rate with nest predation was removed from the model, the simple negative effect of parasitism rate became marginally nonsignificant ($F_{1,121} = 3.23$, $P = 0.075$).

Length of the nestling period differed between parasitism categories (Fig. 2), but this effect depended on nest predation rate (IN: $F_{2,121} = 6.54$, $P = 0.002$). However, parasitism category remained significant even when the interaction with nest predation rate was removed ($F_{2,123} = 4.06$, $P = 0.020$). There was a significant positive effect of adult body mass ($F_{1,121} = 38.04$, $P < 0.001$) and a significant effect of foraging mode ($F_{1,121} = 35.10$, $P < 0.001$; whole model: $R^2 = 0.68$, $F_{7,121} = 36.92$, $P < 0.001$). When phylogeny was controlled, the interaction of parasitism category with nest predation was still significant (IN: $F_{2,118} = 3.83$, $P = 0.024$). However, when this interaction was removed, the simple effect of parasitism category became nonsignificant ($F_{2,120} = 1.08$, $P = 0.342$).

Incubation Period

Length of the incubation period was curvilinearly related to parasitism rate ($F_{1,122} = 7.86$, $P = 0.006$), and this effect depended on adult body mass (IN: $F_{1,122} = 6.04$, $P = 0.015$; Fig. 3). There was also a negative effect of nest predation rate ($F_{1,122} = 14.09$, $P < 0.001$) and a difference between aerial foragers (least squares mean [SE] = 14.5 [1.02] days, $n = 20$) and nonaerial foragers (12.9 [1.01] days, $n = 108$; $F_{1,122} = 25.93$, $P < 0.001$; whole model: $R^2 = 0.52$, $F_{6,122} = 21.87$, $P < 0.001$). In phylogenetic analyses, the interaction of parasitism rate with body mass was no longer significant (IN: $F_{1,119} = 0.03$, $P = 0.856$). Moreover, curvilinear effect of parasitism remained only marginally significant ($F_{1,120} =$

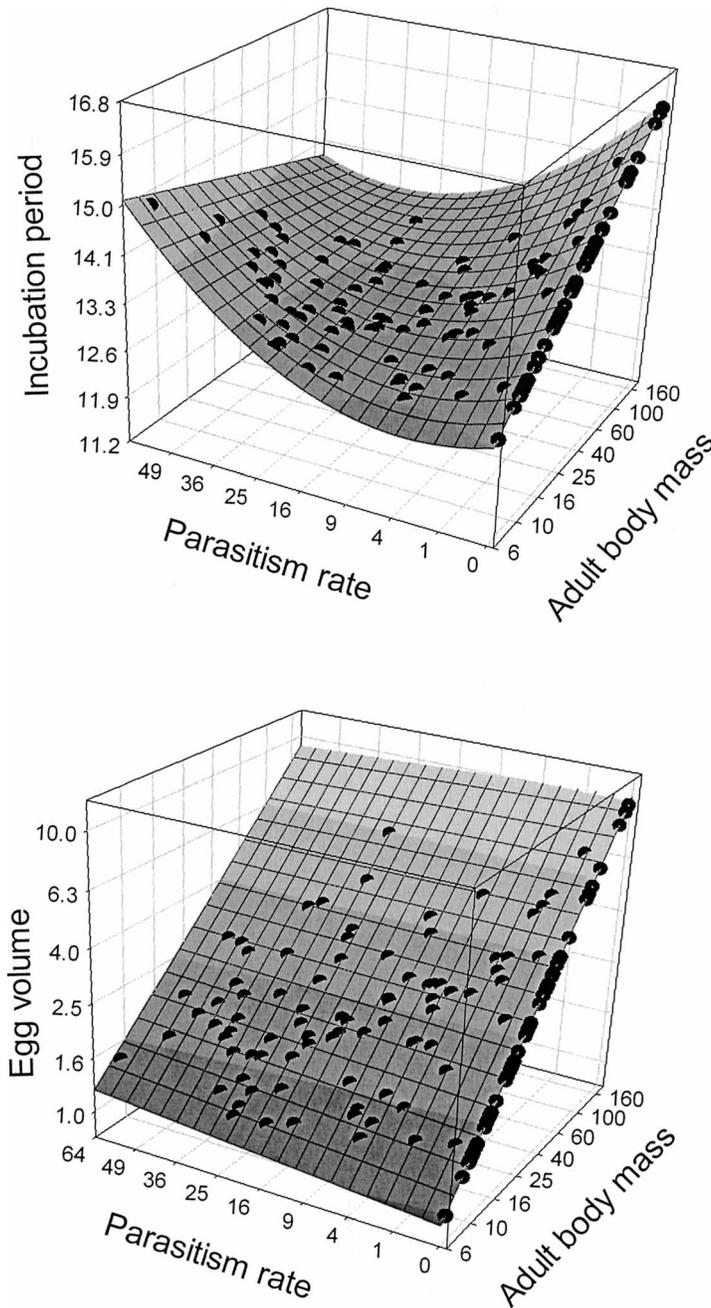


FIG. 3. Relationship between incubation period (day; top) and egg volume (cm³; bottom), and parasitism rate (%) and adult host body mass (g). Shown are predicted relationships for average values of continuous variables controlled for in the analyses reported in Results (nest predation rate = 0.127, clutch size = 4.1) for aerial foragers. Black dots are observations projected on the predicted plane, which should highlight parts of the plane that are most supported by data and thus best interpretable.

3.86, $P = 0.052$), and when removed from the model, parasitism rate had no linear effect on the incubation period whatsoever ($F_{1,121} = 0.04$, $P = 0.836$).

Length of the incubation period differed between parasitism categories, but this effect depended on adult body mass (IN: $F_{2,121} = 4.55$, $P = 0.012$; Fig. 2). There was again a

significant negative effect of nest predation rate ($F_{1,121} = 16.67$, $P < 0.001$) and a significant effect of foraging mode ($F_{1,121} = 18.93$, $P < 0.001$; whole model: $R^2 = 0.50$, $F_{7,121} = 17.38$, $P < 0.001$). In phylogenetically corrected analyses, the interaction of parasitism category with host body mass disappeared (IN: $F_{2,118} = 1.85$, $P = 0.162$), and there was also no effect of the sole parasitism category ($F_{2,120} = 0.67$, $P = 0.511$).

Egg Volume

Egg volume was positively related to parasitism rate, but this effect depended on adult body mass (IN: $F_{1,128} = 5.05$, $P = 0.026$; Fig. 3). There was also a negative effect of clutch size ($F_{1,128} = 9.96$, $P = 0.002$; whole model: $R^2 = 0.96$, $F_{4,128} = 838.89$, $P < 0.001$). The interaction of parasitism rate with host body mass disappeared in phylogeny-adjusted analyses (IN: $F_{1,125} = 2.00$, $P = 0.160$), and there was also no simple effect of parasitism rate ($F_{1,126} = 1.82$, $P = 0.180$).

Egg volume differed between parasitism categories, but this effect depended on adult body mass (IN: $F_{2,126} = 4.41$, $P = 0.014$; Fig. 2). There was also a significant negative effect of clutch size ($F_{1,126} = 8.12$, $P = 0.005$; whole model: $R^2 = 0.97$, $F_{6,126} = 595.59$, $P < 0.001$). Also in the case of parasitism category, both the interaction with host body mass (IN: $F_{2,123} = 0.52$, $P = 0.593$) and simple effect of parasitism category ($F_{2,125} = 1.27$, $P = 0.285$) were not significant in analyses adjusted for phylogeny.

All the analyses of egg volume were performed without *Calcarius ornatus*, which was strongly outlying (standardized residual = 5.9).

DISCUSSION

Brood parasitism caused by the brown-headed cowbird affected growth and development of its North American hosts. At the nestling stage, growth rate increased, mass at fledging decreased, and nestling period duration shortened with increasing parasitism pressure. All these effects were only present in medium and large hosts (roughly above 30 g; Fig. 1). These results were not confounded by relevant covariates (adult body mass, latitude, clutch size, nest predation, foraging technique), which were all controlled for in multivariate analyses. Moreover, these results were also robust to the incorporation of phylogeny into the analyses. The effects were less clear at the incubation stage. Incubation period length was shortest at intermediate levels of parasitism, whereas egg volume increased with parasitism rate (Fig. 3). However, these effects largely disappeared when the analyses were adjusted for phylogeny. These results together lend strong support for the role of sibling competition caused by brood parasitism in shaping growth and development strategies of North American passerine birds. However, it is important to note that although the effects were clear and thus support the general effect of brood parasitism on host growth, they concerned a minority of the studied species. Among 68 hosts, there were only 14 species heavier than 30 g and 31 species heavier than 20 g.

One of the most interesting aspects of these results is the pervasive presence of the interaction between the effects of parasitism rate and adult host body mass on growth and de-

velopment. The general trend at the nestling stage is for a minimum or no effect of parasitism rate in the smallest hosts (up to about 30 g), with the effect increasing up to the largest host body masses (Fig. 1). This agrees with the patterns of host mortality in the presence of the cowbird chick. The smaller the host species, the higher the host young mortality. In the smallest species (mass about 10–20 g), host mortality often reaches 100% (Lorenzana and Sealy 1999; Hauber 2003a; Kilner 2003). The small young are easily outcompeted by much larger cowbird chicks in the begging contest for resources brought by parents (Dearborn 1998; Lichtenstein and Sealy 1998). Since this mortality cannot be escaped by adjusting growth strategies, it has no relevance for the evolution of growth rate (Ricklefs 1969). Similarly, no host chicks of the smallest species are exposed to competition with cowbird young for food (since they all die); thus, there is presumably no selection for early nest leaving. On the contrary, young of the hosts that are comparable to the cowbird in their size are not outcompeted by cowbird nestlings (Dearborn and Lichtenstein 2002), and they fare comparably well even in the company of parasitic nestmates (Davies 2000). Thus, young of these species are exposed to direct competition for resources with the cowbird chick. Moreover, there is still on average about 20% more nestling mortality caused by the presence of the cowbird chick in hosts of this weight category (i.e., 45 g; V. Remeš, unpublished analyses of data from Lorenzana and Sealy 1999; Hauber 2003a; Kilner 2003). Since this mortality can be escaped or alleviated by increasing growth rate (see introduction), it has direct relevance for the evolution of growth strategies. However, cowbird-caused nestling mortality in large hosts (above about 80 g) is negligible, and mortality of the cowbird chick in these hosts is high (Kilner 2003). I would accordingly predict weak to absent effects of cowbird parasitism on growth strategies with host mass substantially outreaching cowbird body mass. Instead, the effect increased up to the highest host masses. This may be caused by the low sample of large hosts that are heavily parasitized, which may have distorted the fitted relationship. Alternatively, there might really be no such weakening, for which fact there seems to be currently no explanation.

Developmental adaptations during incubation were less clear. There was a shortening of the incubation period with increasing parasitism pressure in hosts above about 40 g, whereas in smaller hosts the relationship of incubation period to parasitism was curvilinear (Fig. 3). However, when adjusted for phylogeny, these effects disappeared. This seems surprising since incubation period has clear consequences for host mortality in this system (Hauber 2003a; Kilner 2003) and is as sensitive to another important selective factor, nest predation, as growth rate and nestling period duration (e.g., Bosque and Bosque 1995; V. Remeš, unpubl. data). There are at least two possible explanations. (1) Incubation period in the brown-headed cowbird (10.5 days) is already very short for its body and egg mass. In fact, in the sample of species analyzed here, it lies outside the ranges for this body mass (45 g) or egg volume (3.46 cm³), and is thus by far the shortest incubation period. This may make any significant shortening of the incubation period in the host species as compared to the cowbird physiologically impossible. Moreover, in species

where the incubation period could be shorter than that of the cowbird (i.e., in very small species), this may bring no advantage since their mortality in the presence of the cowbird chick is extremely high anyway (see above). (2) Further shortening of the incubation period may be precluded by costs associated with it. For example, long incubation may bring significant advantages to the development of the immune system (Ricklefs 1992, 1993; Palacios and Martin 2006). Effects of parasitism rate on egg volume were rather weak (Fig. 3) and they disappeared completely after adjusting for phylogeny. This could be explained based on the finding that egg mass variation usually has small effects on subsequent chick mass (reviewed in Williams 1994; Krist et al. 2004). Moreover, egg mass is not evolutionarily sensitive to another major selective factor, nest predation rate (Martin et al. 2006; V. Remeš, unpubl. data).

When host species were categorized as nonhosts versus old hosts versus new hosts, the results were similar, as with simple parasitism rate, but enabled an insight into the tempo of the adjustment of growth strategies in relation to brood parasitism. New hosts have been parasitized for the last 100–200 years (Mayfield 1965), whereas old hosts have been parasitized for at least several thousands of years (see also Hosoi and Rothstein 2000). At the nestling stage, parasitism category interacted with host body mass in affecting growth rate and relative fledging mass, whereas there was a simple effect of parasitism category on nestling period duration (Fig. 2). These effects were largely supported by phylogenetically adjusted analyses. In the case of the nestling period and relative fledging mass, there was a clear effect of the length of coevolution with a cowbird parasite. Old hosts had the shortest nestling period and lowest fledging mass, in new hosts these characteristics were intermediate, and in nonhosts nestling period was longest and fledging mass largest. In the case of relative fledging mass, this was true for host body mass of 50 g and higher, which agrees with body mass-dependent host mortality caused by the cowbird. Growth rate was higher in old hosts than in nonhosts in species weighing 50 g and above, but, surprisingly, it was highest in new hosts (Fig. 2). The effects of parasitism category were less clear during incubation, and completely disappeared after adjusting for phylogeny. Again, developmental characteristics were more flexible at the nestling stage than during incubation. Adjustments of the nestling period duration and relative fledging mass agreed with the length of coevolution with the brood parasite, whereas in growth rate this was not obvious.

There are at least two complications hindering clear-cut interpretation of the results obtained here. First, I analyzed the evolution of growth and developmental allometries in relation to interspecific parasitism; that is, in all analyses, host adult body mass was controlled for. However, it is possible that host species under strong parasitism pressure could adjust adult body mass evolutionarily. Large species do not suffer much from cowbird parasitism (Lorenzana and Sealy 1999); thus, this would be a logical outcome. However, here I was concerned with the evolution of developmental allometries and was not able to analyze possible shifts in host adult body mass. Second, cowbird host selection could play a role. If cowbird females selected hosts with, for example, rapid nestling growth (which could signal high food provisioning),

the relationship between rapid host growth and cowbird parasitism would emerge. However, such an argument would not easily apply to other traits (nestling period, relative fledging mass). Moreover, cowbird females are extreme generalists, laying many eggs during the breeding season to the nests of many hosts (reviewed in Ortega 1998; Davies 2000). Thus, it seems that behavioral adaptations on the side of parasite could not explain results obtained here.

The evolutionary adjustment of growth strategies of cowbird hosts has a direct bearing on the evolution of other antiparasite strategies. The majority of cowbird hosts accept parasitic eggs (Ortega 1998). Antiparasite defenses at the nestling stage may include refusal to feed (Payne et al. 2001), chick desertion (Grim et al. 2003; Langmore et al. 2003), or direct killing (Redondo 1993). However, no such behavior is known in cowbird hosts, and relatively infrequent occurrence of these nestling-stage adaptations in hosts of brood parasites in general has been an enigma and provoked the development of multitude of explanations (reviewed in Grim 2006). No study so far has considered elevated growth rates as a possible host defense against negative effects of parasitism. Moreover, adjustment of growth strategies may even partly explain the puzzling absence of other defenses at the nestling stage. If these growth adjustments mitigate negative effects of parasitic chicks on host young, they may decrease the strength of selection on the evolution of alternative defenses (similar to how egg rejection reduces selection pressure on the host adaptive response to parasitic chicks, see Grim 2006). Then the question remains why the adjustment of growth and development should evolve instead of other defenses. Obviously, it is free of recognition errors, which could be a key advantage over chick discrimination. Moreover, it may be less costly or more evolutionarily flexible. These hypotheses remain to be tested.

This study showed that brood parasitism by the brown-headed cowbird affected the evolution of growth strategies of its hosts. Thus, in addition to juvenile mortality caused by nest predation (Remeš and Martin 2002; Roff et al. 2005), sibling competition caused by the presence of a genetically unrelated nestmate emerged as an important selective factor. This agrees with some previous comparative analyses demonstrating effects of sibling competition on pre- and postnatal development rates in birds (Royle et al. 1999; Lloyd and Martin 2003) and other studies demonstrating effects of parasitism on host life histories (Martin et al. 2001; Møller 2005). Adjustments during nestling stage were more pronounced than during incubation. Growth strategies were surprisingly evolutionarily flexible. The adjustment of growth rate had to take place during the last 100–200 years, because new hosts grew at least as fast as old hosts. In the case of nestling period duration and relative fledging mass, new hosts were intermediate between old hosts and nonhosts, which suggests that these characteristics evolve more slowly and currently lag in their evolutionary response. The recent expansion of the brown-headed cowbird has been enabled by human alteration of habitats, especially forest fragmentation (Lloyd et al. 2005). Human alteration of habitats can thus have strong cascading effects on the evolution of life-history traits in birds (see also Martin and Clobert 1996; Hosoi and Rothstein 2000; Hauber 2003b).

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