

Variation in growth of Brown-headed Cowbird (*Molothrus ater*) nestlings and energetic impacts on their host parents

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Abstract: I tested several hypotheses about the plasticity of avian growth by comparing growth of Brown-headed Cowbird (*Molothrus ater*) nestlings in 20 different host species. Growth of cowbird nestlings was not strongly correlated with host adult mass and nearly all hosts were able to provision cowbirds with enough food to grow at nearly the highest observed rate. Cowbird growth was positively correlated with site latitude (which negatively covaried with maximum temperature) and negatively correlated with the nestling period of the host species. The metabolizable energy expenditure of cowbird and host nestlings was estimated as an approximate measure of the food provisioned by parents. As host adult mass varied from 6 to 113 g, one cowbird nestling was equivalent to 3.4–0.56 host nestlings in terms of peak daily energy intake. Cowbird nestlings impose a substantial energetic demand on smaller host parents that may reduce their future survival or fecundity. The quantity of energy delivered to parasitized nests demonstrates that parents are often willing to provision nests at a much higher rate than for an average clutch of their own young.

Résumé : J'ai éprouvé plusieurs hypothèses sur la plasticité de la croissance des oiseaux en comparant la croissance des oisillons du vacher à tête brune (*Molothrus ater*) dans les nids de 20 espèces hôtes. La croissance des vachers n'était pas en corrélation étroite avec la masse des hôtes adultes et presque tous les oiseaux hôtes ont été en mesure de procurer suffisamment de nourriture aux oisillons parasites pour assurer leur croissance à un taux voisin du plus haut taux observé. La croissance des vachers s'est révélée en corrélation positive avec la latitude du site de nidification (elle-même en corrélation négative avec la température maximale) et en corrélation négative avec la période de nidification de l'espèce hôte. La dépense d'énergie métabolisable des oisillons du vacher et de ceux de l'espèce hôte équivalait approximativement à la quantité de nourriture apportée par les parents. La masse des hôtes adultes se situait entre 6–113 g et la consommation quotidienne maximale d'énergie d'un oisillon parasite équivalait à 3,4–0,56 fois celle des oisillons de l'espèce hôte. Les oisillons du vacher imposent une dépense énergétique importante aux parents d'espèces hôtes de petite taille, ce qui peut diminuer leur survie ou leur fécondité futures. La quantité d'énergie fournie aux nids parasités démontre que les parents sont souvent prêts à investir plus d'efforts à ravitailler les nids parasités qu'à nourrir une couvée moyenne de leurs propres oisillons.

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Introduction

Growth in altricial avian species is regulated by two factors, the rate at which food is delivered to the young and the quality of that food (Boag 1987; Johnston 1993; Starck and Ricklefs 1998a). The rate at which food is delivered to the young reflects a trade-off between the foraging effort of the parent, which may result in decreased survivorship or future fecundity of the parents (Dijkstra et al. 1990; Siikamäki et al. 1997; but see Gustafsson and Sutherland 1988; Pettifor 1993), and the fitness gained through feeding the offspring. This trade-off can result in parent–offspring conflict (Trivers 1974) because the benefit to the offspring of additional provisioning by the parents may not lead to maximization of the parents' fitness. Extreme examples of this are cases of brood parasitism in which the offspring are unrelated to the parent. In this situation one would expect the offspring to attempt to secure

as much food as the parents are willing to provide. Studying the growth of parasitic nestlings offers an opportunity to examine the plasticity of nestling growth in response to different feeding rates of various host species. In addition, the impact of parasitic nestlings on host parents of different sizes and foraging abilities can be estimated in order to understand impacts on parental fitness.

Several studies have examined the plasticity of development in altricial passerines and the degree to which nestling growth is stunted by periods of food shortage (Lack and Lack 1951; Emlen et al. 1991; Lepczyk and Karasov 2000). Growth of nestlings of generalist parasites such as the Shiny Cowbird (*Molothrus bonariensis*) and Brown-headed Cowbird (*Molothrus ater*) represents a situation in which the young grow and develop in nests with parents that vary in body size, diet, and foraging ability, which may lead to differences in the rate of provisioning (Sæther 1994). The degree to which the growth of cowbird nestlings reflects characteristics of their host parents or the nesting environment is only beginning to be studied. Wiley (1986) examined the growth of Shiny Cowbird chicks in three host species varying from 12.8 to 74 g in body mass and found that the mass of cowbird nestlings at fledging increased with the mass of the host. Similarly, Kleven et al. (1999) found that Cuckoo (*Cuculus*

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canorus) nestlings grew faster and fledged heavier in the larger (28.5 vs. 12 g) of two hosts. In contrast, Weatherhead (1989) found the growth rates of Brown-headed Cowbird nestlings to be nearly identical in hosts weighing 9.5 and 52.6 g. Clearly, understanding the relationship between host mass and the growth rate of parasitic young requires substantially larger sample sizes of host species in order to remove the confounding effects of taxonomy, diet, foraging style, resources, and other factors.

Several host species fail to fledge Brown-headed Cowbird (hereinafter cowbird) nestlings and this has been attributed to protein or nutrient deficiencies in the granivorous or frugivorous diet that these hosts provide to their nestlings (Rothstein 1976; Middleton 1991; Kozlovic et al. 1996). Hosts that feed their young an insectivorous diet may fail to fledge cowbirds for other reasons that may be related to interruptions in feeding (e.g., Tree Swallows, *Tachycineta bicolor*; Mills 1988). Analysis of the growth patterns of cowbird nestlings across a range of hosts may illuminate the reasons for poor growth in these otherwise suitable host species.

For hosts that feed their young a primarily insectivorous diet, one would expect the growth of the nestlings to increase with the rate at which food is delivered up to the physiological maximum rate at which the nestlings can process food, or deposit and mature tissue (Lilja et al. 1985; Konarzewski 1988; Ricklefs et al. 1994). Since the foraging and provisioning rate of parents has been shown to be positively and tightly correlated with their mass (Bryant and Westerterp 1980; Sæther 1994), we might expect an asymptotic relationship between adult mass of the host and growth of cowbird nestlings. Below I test the hypothesis that cowbird growth increases with host adult mass, as we would expect if smaller hosts do not provision cowbirds sufficiently.

One factor that might counter this pattern, and lead to decreased growth of cowbird nestlings as host mass increases, is competition for food with nestmates, which is likely to vary with the size of the host nestlings. Cowbird nestlings, in contrast to Cuckoo nestlings, generally do not force host eggs or nestlings from the nest (but see Dearborn 1996) and thus are subject to competition from other nestlings. To determine whether nestling competition is important, one would need to compare cowbird nestling growth in nests with and without nestmates. Data for Dickcissels (*Spiza americana*) (A.M. Kilpatrick, unpublished analyses) suggest that growth of cowbirds in nests with other cowbirds or host nestlings is usually not reduced (in contrast to when they are the lone nest occupant), but this result may not be valid for all host species. Unfortunately, cowbird growth data are rarely, if ever, presented in a format that would allow this comparison. As a result, this question cannot be addressed further.

This paper has two purposes. First, I gathered published and unpublished data on growth of cowbird nestlings in different host species to test hypotheses about the relationships between nestling growth and host and site characteristics. Second, I used the growth patterns of hosts and cowbirds, together with allometric relationships, to estimate the provisioning rate required by host and cowbird nestlings. I used these estimated energetic requirements to assess the impact of cowbird nestlings on their host parents, and I compared this with the effort the parents normally expend on their own young.

The growth of cowbird nestlings below their physiological maximum rate is hypothesized to (i) increase with the adult mass of the parents (Hatch 1983; Wiley 1986; Eckerle and Breitwisch 1997), since provisioning rate increases with adult mass (Bryant and Westerterp 1980; Sæther 1994), (ii) increase with the host growth rate (Hatch 1983), and (iii) increase with latitude through an increase in the number of hours during which parents are able to forage for food each day (Ricklefs 1968). I also tested two alternative hypotheses about the role temperature might play in cowbird growth. Growth may increase with temperature because of decreased thermoregulatory costs of the chicks (Ricklefs 1968; Sullivan and Weathers 1992), or decrease with temperature if heat stress impairs the ability of the parents to provide food for the young (Murphy 1985).

Methods

Nestling growth

I gathered records of cowbird growth through an intensive literature search and by contacting researchers who had worked with cowbirds. Data from hosts for which there were several nestling records suggested that a record of a single nestling was not always representative of cowbird growth for that species. In contrast, the average of any two randomly selected growth records was much more representative. As a result I included only those host species for which there were at least two records of cowbird nestling growth. Increasing this minimum to three records did not change any of the conclusions reported below. In addition, I only included hosts for which cowbird nestling masses were measured through day 8, for reasons discussed below.

I used nonlinear regression to fit the growth data to a logistic equation (Robertson 1923; Ricklefs 1968; Starck and Ricklefs 1998b) of the form

$$M_t = A / \{1 + \exp[-K(t - t_i)]\}$$

where M_t is the mass of the nestling in grams on day t , A is the asymptotic or fledging mass in grams, K is the growth constant with units of days^{-1} , t is the age of the nestling in days, and t_i is the inflection point of the curve in days.

Fitting the logistic equation to growth data in which there is no clear asymptote is somewhat problematic in that the parameters of the model (A , K , and t_i) are sensitive to small changes in the last-measured masses. Unfortunately, several researchers (e.g., Nice 1937; Hatch 1983; Dearborn et al. 1998; J.N.M. Smith, personal communication) stopped measuring nestlings on day 8 (before the asymptote was reached) to avoid "force-fledging" the nestlings prematurely. To overcome this difficulty I used mass at day 8 (hatching occurs at the beginning of day 0) as a second measure of cowbird growth. I tested each hypothesis using both of these growth measures in an effort to make the conclusions drawn from the analyses independent of the growth measure chosen. I chose mass on day 8 for the second measure because this was the latest date that could be obtained for most host species, and thus would be the best estimate of mass at fledging. For many avian species, mass at fledging has been shown to be correlated with fledgling survivorship to independence (e.g., Krementz et al. 1989; Linden et al. 1992; Caffrey 2000; but see Stromborg et al. 1988; Wolf et al.

1988) and thus represents a meaningful end-point in terms of growth.

Because I wanted to compare the growth of cowbird nestlings with the growth of host nestlings, I fit daily masses of host chicks (at the same site where possible) to the same logistic growth model. I also used the nestling period of the host species as a measure of growth rate, because it has been measured for many more nestlings than I had daily masses for, and because it measures a similar quantity to the logistic growth rate, K (Ricklefs 1968).

Energy expenditure

To estimate the energetic impact of cowbird nestlings on their host parents I used the peak daily metabolizable energy (PDME) and total metabolizable energy (sensu Weathers 1992) as estimates of the energy that the host parents would have to supply to their nestlings. Because the daily masses and growth trajectories of cowbirds in different nests varied, I estimated the energetic expenditure of cowbirds for each host species separately. I calculated the energetic expenditure of host and cowbird nestlings using two equations given by Weathers (1992). The first estimates PDME, in kilojoules per day, of a nestling as $11.69 \times M^{0.9082} \times t_{fl}^{-0.428}$, where M is the fledging mass of the nestling in grams and t_{fl} is the nestling period in days (eq. 14 in Weathers 1992). The second estimates the total metabolizable energy from hatching to fledging, in kilojoules, as $6.65 \times M^{0.852} \times t_{fl}^{-0.710}$ (eq. 8 in Weathers 1992). These estimates of nestling energy expenditure are only approximate and are not meant to be exact measures. Nonetheless, they have value in a comparative context, and it is in this way that I use them below.

To estimate the total amount of energy that parents normally deliver to a brood of their own young, I multiplied the energy required by one host nestling by the average clutch size for that species. I also calculated two estimates of the maximum provisioning rate required by the host parents, one using the maximum fledged clutch size recorded for an unparasitized clutch and the other by calculating the largest energetic expenditure of a recorded parasitized clutch in which all nestlings fledged (sources are given in Tables 1 and 3). Since the masses of the chicks in these enlarged clutches were not measured, I assumed that they fledged at the same mass as those in smaller clutches for which I had data.

Finally, the impact of cowbird nestlings on their host parents was estimated by calculating the ratio of the PDME expended by a cowbird nestling divided by that for a single host nestling. This provides an estimate of the “nestling equivalents” of one cowbird young in terms of the energetic demands on the host parents.

Results

Nestling growth

I found records of cowbird nestling growth suitable for fitting to a logistic model for 19 host species (Table 1). In addition, records of cowbird nestling masses on day 8 were found for one additional host species, the Tree Swallow. Sample sizes of nestlings of each species in the analyses varied from 2 to 78 (Table 1). House Finches (scientific names for all species are given in Table 1) and Tree Swallows did

not fledge any cowbird young (Mills 1988; Kozlovic et al. 1996) and were excluded from the analyses below. The growth parameters for cowbird and host nestlings are given in Table 1.

Cowbird growth measured as mass on day 8 did not significantly increase with host adult mass ($r = 0.18$, $p = 0.47$; Fig. 1). Day 8 mass in hosts smaller than adult cowbirds was not significantly different from day 8 mass in hosts larger than adult cowbirds (t test, $t_{[17]} = -1.25$, $p = 0.25$). In addition, there was no significant difference in the variance in cowbird day 8 mass between smaller and larger hosts ($F_{[1,17]} = 1.046$, $p = 0.75$). The coefficient of variation for cowbird day 8 mass among hosts was 0.15. This was similar to the coefficient of variation for individuals within a single host species (e.g., Indigo Bunting 0.17, Ovenbird 0.11, Blue-gray Gnatcatcher 0.15, Song Sparrow 0.14), suggesting that there was greater variation among hosts than would be expected simply as a result of individual variation within hosts. However, this variation was uncorrelated with host adult mass in a univariate analysis (but see below).

Cowbird day 8 mass was negatively correlated with the nestling period of the host ($r = -0.53$, $p = 0.023$) and positively correlated with latitude ($r = 0.57$, $p = 0.013$; Fig. 2A). Day 8 mass was also negatively correlated with the average maximum monthly temperature from May to July at the site (Anonymous 2000) during the years when the growth data were collected ($r = -0.55$, $p = 0.019$; Fig. 2B). However, maximum temperature and latitude were highly negatively correlated ($r = -0.79$, $p < 0.001$), so it is difficult to know which independent variable is responsible for the correlation with cowbird growth, or if both are. A stepwise regression suggested that latitude is slightly more influential than temperature, but the high multicollinearity of the independent variables makes this conclusion questionable.

In a multiple-regression analysis, cowbird day 8 mass was negatively related to nestling period, negatively related to maximum temperature (or positively related to latitude), and positively correlated with adult mass (Table 2). Interestingly, adult mass was significantly correlated with day 8 mass in a multivariate analysis while being uncorrelated in the univariate analysis. Either latitude or maximum temperature (but not both) showed significant effects in a multiple regression with nestling period and adult mass. I present the regression model including maximum temperature (Table 2) rather than latitude because it explains slightly more variance in day 8 mass.

The other measure of cowbird growth, the logistic K , was also unrelated to host adult mass ($r = -0.02$, $p = 0.9$). Although the relationships were all of the same sign as the correlations with day 8 mass, the cowbird logistic K showed much weaker relationships with host nestling period ($r = -0.45$, $p = 0.063$), latitude ($r = 0.38$, $p = 0.12$), and maximum temperature ($r = -0.25$, $p = 0.31$).

Energy expenditure

The PDME of cowbird nestlings was uncorrelated with the adult body mass of the host parents ($r = 0.28$, $p = 0.24$; Fig. 3A). The pattern was similar when provisioning energy was measured as total metabolizable energy ($r = 0.28$, $p = 0.24$; Fig. 3B). There was also no significant correlation between cowbird day 8 mass and the PDME of an average host

Table 1. Host and cowbird nestling growth measures.

	Host				Nestling period (days)	Source(s) for growth data
	K	A	t_i	N		
Western Wood-pewee (<i>Contopus sordidulus</i>)	0.42	16.2	5.9	29	15.5	D.R. Curson and A.M. Kilpatrick, unpublished data
Tree Swallow (<i>Tachycineta bicolor</i>)* [†]	0.53	21.9	6.3	23	20	Paynter 1954
Veery (<i>Catharus fuscenscens</i>)	0.69	26.2	3.5	3	11	Friedmann 1929
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	0.52	6.2	4.2	10	13	Ellison 1992; D.R. Curson and A.M. Kilpatrick, unpublished data
Plumbeous Vireo (<i>Vireo plumbeous</i>)	0.52	15.5	4.8	37	13.5	Marvil and Cruz 1989; Curson and Goguen 1998; D.R. Curson and A.M. Kilpatrick, unpublished data
Red-eyed vireo (<i>Vireo olivaceus</i>) [†]	0.54	15.0		22	11	Starck and Ricklefs 1998b
Yellow Warbler (<i>Dendroica petechia</i>)	0.69	9.5	3.9	74	10.5	Weatherhead 1989
Ovenbird (<i>Seiurus aurocapillus</i>)	0.60	15.5	5.4	3	8.5	Van Horn and Donovan 1994
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)	0.49	46.1	5.7	78	13	Ortega and Cruz 1992a
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	0.56	36.3	4.8	25	12.5	Weatherhead 1989
Common Grackle (<i>Quiscalus quiscula</i>)	0.40	65.7	7.0	40	13.5	Peer and Bollinger 1997b
Northern Cardinal (<i>Cardinalis cardinalis</i>)	0.56	28.7	3.0	25	9.5	Norris 1947; Eckerle and Breitwisch 1997
Indigo Bunting (<i>Passerina cyanea</i>)	0.56	10.8	3.9	70	10.5	Payne 1992; Dearborn et al. 1998; D.C. Dearborn, unpublished data
Lazuli Bunting (<i>Passerina amoena</i>)	0.51	12.8	4.7	18	10	Greene et al. 1996
Dickcissel (<i>Spiza americana</i>)	0.60	18.3	4.2	19	9	Hatch 1983; S.A. Hatch, unpublished data
House Finch (<i>Carpodacus mexicanus</i>)*	0.44	19.1	5.8	11	15.5	Hill 1993; Kozlovic 1998
Henslow's Sparrow (<i>Ammodramus henslowii</i>)	0.71	9.4	3.1	4	9.5	S.A. Hatch, unpublished data
Dark-eyed Junco (<i>Junco hyemalis</i>)	0.52	17.8	4.9	29	11	Wolf 1987
Chipping Sparrow (<i>Spizella passerina</i>) [†]	0.54	11.4	4.2	56	10.5	Reynolds and Knapton 1984
Song Sparrow (<i>Melospiza melodia</i>)	0.47	23.8	5.3	20	10.5	Smith et al. 1982

Note: N is the number of nestlings measured. See Methods for details on estimating growth parameters. Data for several species were taken from

*Host did not fledge cowbird young.

[†]Host and cowbird growth data are from different sites.

clutch ($r = 0.26$, $p = 0.30$), a surrogate for the maximum energy provisioned by parents.

The ratio of the PDME of cowbird nestlings to the peak daily metabolizable energy of a host nestling showed a sharp decrease from almost 3.5 nestling equivalents at a host mass of 6 g (Blue-gray Gnatcatcher) to 1.3 nestling equivalents at 21 g (Song Sparrow) (Fig. 4). It then slowly decreased to ~0.6 nestling equivalents at a host adult mass of 113 g (Common Grackle), intersecting one nestling equivalent at 47 g (Fig. 4), near the approximate mass of an adult cowbird, 48 g (Dunning 1993; sexes averaged).

The maximum clutch size for cowbird hosts was, on average, 39% higher than the average clutch size (Table 3), suggesting that in some conditions host parents are capable of provisioning their young at significantly higher rates than for an average clutch. However, in some parasitized nests, host parents were able to work harder still, provisioning nests at rates 24% higher than the feeding rate for the maximum clutch size for that species (B/A ratios in Table 3), or 69% higher than the provisioning rate for an average clutch.

Discussion

Previous authors have suggested that cowbird nestling growth might increase with the adult or nestling mass of the host (Hatch 1983; Wiley 1986; Eckerle and Breitwisch 1997),

since larger species generally have higher provisioning rates (Sæther 1994). My analyses suggest that cowbird growth is not strongly related to adult mass, and that most hosts are able to provision cowbirds sufficiently for them to fledge within their normal nestling period.

Four host species appeared to be exceptions to this generalization. In these hosts, cowbirds showed substantially lower growth rates, resulting in day 8 masses much lower than the average day 8 mass, 23.9 g. However, in only one species, the Blue-grey Gnatcatcher, did host adult mass appear to be an explanatory factor. At 6 g, Blue-gray Gnatcatchers represent one of the smallest hosts of cowbirds and may simply be unable to provision at a rate sufficient to support the cowbirds' potential for rapid growth. The rate at which gnatcatcher parents provision an average clutch of 4.35 nestlings falls short of that necessary to feed a single cowbird growing at the maximum observed rate (Fig. 3A) and suggests that while cowbirds are able to fledge from gnatcatcher nests, they do so at much smaller sizes and their survivorship to independence may be reduced.

The other three host species in whose nests cowbirds grew poorly were the House Finch, Tree Swallow, and Western Wood-pewee (Table 1). Poor growth in House Finch nests has been previously attributed to protein deficiency of the granivorous diet they feed their nestlings after the first few days following hatching (Kozlovic et al. 1996). Tree Swal-

Cowbird					
K (days ⁻¹)	A (g)	t_i (days)	Day 8 mass (g)	N	Source(s) for growth data
0.45	28.8	6.4	19.5	5	D.R. Curson and A.M. Kilpatrick, unpublished data
			18.0	2	Mills 1988
0.62	30.0	5.2	25.3	2	Friedmann 1929; Norris 1947
0.50	22.5	4.4	19.1	10	D.R. Curson and A.M. Kilpatrick, unpublished data
0.55	26.9	4.9	22.1	43	Marvil and Cruz 1989; D.R. Curson and A.M. Kilpatrick, unpublished data
0.54	36.1	5.6	28.2	4	Friedmann 1929; Herrick 1935
0.59	30.5	4.9	25.4	12	Weatherhead 1989; D.M. Scott, unpublished data
0.70	29.2	4.8	26.3	3	Hann 1937; Norris 1947
0.48	29.1	5.3	21.8	11	Ortega and Cruz 1992a
0.58	31.7	5.1	26.8	23	Weatherhead 1989
0.57	31.9	5.6	26.1	15	Peer and Bollinger 1997a
0.48	33.9	4.5	25.7	3	Norris 1947; Eckerle and Breitwisch 1997
0.56	28.9	4.7	24.6	15	Dearborn et al. 1998; D.C. Dearborn, unpublished data
0.53	29.7	5.4	23.2	8	Greene et al. 1996
0.51	31.1	5.4	24.9	15	Hatch 1983; S.A. Hatch, unpublished data
0.30	25.3	7.6	14.8	23	Kozlovic et al. 1996
0.56	24.9	3.8	22.9	2	S.A. Hatch, unpublished data
0.55	29.0	5.2	24.3	13	Wolf 1987
0.54	30.7	4.2	25.6	2	D.M. Scott, unpublished data
0.58	33.2	4.3	28.1	4	D.M. Scott, unpublished data; J.N.M. Smith, unpublished data

Ehrlich et al. (1988).

lows and Western Wood-pewees both forage on aerial insects, and interruptions in this food supply by rain or wind might be intolerable for a rapidly growing young cowbird (Mills 1988).

One other explanation for the lack of a relationship between host mass and cowbird growth is the fact that nestlings of many smaller hosts in nests containing cowbird nestlings perish, whereas the young of the larger hosts often survive (Weatherhead 1989; Ortega and Cruz 1992a; Greene et al. 1996, and personal observation). As a result, cowbird nestlings in nests of small hosts may receive the undivided efforts of the parents, who would otherwise be unable to sufficiently provision both a cowbird and their own young.

The positive relationship between cowbird growth and latitude (Fig. 2A) could be a result of greater day length at higher latitudes, which would allow host parents more hours in which to forage and feed nestlings each day (Ricklefs 1976). Alternatively, or in addition, heat stress (Fig. 2B) on parents at lower latitudes could result in their spending less time feeding the young (Murphy 1985), leading to poorer growth of the cowbirds. A final possibility, that resource levels were higher at higher latitudes, was not supported by correlations with yearly rainfall (A.M. Kilpatrick, unpublished data), but yearly rainfall may be a poor indicator of prey abundance. There was no support for the hypothesis

that cowbird growth was impacted by higher thermoregulatory costs at colder sites (Fig. 3B).

The negative relationship between host nestling period and cowbird growth is due in large part to the poor growth of cowbirds in nests of three host species from the same arid site in northeast New Mexico (Blue-gray Gnatcatcher, Western Wood-pewee, and Plumbeous Vireo). Cowbird growth was uncorrelated with surrogates of food delivery such as the amount of energy metabolized by the host brood, which suggests that the negative correlation with host nestling period is not a result of decreased provisioning rates. Whether this correlation with nestling period was an artifact of the small sample size of species presented here or represents a real pattern is unclear.

One possible confounding factor merits mention. Adults of one subspecies of Brown-headed Cowbird, *M. a. obscurus*, are significantly smaller than those of the other two subspecies (average male mass: *M. a. obscurus* 40.2 g and *M. a. artemisiae* 47.5 g (Fleischer and Rothstein 1988); *M. a. ater* 48.9 g (Weatherhead and Teather 1987)). Nestlings of *M. a. obscurus* are present at three of the sites and thus are likely represented in the nests of five of the species in this paper (Blue-grey Gnatcatcher, Western Wood-pewee, Plumbeous Vireo, Song Sparrow, and Yellow-headed Blackbird). However, if the growth measures for these species

Fig. 1. Growth of cowbird nestlings measured as day 8 mass plotted against the host adult mass (sexes averaged). House Finches and Tree Swallows did not fledge cowbirds and are not included.

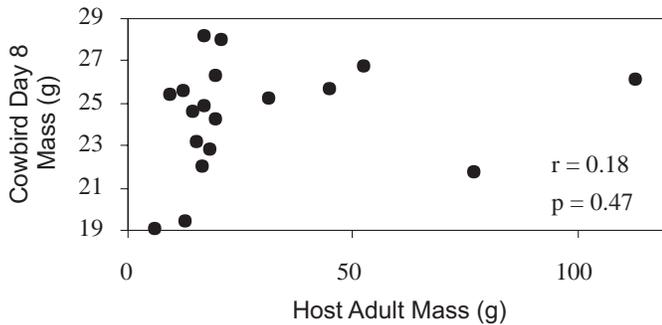
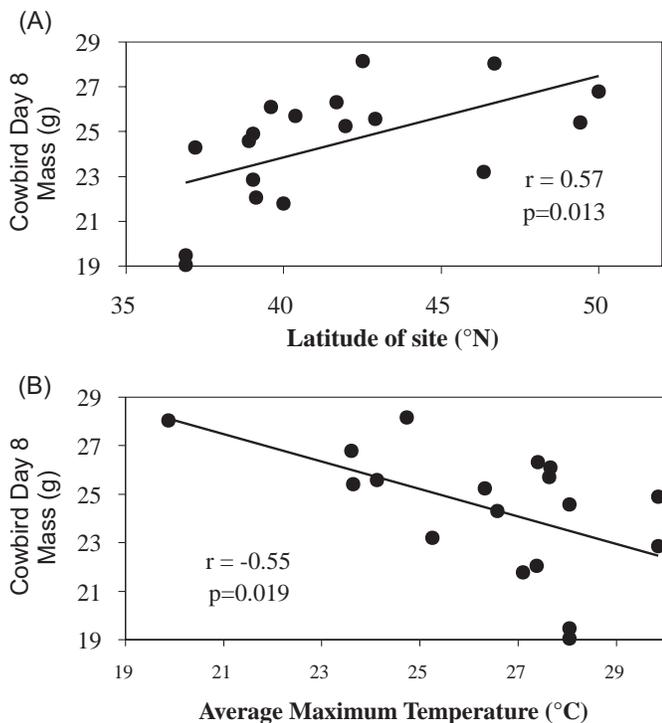


Fig. 2. Growth of cowbird nestlings measured as day 8 mass plotted against the latitude of the site (A) and the average maximum monthly temperature from May to July during the years when the growth data were collected (B). House Finches and Tree Swallows did not fledge cowbirds and are not included.



were 16.5% higher (the size difference of the subspecies), the correlations with latitude and maximum temperature would remain. In addition, at all three of the sites where *M. a. obscurus* occurs, cowbird nestling size is likely to be intermediate between the size of *M. a. obscurus* and the other two subspecies as a result of the relatively new expansion (Ortega and Cruz 1992b) of *M. a. obscurus* into these sites.

Impacts on host parents

Cowbird nestlings require significantly more food than one nestling of most of their common hosts. In cases where hosts are multiply parasitized, nests containing several cowbirds may require more food than a parent would need to

Fig. 3. Logarithmic plot of peak daily metabolizable energy (PDME) of nestlings (A) and total metabolizable energy versus host adult mass (B). The host-brood value is the average clutch size of the host multiplied by the value for one host nestling. The value for the cowbird is calculated from the average growth curve of cowbird nestlings in that host nest.

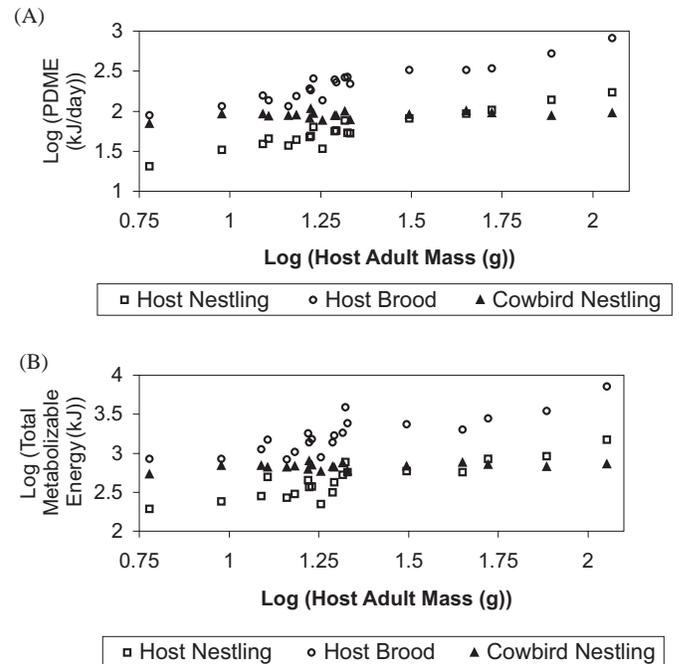


Table 2. Multiple-regression analysis of cowbird day 8 mass.

Predictor	Coefficient	<i>t</i>	<i>p</i>
Constant	48.52	10.93	<0.001
Host nestling period (day)	-0.90	-4.35	0.001
Adult mass (g)	0.04	2.87	0.012
Maximum temperature (°C)	-0.57	-3.89	0.002

Note: The total variance explained (R^2) by this model was 72.2%.

provide to the largest clutch that has ever been recorded for that species (Table 3). Nestling cowbirds appear to be able to elicit a very high rate of foraging from parents, leading to increased stress and perhaps greater predation on the parents. This cost in terms of reduced parental survival compounds the fitness costs of egg removal and reduced host-nestling survival. Two studies (Smith 1981; Sedgwick and Iko 1999) examined whether the future fecundity or survivorship of host parents decreased following parasitism. In both cases, unparasitized and parasitized parents appeared to fare equally well, but the authors of both studies argued that cowbirds appeared to select older or superior parents. My analyses suggest that the energetic impact on the parents may be substantial and argue for further study of this issue. To circumvent the difficulties encountered by Smith (1981) and Sedgwick and Iko (1999), the magnitude of the impact on parents could be directly measured by experimentally removing cowbird eggs from half of the parasitized nests and then following the survivorship and future fecundity of the parents.

Multiply parasitized nests may represent an opportunity to

Table 3. Comparison of peak daily metabolizable energy (PDME) in nests with an average-size clutch, a maximum-size clutch, and a parasitized clutch.

	Adult mass ^a	Avg. clutch size	Avg. brood PDME	Max. clutch size	Max. brood PDME (A)	Max. parasitized clutch ^b	Max. parasitized brood PDME (B)	B/A ratio
Western Wood-pewee	12.8	3	136	4	182			
Veery	31.2	4	325	5	407			
Blue-gray Gnatcatcher	6	4.4	89	5	102	2C	139	1.36
Plumbeous Vireo	16.6	4	192	5	240			
Red-eyed Vireo	16.7	3.75	194	5	245			
Yellow Warbler	9.5	3.5	116	6	198			
Ovenbird	19.4	4.4	248	6	338	3H + 2C	345	1.02
Yellow-headed Blackbird	76.8	3.8	526	5	692			
Red-winged Blackbird	52.6	3.3	341	6	620			
Common Grackle	113	4.8	824	6	1030			
Northern Cardinal	44.7	3.5	329	5	470			
Indigo bunting	14.5	3.1	115	4	148	2H + 2C	249	1.68
Lazuli Bunting	15.3	3.5	154	5	221			
Dickcissel	17	4	256	6	384	3H + 3C	472	1.23
House Finch	21.4	4.2	221	6	316			
Henslow's Sparrow	18	4	137	5	171			
Dark-eyed Junco	19.6	4	229	6	343			
Chipping Sparrow	12.3	4	156	5	195	3H + 1C	209	1.07
Song Sparrow	20.8	3.5	266	6	456	5C	495	1.08
Average	29.0	3.83	259	5.33	362			1.24

Note: For sources see Table 1 plus Friedmann (1929) and Friedmann (1963).

^aFrom Dunning (1993).

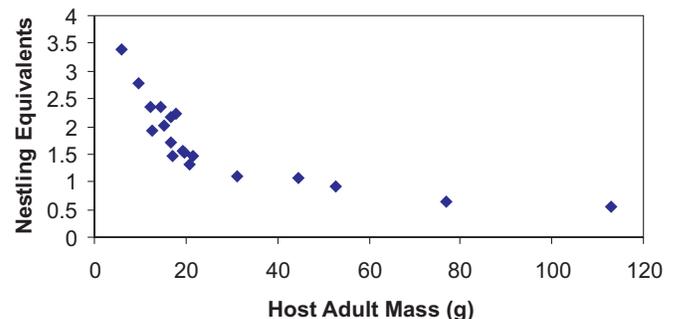
^bThe number of host (H) and cowbird (C) nestlings in the nest.

measure the maximum foraging rate of a host species. The loud, persistent begging calls of cowbird young immediately before and after nearly every delivered meal (A.M. Kilpatrick, personal observation) serve as a strong signal (Brooke and Davies 1989; Kilner et al. 1999) to parents to continue foraging to feed the nestling. Because cowbirds are unrelated to their parents and their nestmates, cowbird nestlings' fitness would be unaffected by overworking their parents, provided the parents live long enough to raise the cowbirds to independence. Parasitized clutches provide tests of hypotheses about the maximum levels of parental care that parents are willing to perform both for a brood, and for a single nestling. For a Blue-gray Gnatcatcher, one cowbird is nearly the equivalent of an entire clutch of its own young. That the parents are willing to feed cowbird nestlings to fledging and beyond suggests that the growth of a single host nestling is not limited by the maximum effort a parent will devote to one nestling.

The data in Fig. 3 and Table 3 can also be used to make predictions about which hosts would be able to raise multiple cowbirds, and how many. For example, Yellow Warbler parents are much less likely to be able to raise multiple cowbirds than are Red-winged Blackbirds, owing to much lower PDMEs. The larger number of cowbird eggs in Red-winged Blackbird nests than in Yellow Warbler nests (Weatherhead 1989) may be a reflection of nest-site characteristics, but may also be due to female cowbirds' assessment of the likelihood that the host will be able to raise multiple cowbirds.

Parasitism by Brown-headed Cowbirds has a substantial impact on many songbird species across North America. Several control programs include removal of adult cowbirds through trapping and shooting (e.g., Eckrich et al. 1999),

Fig. 4. Numbers of "nestling equivalents" (cowbird PDME / host PDME) plotted against host adult mass. See Methods for further explanation.



while others have also implemented egg and nestling removal of cowbirds (Whitfield et al. 1999). The results of this study suggest that removal of cowbird eggs from host nests will have the dual benefit of increasing the likelihood that the host will fledge some of its own young and decreasing the substantial energetic impact of cowbird nestlings on their host parents.

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