

# EFFECTS OF COWBIRD PARASITISM ON PARENTAL PROVISIONING AND NESTLING FOOD ACQUISITION AND GROWTH<sup>1</sup>

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**Abstract.** Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) is known to affect the fitness of many hosts by causing a reduction in the number of chicks that fledge from parasitized nests. However, little is known about less immediate effects on host fitness. We studied nestling growth and food acquisition and parental provisioning in parasitized and unparasitized nests of the Indigo Bunting (*Passerina cyanea*). Indigo Bunting nestlings in parasitized nests exhibited reduced rates of mass gain, but not tarsus growth, relative to bunting chicks in unparasitized nests. Bunting nestlings in parasitized nests received less food than did buntings in unparasitized nests. Buntings in parasitized nests spent more time begging than did those in unparasitized nests, but energy expended in this behavior may not have detracted greatly from the amount of energy available for growth. Adults at parasitized nests exhibited a higher provisioning rate than those at unparasitized nests. Increased provisioning by adult buntings at parasitized nests did not come at the expense of time spent brooding nestlings, but increased provisioning has the potential to affect the survival and future reproductive success of host adults. Because cowbird parasitism appears to impose substantial costs on Indigo Bunting nestlings and adults, concern over the conservation implications of parasitism should not be limited to species that suffer total reproductive failure when parasitized.

**Key words:** begging behavior, brood parasitism, Indigo Bunting, *Molothrus ater*, nestling growth, parental provisioning, *Passerina cyanea*.

## INTRODUCTION

Understanding the impact of brood parasitism on host species is an important aspect of songbird conservation (May and Robinson 1985, Trail and Baptista 1993, Robinson et al. 1995). For some host species of the Brown-headed Cowbird (*Molothrus ater*), parasitism typically results in the eventual death of all host nestlings due to starvation (Marvil and Cruz 1989). For other host species, some or all host young are able to fledge from parasitized nests (Petit 1991). For those species in which hosts are capable of fledging mixed broods of host and parasitic young, our knowledge about the costs that parasitized hosts incur during the nestling period is limited.

Researchers have tested for a negative effect

of parasitism on the growth of host nestlings; however, no study has examined the causal factors involved in the decreased growth rate of host nestlings in nests parasitized by Brown-headed Cowbirds. Host chicks in parasitized nests could exhibit low growth rates due to reduced food acquisition as a result of preferential feeding of the parasitic nestling (Soler et al. 1995, Dearborn, in press), increased energy spent on begging as host chicks try to compete for food with the parasitic nestling, or increased energy spent on thermoregulation as parents spend less time brooding nestlings due to increased rates of provisioning at parasitized nests.

In addition to costs borne by nestlings, adults of small host species also may incur costs as a result of parasitism because they may increase their rate of provisioning nestlings if they are feeding a cowbird that is much larger than a typical host nestling (Luther 1974). Such an in-

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crease in provisioning can affect both current and future reproductive efforts. The current reproductive attempt may be affected if an increase in time spent provisioning nestlings results in a decrease in the time that the parents are near the nest and available for nest defense. Increases in nest provisioning can reduce future reproductive success by decreasing adult survival, decreasing energy available for investment in subsequent broods, or increasing the time until the next reproductive attempt (Stearns 1992). Thus, the presence of a cowbird nestling in the nest of a small host has the potential to impose costs on host nestlings and host adults.

In this paper, we investigate the effect of cowbird parasitism on nestling growth and parental provisioning in the Indigo Bunting (*Passerina cyanea*). First, we compare the growth of nestlings in parasitized and unparasitized nests and examine three factors that may affect the amount of energy that host nestlings can invest in growth: the amount of food acquired by host nestlings, the amount of time that host nestlings spend begging, and the amount of time that parents spend brooding nestlings. Second, we quantify the overall rate at which parents provision parasitized and unparasitized nests.

## METHODS

Indigo Buntings are frequent cowbird hosts and are typical hosts in two important respects (Friedmann and Kiff 1985): they are much smaller in body size than are Brown-headed Cowbirds (mean of male and female adult body mass is 14.5 g for Indigo Buntings and 43.9 g for Brown-headed Cowbirds; Dunning 1993), and they are in the same family as many cowbird hosts (Family Emberizidae; AOU 1997). We located and monitored parasitized and unparasitized Indigo Bunting nests in old-field and forest edge habitat at the University of Missouri's Thomas S. Baskett Wildlife Research Area in Boone County, Missouri, in 1995–1996. All parasitized nests used in this study were singly-parasitized. Unparasitized nests were studied only during the portion of the breeding season when other nests were being parasitized by cowbirds. Within a nest, cowbird eggs and bunting eggs almost always hatched on the same day.

We measured nestlings daily through day 7 of the 10-day nestling period (day of hatch = day 0). We did not make measurements after day 7 because nestlings may fledge prematurely if han-

dled after that age. We measured both mass to the nearest 0.1 g with a digital scale and tarsometatarsus length (hereafter "tarsus") to the nearest 0.1 mm with dial calipers. In 1995, we made video recordings of nest activity for 2 hr on the morning of day 6 of the nestling period. In 1996, we made video recordings on the morning of days 2, 4, and 6. Due to nest predation and a limited number of video cameras, some 1996 nests were videotaped at only one age, whereas others were videotaped at two or three different ages. Cameras were set up at a distance of 1.5–3 m from the nest, pointing down at approximately a 30 degree angle. Recordings were started between 06:00 and 07:30. Chicks were individually marked on the top of the head with a black nontoxic marker. These marks were not visible to the parent when a chick's head was tilted back during begging.

## STATISTICAL ANALYSES

The relationships between mass and age and between tarsus length and age were linear over the 8 days that we measured nestlings. Consequently, we performed a regression of mass versus age and tarsus versus age for each individual nestling and used the slope of these regression lines as measures of nestling growth rates. Because our two measures of nestling size changed linearly over the days that we measured them, it was not necessary to use an asymptotic function (sensu O'Connor 1984) to quantify growth rates. By calculating a single value for each chick's rate of mass gain, we avoided the treatment of multiple measurements from the same individual as independent data points. We calculated growth rates based upon a mean of 5.04 days of measurements per chick (range: 2–8). The calculation of slopes from two data points is likely to yield an accurate measure of growth rates, as the  $r^2$  values for the growth regressions were high among chicks for which we had a larger number of measurements (for 81 chicks measured on six, seven, or eight days, mean  $r^2 = 0.98$  for tarsus regressions and mean  $r^2 = 0.98$  for mass regressions).

We used ANOVAs to test for an effect of cowbird parasitism on host nestling growth, using rate of mass gain as the dependent variable in one analysis and rate of tarsus growth as the dependent variable in a second analysis. In each analysis, we used parasitism (yes or no) and total brood size (2, 3, or 4, including the cowbird,

if present) as crossed factors and nest as a third factor nested within parasitism and brood size. The incorporation of nest as a factor in the analysis allowed for the use of data from each nestling but controlled for variation among nests in growth rates that may reflect differences in factors such as parental quality. We used nest as a fixed factor rather than as a random factor because we used data from all nests that we found rather than from a random sample of nests found (Neter et al. 1990).

Because we detected an effect of parasitism on rate of mass gain (see Results), we performed analyses to determine whether all bunting chicks in parasitized nests experienced reduced growth rates or, alternatively, whether some chicks suffered very reduced rates of mass gain while their healthier nestmates gained mass at a more normal rate. First, we used an ANOVA to test for effects of parasitism and brood size on the rate of mass gain for the slowest-growing chick from each nest. Second, we used an ANOVA to test for effects of parasitism and brood size on the rate of mass gain for the fastest-growing chick from each nest. Because both of these analyses detected an effect of parasitism on rate of mass gain (see Results), we performed a final analysis to examine the difference in rate of mass gain between the fastest- and slowest-growing bunting chick in each nest. After subtracting the slowest growth rate from the fastest growth rate for each nest, we used a Wilcoxon rank sum test to compare these difference scores between parasitized and unparasitized nests (difference scores were not normally distributed). For all three of these follow-up analyses, we used data only from broods of three or four because in smaller broods there was only one bunting chick in nests that were parasitized.

To quantify food acquisition from the videotapes, we counted the size and number of items fed to each bunting chick per hour. We scored the size of items by comparing the volume of the item to the volume of the parent's bill, using 4 size classes: 0.25, 1, 1.75, and 2.50 bill-equivalents. The feeding rate for a given chick was expressed as total bill-equivalents of food received per hour. We compared food acquisition by bunting chicks in parasitized and unparasitized nests with an ANOVA with parasitism and brood size as crossed factors and nest as a factor nested within the two crossed factors. We performed separate analyses for 2-day-old, 4-day-

old, and 6-day-old chicks. Exploratory analyses detected no effect of brood size ( $P > 0.3$ ) and no brood size by parasitism interaction ( $P > 0.3$ ), so we dropped these factors from the final model in order to conserve degrees of freedom for testing our primary hypothesis regarding effects of parasitism.

To examine time spent begging, we transcribed from the videotapes the rate at which each bunting chick begged (total sec begging  $\text{hr}^{-1}$ ). As with our analysis of food acquisition, we analyzed these data using an ANOVA with parasitism and brood size as crossed factors and with nest as a factor nested within the two crossed factors. We performed separate analyses for 2-day-old, 4-day-old, and 6-day-old chicks. Because we detected an effect of parasitism on time spent begging (see Results), we developed a model to estimate the energetic cost of this behavior. First, for each age we calculate the difference between parasitized and unparasitized nests in the rate at which individual bunting chicks beg ( $\text{sec hr}^{-1}$ ). Assuming that buntings beg at this rate for  $12 \text{ hr day}^{-1}$ , we calculate the difference in time spent begging over the course of the day. We then incorporate a recent estimate of the energetic cost of begging by Tree Swallow (*Tachycineta bicolor*) nestlings ( $0.008 \text{ J g}^{-1} \text{ sec}^{-1}$ ; McCarty 1996). For 2-, 4-, and 6-day-old nests, we multiply the extra time spent begging by parasitized bunting chicks ( $\text{sec day}^{-1}$ ) times the mean mass of nestlings in parasitized nests (g) times McCarty's incremental cost of begging ( $0.008 \text{ J g}^{-1} \text{ sec}^{-1}$ ). Finally, we perform a series of calculations to estimate the energetic content of a typical nestling food item in order to examine the energetic cost of the extra begging by chicks in parasitized nests.

From each videotape, we also measured the time that the female spent brooding nestlings. Because we were interested in potential thermoenergetic costs to the nestlings, we included both time that the female spent sitting on the nestlings and time that the female spent on the nest rim shading the nestlings. Males did not participate in either of these activities. We analyzed time spent brooding using an ANOVA, initially including parasitism and brood size as crossed factors. Exploratory analyses detected no effect of brood size ( $P > 0.4$ ) and no brood size by parasitism interaction ( $P > 0.6$ ), so we dropped these factors from the final model in order to conserve degrees of freedom for testing

our primary hypothesis regarding effects of parasitism.

Finally, we examined the overall rate at which adult buntings provisioned parasitized and unparasitized nests. Total parental provisioning rates were analyzed using an ANOVA, initially including parasitism and brood size as crossed factors. Exploratory analyses detected no effect of brood size ( $P > 0.3$ ) and no brood size by parasitism interaction ( $P > 0.3$ ), so we dropped these factors from the final model. The majority of feedings were made by females. To analyze male provisioning effort at parasitized and unparasitized nests, we could not use an ANOVA approach because we observed males feeding nestlings at only 5 of 35 (14.3%) nests. Thus, we used a Fisher exact test to compare the proportion of parasitized and unparasitized nests at which males fed nestlings at least once.

We used SAS (SAS 1989) for all statistical analyses. Critical assumptions were met for all statistical tests. Significant ANOVAs were followed by Tukey HSD multiple comparisons that controlled for an overall alpha of 0.05. Means are presented  $\pm$  SE. In the case of multifactor ANOVAs, we present least squares marginal means rather than unadjusted means. For statistical tests in which we failed to reject the null hypothesis of no effect of parasitism, we performed post-hoc power calculations using G-Power (Buchner et al. 1996). We estimated effect sizes ( $f$ ) based upon a desire to detect a 20% difference between treatment means, using sample sizes and estimates of standard deviations from our data. We then calculated power using this measure of effect size in conjunction with  $\alpha = 0.05$  and total sample size =  $kn$  where  $k$  = number of treatments and  $n$  = harmonic mean of our sample size from each treatment. Finally, we also calculated power in this manner using Cohen's (1988) conventional "small," "medium," and "large" effect sizes ( $f = 0.10, 0.25, \text{ and } 0.40$ , respectively, for ANOVAs).

## RESULTS

### NESTLING GROWTH

We located and monitored 152 Indigo Bunting nests, 61 (40.1%) of which were parasitized; 74 nests survived long enough for us to measure nestling growth. We measured growth rates for 29 bunting chicks in 15 parasitized nests and

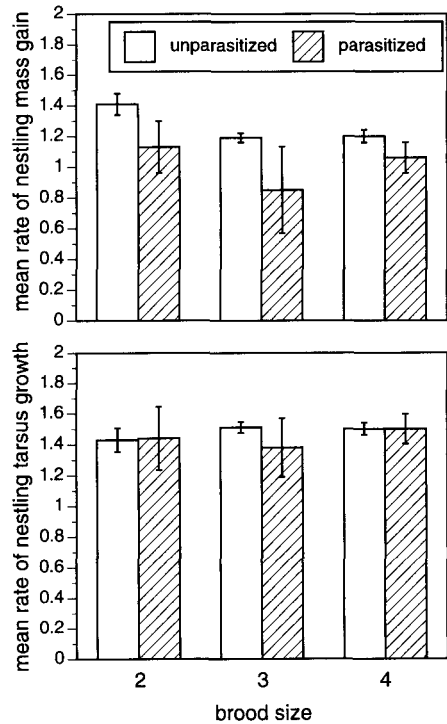


FIGURE 1. Rate of growth of Indigo Bunting nestlings ( $\pm$  SE), measured as the slope of a regression of mass versus age and tarsus versus age for each nestling. Rate of mass gain varied significantly with parasitism, brood size, and nest (nested within the two crossed factors). Rate of tarsus growth varied with nest but not with parasitism or brood size.

147 buntings in 53 unparasitized nests, excluding data from 6 nests that contained only 1 chick each. Indigo Bunting nestlings in parasitized nests exhibited lower rates of mass gain than did buntings in unparasitized nests ( $F_{1,109} = 20.9, P < 0.001$ ; Fig. 1). There was a trend for variation in mass gain among brood sizes, with chicks in broods of two tending to gain mass faster than chicks in broods of three or four ( $F_{2,109} = 7.3, P < 0.001$ ). There was no interaction between parasitism and brood size ( $F_{2,109} = 2.5, P > 0.05$ ), but there was significant variation in chick mass gain among nests ( $F_{61,109} = 3.8, P < 0.001$ ). Rate of tarsus growth did not vary with parasitism ( $F_{1,109} = 0.7, P > 0.4$ ; Fig. 1) or brood size ( $F_{2,109} = 1.2, P > 0.3$ ). There was no interaction between parasitism and brood size ( $F_{2,109} = 0.8, P > 0.4$ ), but there was significant variation in tarsus growth rates among nests ( $F_{61,109} = 4.9, P < 0.001$ ). Power to detect an effect of parasitism

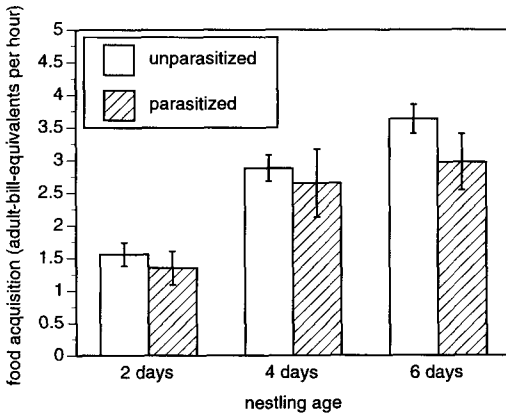


FIGURE 2. Amount of food (adult bunting bill-equivalents  $\text{hr}^{-1} \pm \text{SE}$ ) acquired by individual Indigo Bunting nestlings in unparasitized and parasitized nests. We detected a significant difference in food acquisition by chicks in parasitized and unparasitized nests at the age of 6 days, but not at 2-day-old or 4-day-old nests, although power was low ( $1 - \beta < 0.15$ ).

on tarsus growth was relatively high (for calculated effect size of  $f = 0.272$ ,  $1 - \beta = 0.752$ ; for  $f = 0.10, 0.25$ , and  $0.40$ ,  $1 - \beta = 0.164, 0.683$ , and  $0.974$ , respectively).

Rate of mass gain was still lower in parasitized nests when we restricted our analyses to the slowest-growing chicks ( $F_{1,43} = 5.1$ ,  $P < 0.05$ ;  $0.71 \pm 0.16 \text{ g day}^{-1}$  for parasitized nests,  $1.01 \pm 0.07 \text{ g day}^{-1}$  for unparasitized nests) or the fastest-growing chicks ( $F_{1,43} = 5.8$ ,  $P < 0.05$ ;  $1.16 \pm 0.17 \text{ g day}^{-1}$  for parasitized nests,  $1.32 \pm 0.03 \text{ g day}^{-1}$  for unparasitized nests). Furthermore, we found that the difference in rate of mass gain between the fastest- and slowest-growing buntings was larger in parasitized than in unparasitized nests (Wilcoxon rank sum test, normal approximation with continuity correction:  $Z_c = 1.99$ ,  $P < 0.05$ ; median difference in rate of mass gain =  $0.425 \text{ g day}^{-1}$  for parasitized nests,  $0.177 \text{ g day}^{-1}$  for unparasitized nests).

#### FOOD ACQUISITION

We made 5, 3, and 9 videotapes at parasitized nests of ages 2, 4, and 6 days, respectively, and 7, 14, and 20 videotapes at unparasitized nests of ages 2, 4, and 6 days, respectively. Two-day-old bunting chicks in parasitized nests did not receive less food (adult bill-equivalents  $\text{hr}^{-1}$ ) than did 2-day-old buntings in unparasitized nests, although the difference was in the predicted direction ( $F_{1,22} = 0.5$ ,  $P > 0.5$ ; Fig. 2).

Four-day-old bunting chicks in parasitized nests did not receive less food than did 4-day-old buntings in unparasitized nests, although the difference was again in the predicted direction ( $F_{1,27} = 1.5$ ,  $P > 0.2$ ; Fig. 2). There was significant variation in food acquisition among nests of 4-day-old chicks ( $F_{13,27} = 2.5$ ,  $P < 0.05$ ). Six-day-old bunting chicks in parasitized nests received less food than did 6-day-old buntings in unparasitized nests ( $F_{1,38} = 4.0$ ,  $P < 0.05$ ; Fig. 2). There was significant variation among nests at this age also ( $F_{21,38} = 2.7$ ,  $P < 0.005$ ). Power to detect an effect of parasitism on food acquisition was low at both 2-day-old nests (for calculated effect size of  $f = 0.178$ ,  $1 - \beta = 0.128$ ; for  $f = 0.10, 0.25$ , and  $0.40$ ,  $1 - \beta = 0.074, 0.208$ , and  $0.449$ , respectively) and 4-day-old nests (for calculated effect size of  $f = 0.141$ ,  $1 - \beta = 0.094$ ; for  $f = 0.10, 0.25$ , and  $0.40$ ,  $1 - \beta = 0.072, 0.193$ , and  $0.413$ , respectively).

#### BEGGING RATE

Two-day-old bunting chicks in parasitized nests begged more than 2-day-old buntings in unparasitized nests ( $F_{1,15} = 13.8$ ,  $P < 0.005$ ;  $99.3 \pm 14.6 \text{ sec hr}^{-1}$  for parasitized nests,  $34.1 \pm 9.7$  for unparasitized nests; Fig. 3). There also were significant effects of brood size ( $F_{2,15} = 13.2$ ,  $P < 0.001$ ) and nest ( $F_{3,15} = 7.5$ ,  $P < 0.005$ ). Four-day-old bunting chicks in parasitized nests spent significantly more time begging than 4-day-old chicks in unparasitized nests ( $F_{1,27} = 11.8$ ,  $P < 0.005$ ;  $99.3 \pm 10.7 \text{ sec hr}^{-1}$  for parasitized nests,  $59.8 \pm 4.1$  for unparasitized nests; Fig. 3). There also were effects of brood size ( $F_{2,27} = 88.9$ ,  $P < 0.001$ ), parasitism by brood size interaction ( $F_{2,27} = 22.9$ ,  $P < 0.001$ ), and nest ( $F_{9,27} = 42.8$ ,  $P < 0.001$ ). Six-day-old bunting chicks in parasitized nests spent more time begging than 6-day-old chicks in unparasitized nests ( $F_{1,35} = 52.5$ ,  $P < 0.001$ ;  $133.9 \pm 9.6 \text{ sec hr}^{-1}$  for parasitized nests,  $56.5 \pm 4.4$  for unparasitized nests; Fig. 3). There also were effects of brood size ( $F_{2,35} = 22.3$ ,  $P < 0.001$ ), parasitism by brood size interaction ( $F_{2,35} = 50.0$ ,  $P < 0.001$ ), and nest ( $F_{16,27} = 6.6$ ,  $P < 0.001$ ).

For 2-, 4-, and 6-day-old buntings, our calculations suggest that individual chicks in parasitized nests beg for approximately 780, 480, and 924  $\text{sec day}^{-1}$ , respectively, more than do chicks in unparasitized nests. The mean mass of 2-, 4-, and 6-day-old buntings in parasitized nests was 3.3, 5.8, and 9.3 g, respectively. Thus,

our model suggests that the daily cost of extra begging by each bunting in parasitized nests is approximately 21, 22, and 69 J for 2-, 4-, and 6-day-old chicks, respectively. A Lepidopteran larva approximately 15 mm long is typical of the food items that we observed Indigo Bunting

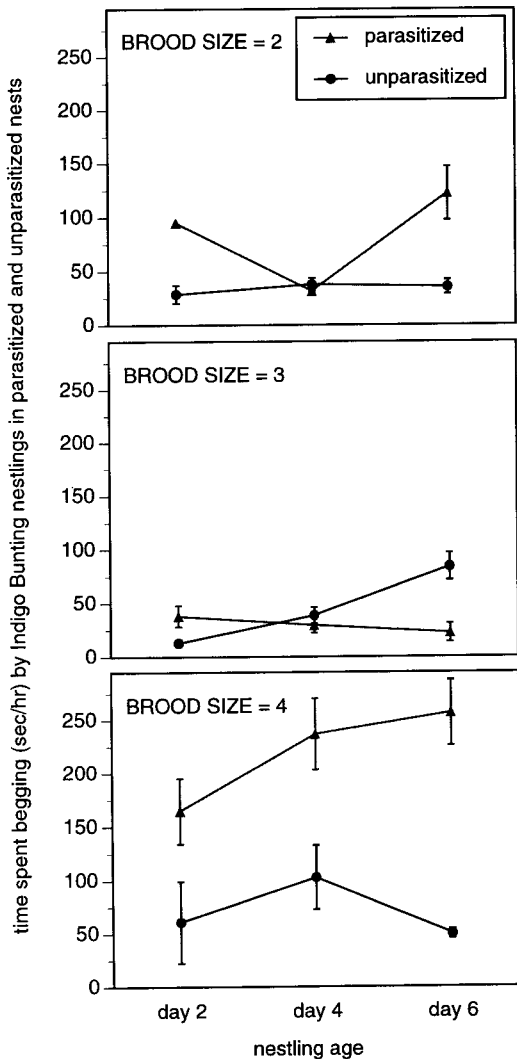


FIGURE 3. Time spent begging ( $\text{sec hr}^{-1} \pm \text{SE}$ ) by individual 2-, 4-, and 6-day-old Indigo Bunting nestlings. For 2-day-old nestlings, time begging varied with parasitism, brood size, and nest. For 4-day-old nestlings, time begging varied with parasitism, brood size, parasitism by brood interaction, and nest. For 6-day-old nestlings, time begging varied with parasitism, brood size, parasitism by brood size interaction, and nest. For 2- and 4-day-old parasitized nests with brood size of two, standard error bars are missing because  $n = 1$ .

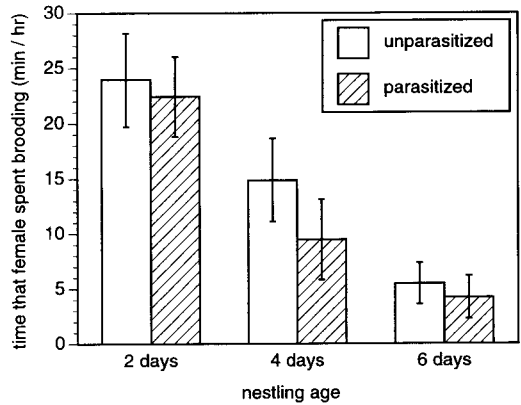


FIGURE 4. Time that adult female Indigo Buntings spent brooding nestlings ( $\text{min hr}^{-1} \pm \text{SE}$ ) at parasitized and unparasitized nests. Females at parasitized nests did not differ from those at unparasitized nests in the amount of time spent brooding 2-day-old nestlings, 4-day-old nestlings, or 6-day-old nestlings, although power was low ( $1 - \beta < 0.10$ ).

adults feeding to nestlings. Using equations developed by Sage (1982), the approximate dry mass of a 15 mm caterpillar is 0.009832 g. The gross energetic content of insects is approximately 24.68  $\text{kJ g}^{-1}$  (Bryant and Bryant 1988, Karasov 1990), and the efficiency with which altricial nestlings assimilate insect food is approximately 69.2% based upon 10 studies reviewed in Bryant and Bryant (1988). Thus, the net energy that an Indigo Bunting chick gains from a typical food item is approximately  $(0.009832 \text{ g})(24.68 \text{ kJ g}^{-1})(0.692) = 168 \text{ J}$ .

#### PARENTAL BEHAVIOR

Adult females at parasitized nests did not differ from those at unparasitized nests in the amount of time spent brooding 2-day-old nestlings ( $F_{1,11} = 0.1$ ,  $P > 0.8$ ; Fig. 4), 4-day-old nestlings ( $F_{1,15} = 0.4$ ,  $P > 0.5$ ; Fig. 4), or 6-day-old nestlings ( $F_{1,27} = 0.2$ ,  $P > 0.6$ ; Fig. 4). Power to detect an effect of parasitism on time brooding was low for 2-day-old nests (for calculated effect size of  $f = 0.207$ ,  $1 - \beta = 0.100$ ; for  $f = 0.10$ , 0.25, and 0.40,  $1 - \beta = 0.061$ , 0.123, and 0.241, respectively), 4-day-old nests (for calculated effect size of  $f = 0.076$ ,  $1 - \beta = 0.055$ ; for  $f = 0.10$ , 0.25, and 0.40,  $1 - \beta = 0.059$ , 0.108, and 0.201, respectively), and 6-day-old nests (for calculated effect size of  $f = 0.066$ ,  $1 - \beta = 0.062$ ; for  $f = 0.10$ , 0.25, and 0.40,  $1 - \beta = 0.077$ , 0.224, and 0.483, respectively).

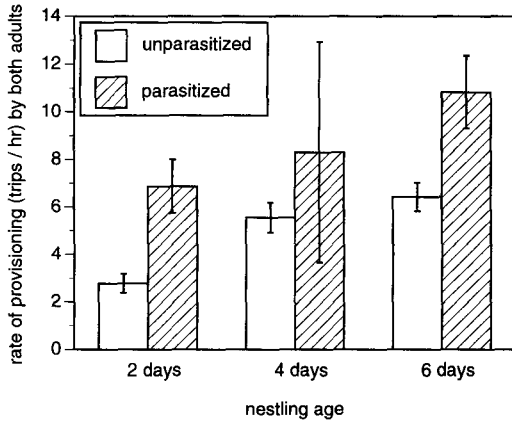


FIGURE 5. Rate at which adult Indigo Buntings provisioned parasitized and unparasitized broods (trips  $\text{hr}^{-1} \pm \text{SE}$ ). We detected a significant difference in provisioning rate between parasitized and unparasitized nests at ages 2 days and 6 days, but not 4 days. Data include trips by both males and females, although 94.6% of trips were made by females.

In 2-day-old nests, parents provisioned parasitized nests at a higher rate than unparasitized nests ( $F_{1,10} = 15.0$ ,  $P < 0.005$ ; Fig. 5). In 4-day-old nests, parents did not provision parasitized nests more than unparasitized nests ( $F_{1,15} = 1.4$ ,  $P > 0.2$ ), although the difference was in the predicted direction (Fig. 5) and power was low (for calculated effect size of  $f = 0.092$ ,  $1 - \beta = 0.058$ ; for  $f = 0.10, 0.25$ , and  $0.40$ ,  $1 - \beta = 0.059, 0.108$ , and  $0.201$ , respectively). In 6-day-old nests, parents provisioned parasitized nests at a higher rate than unparasitized nests ( $F_{1,27} = 10.8$ ,  $P < 0.005$ ; Fig. 5). Males fed nestlings at least once at 4 of 11 (36.4%) parasitized and 1 of 29 (3.4%) unparasitized nests (Fisher exact test,  $P = 0.015$ ).

## DISCUSSION

Indigo Bunting nestlings in parasitized nests exhibited lower rates of mass gain than did bunting chicks in unparasitized nests, and this difference was relatively constant across brood sizes (Fig. 1). Bunting tarsus growth, however, did not differ between parasitized and unparasitized nests (Fig. 1). These results suggest that bunting nestlings in parasitized nests are exhibiting structural development that is comparable to their unparasitized counterparts, but chicks in parasitized nests are in worse condition. We also found that the lower rate of mass gain for chicks in parasitized nests was due to slow mass gain by both

the fastest- and the slowest-growing chick in each nest. However, the disparity in rate of mass gain between fast-growing and slow-growing chicks was exaggerated in parasitized nests, suggesting that the growth-related costs of parasitism are affecting nestmates unequally. Several studies have shown that low nestling growth rates or low mass at fledging are correlated with low post-fledging survival probabilities (Perrins 1963, Dhont 1979, Magrath 1991). Thus, although bunting chicks do frequently fledge from parasitized nests, they may experience reduced post-fledging survival relative to buntings from unparasitized nests, and this effect may be more pronounced for the slowest-growing chick in each nest.

The lower rate of mass gain by chicks in parasitized nests appears to be related to food acquisition. Six-day-old chicks in parasitized nests received a significantly lower volume of food per hour than did chicks in unparasitized nests. Although adults provisioned parasitized nests at a higher rate than unparasitized nests (see below), bunting chicks in parasitized nests experienced reduced food acquisition because a disproportionate share of food was given to the cowbird nestling (Dearborn, in press). We did not detect an effect of parasitism on food acquisition among 2-day-old and 4-day-old bunting chicks (Fig. 2), but we had very low statistical power. In addition to receiving less food than chicks in unparasitized nests, buntings in parasitized nests could be receiving food that is of lower nutritional quality if adults provisioning those nests must forage more quickly than adults provisioning unparasitized nests.

Indigo Bunting chicks in parasitized nests spent more time begging for food than did chicks in unparasitized nests, although the results varied across ages and brood sizes (Fig. 3). Our model estimating energetic costs suggests that the increase in time spent begging by bunting nestlings in parasitized nests costs less than  $100 \text{ J day}^{-1}$ . This cost is less than our estimate of the energetic gain from one food item. Thus, our results suggest that the energetic cost of increased begging may contribute relatively little to the lower rates of mass gain by chicks in parasitized nests. However, we compared the begging of parasitized and unparasitized buntings only in terms of time spent begging; we were not able to quantify the intensity of begging. It is possible that bunting chicks in parasitized

nestlings expended extra energy by begging more intensely as well as begging for more seconds per hour (McCarty 1996). It also is possible that increased begging can cause an increase in the risk of nest predation (Haskell 1994, Dearborn 1997).

A final potential energetic cost to nestlings in parasitized nests is a decrease in the amount of time that parents spend brooding. Altricial nestlings are incapable of thermoregulation when they first hatch, but studies using doubly-labeled water to quantify energy expenditure indicate that the combined cost of activity and thermoregulation account for roughly 30% of a chick's total metabolizable energy budget over the length of the nestling period (Weathers 1996). Because adult buntings are making more provisioning trips at parasitized nests they may spend less time brooding. We did not detect a difference between parasitized and unparasitized nests in the amount of time that females spent brooding chicks, but our power to detect a difference was low.

Adult Indigo Buntings at parasitized nests made more provisioning trips per hour than did adults at unparasitized nests (Fig. 5). Although the vast majority of provisioning trips (796 of 841 = 94.6%) were made by females, males were more likely to provision nestlings at parasitized nests than at unparasitized nests. This difference in provisioning rate has the potential to increase predation probability of the current brood and decrease adult survival or future reproductive success. Nest attendance by adults may be important in deterring nest predators (Blancher and Robertson 1982, Winkler 1992; but see Sealy 1994). In 124 hr of videotapes at nestling-stage Indigo Bunting nests and 41 hr of videotapes at nestling-stage Northern Cardinal (*Cardinalis cardinalis*) nests, we observed two events that indicate the potential importance of host adults in nest defense. At an Indigo Bunting nest containing one 6-day-old cowbird and three 6-day-old buntings, we observed a predation attempt by a Blue Racer (*Coluber constrictor*) that was interrupted by an adult male and female bunting. The 1-m snake had grabbed one of the nestlings by the head and was attempting to remove it from the nest when the adult buntings flew into view of the camera and dove at the snake, which then let go of the nestling and left the field of view. At a Northern Cardinal nest containing one 6-day-old cowbird chick and one

6-day-old cardinal chick, we observed an adult female Brown-headed Cowbird attack the nestlings. The adult cowbird pecked at the cowbird nestling twice and the cardinal nestling once, at which point the adult female cardinal flew into view and struck the cowbird, driving it from the nest. These observations, and other reported incidents of successful nest defense (Winkler 1992), suggest that nest attendance by parents can be an important component of nest success. Female buntings did not greatly reduce the amount of time spent brooding nestlings, and thus may have made a tradeoff between nest attendance and foraging. Females may have been foraging less for themselves or they may have been foraging in a faster but riskier fashion (i.e., being less vigilant). This could result in decreased survival or a reduction in energy available for future reproductive attempts (Stearns 1992). A shift in males' time budgets to provision nestlings could impact fitness by decreasing time available for territory defense or for seeking extra-pair copulations.

Our results indicate that host species that are capable of fledging mixed broods of host and parasitic young still incur costs of raising a cowbird. The reduction in growth of host nestlings may result in low post-fledging survival, and the increased effort at provisioning nestlings may result in reduced survival or future reproductive success of adults. Concern over the conservation implications of cowbird parasitism should not be restricted to host species in which host young do not fledge from parasitized nests.

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