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COSTS OF PARASITISM INCURRED BY TWO SONGBIRD SPECIES AND THEIR QUALITY AS COWBIRD HOSTS[1]

DIRK E. BURHANS AND FRANK R. THOMPSON III
North Central Research Station, USDA Forest Service, 202 Natural Resources Building, University of Missouri, Columbia, MO 65211-7260, e-mail: dburhans/nc_co@fs.fed.us

JOHN FAABORG
Division of Biological Sciences, 110 Tucker Hall, University of Missouri, Columbia, MO 65211-7260

Abstract. We measured the costs of Brown-headed Cowbird (*Molothrus ater*) parasitism incurred by Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*). We predicted that the frequent occurrence of nest desertion as a response to cowbird parasitism in Field Sparrows would be reflected by a higher cost of parasitism for that species. We also compared growth and survival of cowbird nestlings between hosts, predicting that they would do poorly at Field Sparrow nests because the latter appear to be avoided by cowbirds. Both species experienced reduced body mass gain in parasitized broods, but only Indigo Bunting suffered reduced tarsus growth. Both species experienced reductions in clutch size, hatching success, and nestling survival due to parasitism, but these losses did not differ among the two hosts. Multiple parasitism did not affect hatching success or nestling survival more than single parasitism for Indigo Buntings. Once accepted, cowbird offspring fared equally well in nests of both species, but almost half of all cowbird eggs laid in Field Sparrow nests were lost through nest abandonment. As parasitism costs to both species appear to be substantial, the rarity of nest desertion in Indigo Buntings may be due to other factors. Infrequent parasitism of Field Sparrows is consistent with host avoidance by cowbirds but other explanations should be explored.

Key words: brood parasitism, Molothrus ater, *nest desertion, nestling growth,* Passerina cyanea, Spizella pusilla.

INTRODUCTION

The finding that brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) reduces reproductive success of host songbirds has led to a significant amount of recent research on parasitism of North American songbirds (Robinson et al. 1995, Ortega 1998). Not all research on cowbird brood parasitism has directly studied costs of parasitism to hosts, but many studies have demonstrated that parasitized hosts fledge fewer or none of their own young compared to unparasitized hosts. The mechanisms behind the reduction of fledged host young may include egg removal by cowbirds (Sealy 1992, Clotfelter and Yasukawa 1999), disruption of host incubation (McMaster and Sealy 1998), reduced growth or loss of host chicks in competition with cowbird nestmates (Marvil and Cruz 1989, Dearborn et al. 1998), increased nest predation possibly due to the presence of cowbird chicks (Payne and Payne 1998, Dearborn 1999), delayed host reproduction by renesting via nest desertion (Clotfelter and Yasukawa 1999), and reduced post-fledging survival of young in parasitized broods (Payne and Payne 1998).

The costs of brood parasitism incurred by songbird hosts should be a major factor in the evolution of defenses against parasitism. Hosts incurring high costs should be under strong selection to evolve defenses, whereas hosts incurring little or no costs should be under weaker selection for defenses. Even though Brown-headed Cowbirds are generalist brood parasites that parasitize a variety of songbird hosts (Rothstein 1990), they should avoid hosts that are unlikely to raise cowbird young, whatever the reason. Such hosts may include those that have defenses against brood parasitism such as egg rejection or nest desertion (Rothstein 1990), hosts having important differences in size, incubation, or hatching (Scott and Lemon 1996), or hosts providing inappropriate food for cowbird chicks (Kozlovic et al. 1996).

Field Sparrows (*Spizella pusilla*) and Indigo Buntings (*Passerina cyanea*) are songbird species that nest in old field habitats, are of similar size (13–15 g), and feed their young arthropods. However, Field Sparrows frequently desert par-

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asitized nests (Carey et al. 1994), whereas Indigo Buntings, although occasionally deserting parasitized nests (Phillps 1951, Terrill 1961), usually accept and raise cowbird young (Payne 1991). One explanation for the presence of a defense in Field Sparrows and its rarity in Indigo Buntings could be that a greater cost of parasitism has selected for defenses in Field Sparrows. In a recent analysis of nest desertion, Hosoi and Rothstein (in press) found that non-forest species incurring higher costs of parasitism had higher frequencies of nest desertion than non-forest species that incurred lower costs. Accordingly, we quantified the costs of parasitism for Field Sparrows and Indigo Buntings, predicting that the presence of a defense in Field Sparrows would be reflected in a higher cost of parasitism. We also compared the fates of cowbird offspring at nests of Field Sparrows and Indigo Buntings. As Field Sparrows desert parasitized nests more frequently than buntings, it follows that they may be less desirable cowbird hosts; however, we measured other fitness decrements potentially incurred by cowbird young to determine costs to cowbird fitness in addition to nest desertion.

METHODS

We located Field Sparrow and Indigo Bunting nests in old fields and adjoining forests from April through July 1992–1994 and 1997–1998 at the Thomas S. Baskett Wildlife Research and Education Center near Ashland, Missouri (Boone County; described in Burhans 1997). In 1995, we monitored Field Sparrow nests only until the first week of July and did not monitor Indigo Bunting nests. We searched sites daily for nests and marked them with plastic flagging from at least 3 m distance. We noted the presence of eggs or nestlings of the Brown-headed Cowbird and categorized nests as parasitized or unparasitized. Nests were monitored every 2–3 days until fledging approached, after which we monitored them daily to document fledging. We documented fledging either by video camera (Thompson et al. 1999) or by behavioral evidence during early morning visits on the expected day of fledging. We concluded fledging from behavioral evidence (fledgling begging calls, the sight of fledglings, parents carrying food, or parents chipping rapidly nearby) only for nests having no adjacent neighbors that could have fledged at the same date. Nests empty prior to this were considered depredated; nests active up to the expected fledging date for which fledging was unconfirmed were classified as unknown. To control for seasonal effects, we included only active nests initiated before the last parasitized nest for a given year (range 7–22 July).

We measured nestlings daily from the hatching day (day 0) up to nestling day 7, but also took measurements if nestlings were found several days after hatching. We took measurements at about the same time daily (± 20 min) but did not measure on cold or wet days. We took body mass measurements to the nearest 0.1 g with a portable digital scale and obtained tarsus measurements (to the nearest 0.1 mm) with dial calipers. We excluded tarsus data from the analysis if more than one person took measurements at the same nest.

STATISTICAL ANALYSES

Nestling growth rates. We followed the protocol of Dearborn et al. (1998) for analyzing nestling growth. We calculated a growth rate for each chick to reduce error from among-chick variability that occurs if daily means are used across chicks of the same age, as body mass measurements can vary up to 1.0 g on nestling day 0 among host chicks apparently hatched on the same day (unpubl. data). For each host or cowbird chick, we regressed daily body mass or tarsus length on age (in days) and used the slopes of the regression equations as the growth rate. We inspected graphs of the slopes to make sure that the linear function was appropriate and that growth rate did not reach an asymptote. We retained measurements for Field Sparrows and Indigo Buntings up to nestling day 4 (mean number days 3.6, range 2–5, each species) and for Brown-headed Cowbird chicks up to nestling day 6 (Field Sparrows: mean number days 3.5, range 2–5; Indigo Buntings: mean number days 4.1, range 2–7). Slopes for nestlings with only two days of measurements are likely to be an accurate measure of growth rate, as r^2 values for nestlings with greater than two measurements were high also (body mass: mean $r^2 = 0.98$, all three species; tarsus: Field Sparrows, mean $r^2 = 0.98$; Indigo Buntings and Brown-headed Cowbirds, mean $r^2 = 0.97$).

We analyzed host nestling growth rates with an ANOVA model (Dearborn et al. 1998). We used growth rates of individual chicks as the dependent variable and included factors for species

(Field Sparrow or Indigo Bunting), parasitism (parasitized or not), and total number of chicks in the nest (2–5), including cowbirds if parasitized. When calculating total brood size, we used the maximum number of host and cowbird chicks hatched in a nest, including nestlings that later died or disappeared from the nest prior to termination. We did not consider the number of cowbird chicks in the nest separately from total brood size, as few host chicks in parasitized nests that we measured had more than one cowbird nestmate. To account for variability between nests, we added nest as a fourth factor nested within parasitism, total brood size, and species. We interpreted species × parasitism interactions as indicating differences in host nestling growth between species due to parasitism. We tested for differences in growth between parasitized and unparasitized nests within species using least-significant difference tests (LSMEANS; SAS 1990). This test uses a *t*-value with the degrees of freedom from the standard error of the means (Day and Quinn 1989). We used a sequential Bonferroni test (Rice 1989) to determine the accepted significance level for the multiple comparisons. We analyzed growth of cowbird chicks similarly at parasitized nests of both hosts. In this model, we interpreted a significant species effect as indicating a difference in host quality between Field Sparrows and Indigo Buntings.

We used PASS V. 6.0 (Hintze 1996) to conduct power analyses for the factors of interest (parasitism, species × parasitism, and species) in the ANOVA analyses if differences were not significant. Sample sizes of Field Sparrows and Indigo Buntings and cowbirds in their respective nests were not equal, so we used the average sample size in calculating sample size within a cell. We calculated power for effect sizes (*f*) defined by Cohen (1988) as small, medium, and large ($f = 0.1, 0.25, 0.4$, respectively).

Other costs of parasitism. In addition to nestling growth, we compared four potential fitness decrements from cowbird parasitism that could differ between host species: (1) cost of egg removal by cowbirds, (2) reduced hatching success of host eggs in parasitized clutches, (3) reduced host chick survival in parasitized nests, and (4) number of young fledged from parasitized and unparasitized nests.

Numbers of eggs or offspring ranged from 0 to 5 and did not fit the assumptions of a continuous normal distribution, so where applicable we used categorical data analysis to analyze the above costs to hosts (PROC CATMOD; Stokes et al. 1995). This approach uses a weighted-least-squares estimation method, and, as with standard ANOVA, allows partitioning of the variation (among mean response functions) into the sources of interest (species, parasitism, species × parasitism). We interpreted significant species × parasitism interactions as indicating differences in the effects of parasitism according to host.

We compared mean host clutch sizes of parasitized and unparasitized nests using the final number of eggs before hatching to analyze costs of egg removal by cowbirds. We calculated host hatching success by subtracting the number of host young hatched from the final host clutch size for each nest; to account for asynchronous hatching we included nests visited at least one additional day after hatching. As sample sizes of multiply-parasitized Field Sparrow nests were small, for parasitized Indigo Bunting nests only, we compared the number of unhatched eggs by frequency of single or multiple parasitism, for which any nest with > 1 cowbird egg was considered multiply parasitized.

When analyzing host young lost during the nestling stage, we subtracted the number of young counted at the last visit (before nest termination) from the number of young hatched. We calculated fledging of host young similarly for nests that fledged either host or cowbird young. For Indigo Bunting nests, we compared the number of lost host nestlings by frequency of single or multiple parasitism as with the hatching analysis above. We also compared the number of host young fledged from parasitized and unparasitized bunting nests with the weighted least-squares approach described previously. We removed cowbird eggs from 10 Indigo Bunting nests and classified these nests as parasitized for the parasitism frequency and host clutch size analyses because we assumed that this would not affect host egg removal by cowbirds. We eliminated these nests from the subsequent analyses, except for a bunting nest where one cowbird egg was left to hatch. We excluded 10 unparasitized Field Sparrow nests for which clutch size was manipulated.

Quality of hosts and potential costs to cowbirds. For cowbirds, we evaluated quality of hosts similarly by comparing number of cowbird eggs, hatching success, nestling survival, and fledging success between Field Sparrows and Indigo Buntings. However, as sample sizes of parasitized Field Sparrow nests were small, we were not able to compare host quality statistically for all of these measurements.

When analyzing nest desertion, we excluded nests that were apparently abandoned before hosts had commenced laying (Payne 1991), because such nests may be deserted due to generalized disturbance rather than cowbird parasitism. We also excluded nests that were depredated before desertion could be confirmed.

We calculated the proportion of cowbird eggs hatched and cowbird chicks surviving. For all parasitized nests (excluding Indigo Bunting nests where cowbird eggs were removed), we calculated the proportion of all cowbird eggs lost to desertion, predation, and other causes (weather, flooding, and animal trampling), excluding several nests apparently abandoned due to placement of video cameras (Thompson et al. 1999).

For all nests except the manipulated nests (see above), we evaluated nesting success using the Mayfield method (Mayfield 1975). For each nest, we added half the number of days between subsequent visits over which a nest was empty to the previous days the nest survived to obtain the total number of observation days. We calculated survival probabilities and variances with standard errors according to Johnson (1979) and compared survival probabilities using CONTRAST (Hines and Sauer 1989). For this analysis, we included all sources of nest mortality, because our goal was to determine which host should be preferred by cowbirds considering nest failure from any cause. A Field Sparrow nest not monitored between building and the time we realized it was parasitized and deserted was eliminated from the latter analysis because we could not determine the number of observation days. For all analyses, we accepted $P \leq 0.05$ as the level of statistical significance. Results of tests reporting means are indicated as mean ± SE.

RESULTS

NESTLING GROWTH RATES

Host chicks of both species suffered reduced body-mass growth rate in parasitized nests (Fig. 1; ANOVA: $r^2 = 0.78$, overall $F_{81,128} = 5.7$, $P < 0.001$, parasitism: $F_{1,128} = 37.1$, $P < 0.001$).

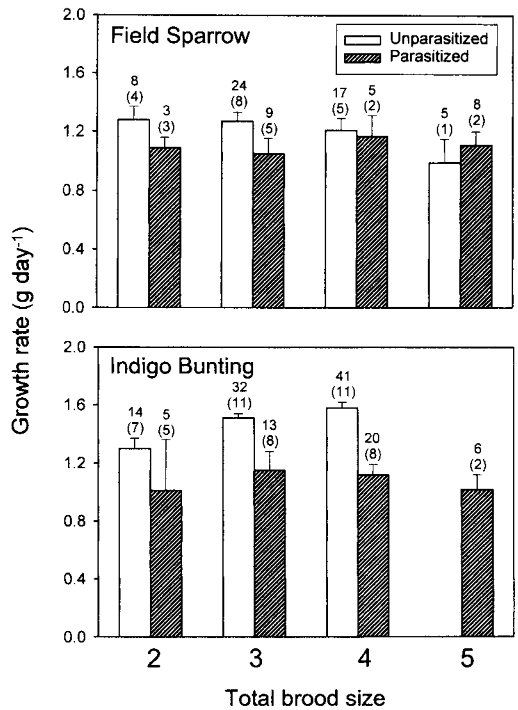

FIGURE 1. Mean rate of daily host nestling mass gain (± SE) by total brood size (including cowbird chicks if present) for Field Sparrows and Indigo Buntings. Sample sizes of chicks (nests) above bars. Brood size is based on number of chicks initially hatched; sample size is number of chicks measured at least twice.

The difference between host body-mass growth rate at parasitized versus unparasitized nests was greater at Indigo Bunting nests than Field Sparrow nests (species × parasitism interaction: $F_{1,128} = 6.6$, $P = 0.01$). Bunting chicks at parasitized nests experienced reduced body-mass growth rate compared to chicks at unparasitized nests for total brood sizes of 2, 3, and 4 (Fig. 1), whereas Field Sparrow chicks at parasitized nests only experienced reduced growth rate in total brood sizes of 3 (least significant difference tests with sequential Bonferroni adjustments). The main effects of total brood size ($F_{3,128} = 2.8$, $P < 0.05$) and species ($F_{1,128} = 5.4$, $P < 0.05$) accounted for significant variation in mean body-mass growth rate. Differences between nests also accounted for significant variation in rate of body mass growth rate ($P < 0.001$).

The ANOVA model analyzing differences in tarsus growth rate was significant (Fig. 2; $r^2 = 0.78$, overall $F_{78,126} = 5.9$, $P < 0.001$). The main

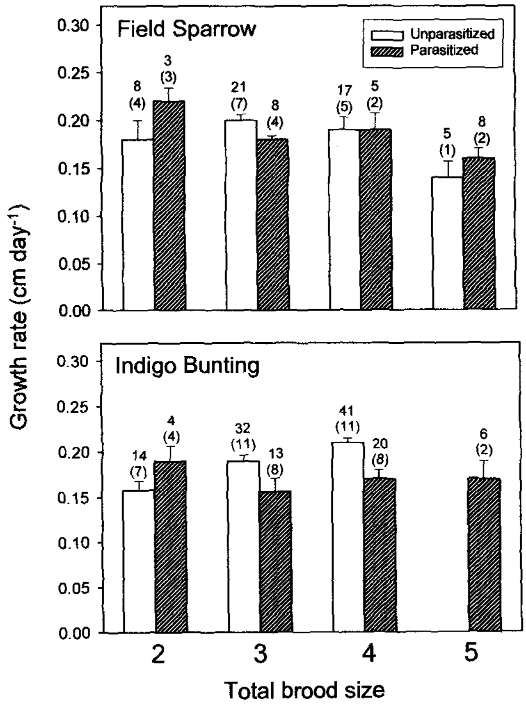

FIGURE 2. Mean rate of daily host nestling tarsus gain (± SE) by total brood size (including cowbird chicks if present) for Field Sparrows and Indigo Buntings. Sample sizes as in Figure 1.

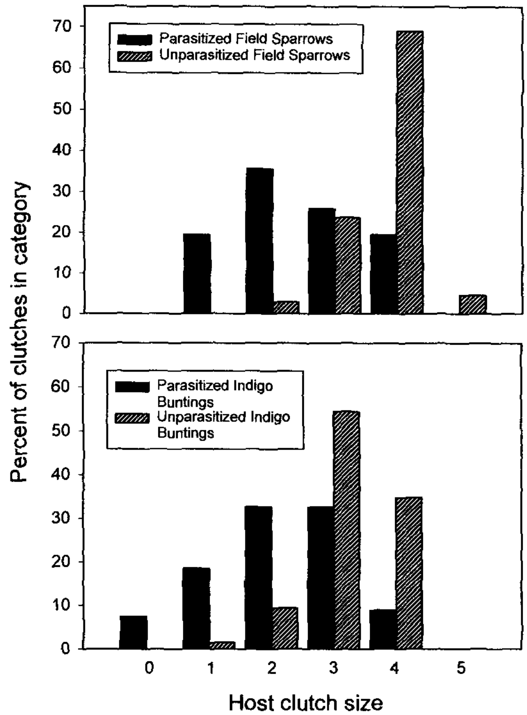

FIGURE 3. Distribution of parasitized (n = 31 Field Sparrow nests, n = 135 Indigo bunting nests) and unparasitized (n = 355 Field Sparrow, n = 138 Indigo Bunting nests) host clutch sizes, based on final number of host eggs observed before hatching.

effect of parasitism alone did not explain tarsus growth (P = 0.4), but species was significant ($F_{1,126}$ = 5.2, $P < 0.05$). Power to detect a difference in the parasitism effect was high for medium and large effect sizes (f = 0.1, 0.25, and 0.4: $1 - \beta$ = 0.30, 0.95, and 0.99, respectively). Parasitism affected growth rate differently according to species (species × parasitism interaction: $F_{1,126}$ = 4.2, $P < 0.05$). Bunting chicks at parasitized nests experienced reduced tarsus growth rate compared to chicks at unparasitized nests for total brood sizes of 3 and 4 (Fig. 2), whereas Field Sparrow chicks at parasitized nests did not experience reduced tarsus growth due to parasitism.

We measured body mass and tarsus growth for 15 cowbird chicks at 13 Field Sparrow nests and 39 cowbird chicks at 32 Indigo Bunting nests. Neither overall body mass or tarsus growth rate ANOVA models for Brown-headed Cowbird chicks were significant (mass model r^2 = 0.89: overall $F_{45,8}$ = 1.4, P = 0.3; tarsus model r^2 = 0.93: overall $F_{45,8}$ = 2.6, P = 0.08). Mean body-mass growth rate did not differ between cowbird chicks at Field Sparrow and Indigo Bunting nests (cowbirds in Field Sparrow nests: 2.9 ± 0.2 g day^{-1}, n = 15 chicks; Indigo Buntings 3.1 ± 0.2 g day^{-1}, n = 39 chicks). Similarly, none of the main effects or interactions explained mean rate of tarsus growth rate for cowbird chicks (cowbirds in Field Sparrow nests: 0.25 ± 0.02 cm day^{-1}, n = 15 chicks; cowbirds in Indigo Bunting nests: 0.25 ± 0.01 cm day^{-1}, n = 39 chicks). Power to explain the species effect was low except for large effect sizes (both models: f = 0.1, 0.25, and 0.4: $1 - \beta$ = 0.11, 0.44, and 0.82, respectively).

OTHER COSTS OF PARASITISM

Parasitism accounted for significant reductions in host clutch size but its effects did not vary between species (parasitism χ^2_1 = 121.7, $P < 0.001$; species χ^2_1 = 14.4, $P < 0.001$; species × parasitism interaction χ^2_1 = 1.3, P = 0.3; Fig. 3). Parasitism also affected hatching of host eggs for both species (parasitism χ^2_1 = 5.0, $P < 0.05$;

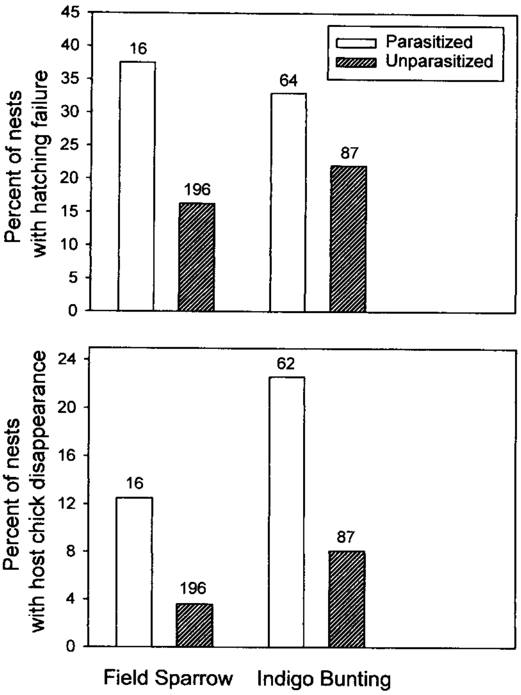

FIGURE 4. Top: percent of nests surviving through hatching in which at least one host egg failed to hatch by species and category of parasitism. Bottom: percent of hatched nests in which at least one host chick disappeared by species and category of parasitism (total sample sizes of parasitized and unparasitized nests above bars).

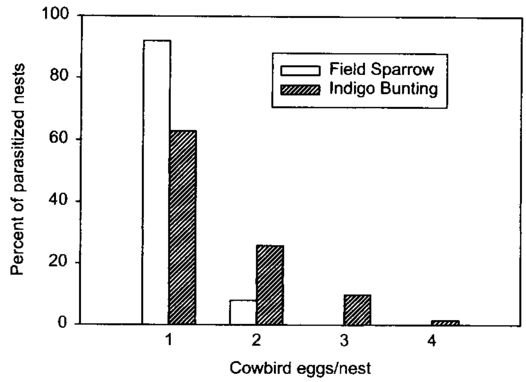

FIGURE 5. Distribution of Brown-headed Cowbird eggs by host species (n = 50 parasitized Field Sparrow, n = 132 parasitized Indigo Bunting nests).

Fig. 4), but there was no difference in host hatching success by species (P = 1.0) and no difference in hatching success between species according to parasitism status (species × parasitism interaction: P = 0.5). Additional cowbird eggs did not reduce the chances of at least one host egg failing to hatch at Indigo Bunting nests (singly parasitized nests: 13 host egg failures/40 nests; multiply parasitized nests: 8 host egg failures/24 nests; χ^2_1 = 0.01, P = 1.0). Parasitism affected loss of host chicks for both species (parasitism χ^2_1 = 5.0, P < 0.05; Fig. 4), but there was no difference in chick loss by species (P = 0.2) and no difference in chick loss between species according to parasitism status (species × parasitism interaction: P > 0.5). We noted 2 cases where one Field Sparrow chick died or disappeared from a parasitized nest and 17 cases at 13 parasitized Indigo Bunting nests (including several cases where > 1 host chick perished at the same nest; Fig. 4). In Indigo Bunting nests where both cowbirds and buntings hatched, additional cowbird chicks did not increase loss of bunting chicks (singly parasitized nests: 9 nests with ≥ 1 bunting chick perishing, n = 40 nests; multiply-parasitized nests: 4 nests with ≥ 1 bunting chick perishing, n = 10 nests; Fisher exact test, P = 0.2). Comparing nests that fledged either host or cowbird young, Field Sparrows fledged an average of 2.5 ± 0.7 host young at parasitized nests (n = 4 parasitized nests surviving to fledging) compared to 3.4 ± 0.1 host young at unparasitized nests (n = 93 nests). Parasitized Indigo Buntings fledged an average of 1.6 ± 0.2 host young (n = 25 parasitized nests surviving to fledging) compared to 2.8 ± 0.1 young at 55 unparasitized nests (χ^2_1 = 23.5, P < 0.001).

QUALITY OF HOSTS AND POTENTIAL COSTS TO COWBIRDS

Indigo Buntings were more frequently parasitized than Field Sparrows (Field Sparrows: 11.3%, n = 443 nests; Indigo Buntings: 48%, n = 295 nests; χ^2_1 = 124.9, P < 0.001). Indigo Buntings experienced more cases of multiple parasitism but sample sizes of parasitized Field Sparrow nests were small for comparison (Fig. 5). In parasitized Field Sparrow nests that survived long enough for either hosts or cowbirds to hatch (n = 16 nests), only 1 cowbird egg failed to hatch, whereas 28 cowbird eggs in comparable Indigo Bunting nests failed to hatch (n = 65 nests). One cowbird chick was lost from one Field Sparrow nest; two were lost from one Indigo Bunting nest. Of parasitized nests for which desertion could be determined, Field Sparrows deserted 45% of 47 parasitized nests, whereas buntings abandoned 3.5% of 142 parasitized nests (χ^2_1 = 50.4, $P < 0.001$). After losses to nest predation and desertion, 4 cowbird chicks fledged from 4 parasitized Field Sparrow nests out of 54 cowbird eggs in 50 parasitized nests, whereas 33 cowbird chicks fledged from 25 Indigo Bunting nests out of an original total of 194 cowbird eggs in 128 parasitized nests. Including nests where desertion was a component of mortality, parasitized Field Sparrow nests had significantly lower daily survival than parasitized Indigo Bunting nests (Field Sparrows: 0.88 ± 0.02, n = 376.5 observation days, 49 nests; Indigo Buntings: 0.92 ± 0.01, n = 1,288 observation days, 132 nests; χ^2_1 = 4.6, $P < 0.05$). Unparasitized Field Sparrow and Indigo Bunting nests did not have different daily survival estimates (Field Sparrows: 0.92 ± 0.004, n = 3,726 observation days, 383 nests; Indigo Buntings: 0.93 ± 0.006, n = 1,467 observation days, 153 nests; χ^2_1 = 1.9, P = 0.2).

DISCUSSION

Both hosts incurred significant costs of parasitism. Field Sparrows, however, did not experience greater costs of parasitism, as Indigo Buntings raised with cowbirds experienced slightly greater reductions in body mass and tarsus growth by comparison (Fig. 1 and 2). Indigo Buntings and Field Sparrows did not differ for other costs of parasitism that we measured. Although Field Sparrows did not experience greater costs of parasitism than Indigo Buntings, they still experienced significant reductions in nestling growth, clutch size, and hatching success, as well as apparent loss of chicks in the nest due to competition with cowbirds.

Unlike other small hosts (Marvil and Cruz 1989), neither of these hosts regularly experienced entire reproductive failure when parasitized. Longer incubation periods of many hosts appear to contribute to brood reduction in parasitized nests (Robinson et al. 1995) because cowbirds have short incubation periods of 10–12 days (Lowther 1993). Both hosts in this study have incubation periods similar to cowbirds (Field Sparrows 11 days, Indigo Buntings 12–13 days; Payne 1991, Carey et al. 1994). Although we did not always visit nests on consecutive days during hatching, in many cases, the host chicks that hatched one or more days after cowbirds and host nestmates were the ones that perished; Field Sparrow chicks in particular tended to hatch on the same day as cowbird nestmates.

In another study of the same population of Indigo Buntings during different years, Dearborn et al. (1998) showed that buntings experienced reduced rates of body mass gain, but not tarsus growth, at parasitized nests. Although we detected both decreased body mass and tarsus gain at parasitized bunting nests, we did not detect an overall trend for reduced tarsus growth for both host species, and our sample size of parasitized bunting nests was slightly larger than that of Dearborn et al. (1998). Payne and Payne (1998) found similar costs for buntings in host egg removal and reduction of host young fledged; they also found lower post-fledging survival of buntings fledged with cowbirds. We did not find that multiple parasitism further reduced hatching or nestling survival for Indigo Buntings, although other studies have found reduced host nestling survival or fledging with multiple parasitism (Rogers et al. 1997, Payne and Payne 1998).

In a study of another pair of small hosts, Briskie et al. (1990) found that Yellow Warblers (*Dendroica petechia*) were parasitized six times more frequently than Least Flycatchers (*Empidonax minimus*) nesting in the same habitat, despite the fact that Yellow Warblers frequently rejected cowbird eggs by burying them. They similarly found no differences in host quality between the two species other than differences in acceptance of cowbird eggs. In our study, the frequently-deserting species (Field Sparrow) was parasitized four times less than the rarely-deserting species (Indigo Bunting). Underestimation of parasitism could result if deserted nests are less likely to be found (Burhans, in press). However, our nest-finding efforts, particularly for Field Sparrows, included observing nest-building behavior of monitored pairs. We found many Field Sparrow nests in the building or laying stages; thus we feel that the reported parasitism frequencies are not far from the true difference between the two species.

Other studies of concurrently nesting Field Sparrows and Indigo Buntings indicate that buntings are either parasitized at greater (≥ 10% higher) frequencies than Field Sparrows (Berger 1951, Batts 1958, Strausberger and Ashley 1998) or at similar frequencies (Hicks 1934, Trautman 1940, Sutton 1959, 1960; Nolan 1963, Robertson and Norman 1977). Nest desertion due to parasitism for Field Sparrows ranges from 45% (this study) to 63% (B. Strausberger, unpubl. data; reviewed in Carey et al. 1994). Desertion for Indigo Buntings in two large studies, our's and Payne's (1991), usually occurred only when cowbird eggs were laid before host eggs (Payne 1991, D. Burhans, pers. observ.). Studies with smaller sample sizes report desertion frequencies between 7% and 100% for buntings (Twomey 1945, Phillips 1951, Terrill 1961, Nolan 1963, Morgan 1976), although the criteria used when determining desertion in these studies is not always clear.

Unparasitized nests of both hosts had similar daily survival estimates, indicating that parasitized hosts should fledge cowbird young equally in the absence of differences in fostering ability. However, nest abandonment by Field Sparrows resulted in loss of almost half of all cowbird eggs, culminating in significantly lower daily survival estimates for parasitized Field Sparrows than comparable Indigo Bunting nests. These results are consistent with the possibility that cowbirds prefer Indigo Buntings over Field Sparrows because the latter species frequently abandons parasitized nests. Cowbirds are thought to be generalist brood parasites, and although they appear to avoid parasitizing certain hosts (Sealy and Bazin 1995, Peer and Bollinger 1997), this "avoidance" could be for many reasons other than host preference. For instance, cowbirds may prefer certain habitats (Zimmerman 1983, Burhans 1997), respond to certain structural features in the vicinity of host nests (Brittingham and Temple 1996, Clotfelter 1998), or use behavioral cues from hosts to find nests (Uyehara and Narins 1995, Clotfelter 1998). Species differences in characteristics such as these, rather than host preference, could explain the disparity in parasitism frequencies between Field Sparrows and Indigo Buntings. However, a previous study showed few differences between nest-site and microhabitat characteristics in old field nests of these two species (Burhans 1997).

Unlike some hosts, e.g., Solitary Vireo (*Vireo solitarius*; Marvil and Cruz 1989), Field Sparrows and Indigo Buntings are able to fledge their own young with cowbirds, and parasitism rarely resulted in total brood loss. However, like Dearborn et al. (1998), our results indicate that parasitism can incur additional costs resulting in reduced numbers of fledged host young. In their analysis and review of nest desertion by cowbird hosts, Hosoi and Rothstein (in press) found that desertion was most frequent among non-forest compared to forest host species when effects due to predation, sympatry, parasitism frequency, host laying season, phylogeny, and cost of parasitism were included. However, within non-forest species, they found that species incurring larger costs when parasitized had higher frequencies of desertion. As differences in the costs of parasitism between these two hosts appear to be minimal, other factors may explain the frequent occurrence of cowbird-induced nest desertion in Field Sparrows and its apparent rarity in Indigo Buntings.

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