Brood parasitism by cowbirds: risks and effects on reproductive success and survival in indigo buntings

Robert B. Payne and Laura L. Payne

*Department of Biology, University of Michigan, Ann Arbor, MI 48109-1079, USA

We observed brood parasitism by brown-headed cowbirds (Molothrus ater) on indigo buntings (Passerina cyanea) and estimated the impact of parasitism on the success of the individual buntings in their current nests and in their future reproduction. Rates of parasitism over 8 years were 26.6% in 1040 nests and 19.8% in 693 nests in two areas in southern Michigan. Risk of parasitism was high early in the season; half the buntings were begun after the end of the cowbird season. Risk was independent of female age, plant containing the nest, or habitat. The immediate cost of parasitism was 1.19 and 1.26 fewer buntings fledged per nest. Breeding success was lower in parasitized nests with cowbird eggs (nests were more likely to be deserted or predated), lower when the cowbird nestling failed (nests were more likely to be predated), and lower when the cowbird fledged (fewer buntings fledged) compared to nonparasitized nests. Costs were due to removal of a buntings egg and to competition for parental care of the cowbird and bunting nestlings. Buntings that fledged from nests where a cowbird also fledged were only 18% as likely to survive and return to their natal area in the next year as buntings from nests where a cowbird did not. Long-term effects of cowbird parasitism on adult breeding later in the season, survival to the next season, and reproductive success in the next season were negligible when compared between birds that reared a cowbird and those that reared only a bunting brood, or between birds that were parasitized and birds that escaped parasitism. The results indicate little long-term cost of brood parasitism on individual fitness of adult buntings beyond the impact on the current nest and the survival of buntings that fledge from it; nearly all cost is to the parasitized brood. Key words: breeding seasons, brood parasitism, brown-headed cowbirds, cost of parasitism, cost of reproduction, indigo buntings, individual fitness, Molothrus ater, natal philopatry, nest predation, nestling competition, Passerina cyanea, postfledging survival, reproductive success. [Behav Ecol 9:64-73 (1998)]
later breeding attempts (Leszella, 1993; Partridge, 1989; Renick, 1985; Stearns, 1992; Williams, 1966). Observations and experimental tests give some support for this hypothesis. For example, great tits (Parus major) that rear larger broods early in the season are less likely to have a second brood within the same season (Perrins, 1983). House sparrows (Passer domesticus) that rear larger broods early in the season have smaller broods later in the season (McGillivray, 1983). Rooks (Corvus frugilegus) and pied flycatchers (Ficedula hypoleuca) that rear enlarged broods in one season have lower reproductive success in the next season (Gustafsson and Pärt, 1990; Gustafsson and Sutherland, 1988; Reskaf, 1985). Finally, blue tits (Parus caeruleus) that rear enlarged broods have lower survival into the next season (Petitiir, 1993). In other studies, the birds that rear a naturally large brood or an experimentally enlarged brood sometimes show a lower survival or reproductive success (Högstedt, 1981; Leszella, 1993; Lindén and Moller, 1988; Nur, 1988; Orell et al., 1996; Partridge, 1989; Smith, 1981b; Wheelwright et al., 1991; Winkler and Wilkinson, 1988; Verhulst and Hut, 1996).

We observed brood parasitism of brown-headed cowbirds on the indigo bunting (Passerina cyanea), a small songbird of eastern North America. We determined the effect of cowbird parasitism on the reproductive success of individual birds at each nest and throughout the breeding season, their survival and reproductive success in the next year, and survival of their fledglings to the next year. If parasitism affects the ability of a bunting to rear a later brood, then we predict that fewer nests will be started after a parasitized nest than after an unparasitized nest of the pair and that earlier parasitism will affect the success of the later nest, especially when the earlier nest was successful and a cowbird fledged. If rearing a cowbird affects the survival of adult buntings, then we predict that fewer buntings will return in the year after they fledged a cowbird than after they fledged only their own brood or failed to rear any brood. Finally, if rearing a cowbird affects reproductive success in a later year, then we predict that few buntings will be fledged in the following year. For this prediction we tested the female buntings, as they provide the parental care to the time of fledging and are the sex most likely to show a cost of parasitism.

**METHODS**

**Study areas, populations, and reproductive success**

We observed indigo buntings in southern Michigan, USA (Payne, 1989, 1992; Payne and Payne, 1990, 1995a,b; Payne et al., 1988). We color banded the breeding birds and found nearly all nests in two study areas, one near Niles (41°55' N, 86°14' W) which was 4 km², the other at the E. S. George Reserve and neighboring lands (42°27' N, 84°00' W) which was 12 km². We located the position of each male, the territory occupied, and all nests on maps and a series of aerial photographs of the study areas.

For each male we categorized the territory according to whether it occupied one of five major habitats: upland woods, aspen Populus grandidentata), black locust Robinia pseudoacacia thickets, upland old fields, swamps, or edge of field and woods, as determined by field observations and aerial photographs. Bunting nests generally were within 1.2 m of the ground under the canopy of a dense herb or shrub. We identified 58 kinds of plants in which the nests were built; most were in shrubs of black raspberry (Rubus occidentalis) or gray dogwood (Cornus racemosa) and others with 10 or more nests were in saplings especially maple, in shrubs (staghorn sumac Rhus typhina, multiflora rose Rosa multiflora, gooseberry Ribes cynosbati, honeysuckle Lonicera spp.), and in low herbs (bracken Pteridium aquinum, goldenrod Solidago spp.). We compared the proportion of nests parasitized by cowbirds in these habitats and nest plants.

We determined the date of the first egg in each nest. The earliest egg in any year was laid on 14 May; the latest date for nestlings was 7 September. Nest building took up to 8 days in early spring but sometimes only 2 days in summer. Clutch size was usually three or four. The incubation period was 12–14 days for buntings and 11 days for cowbirds. Young buntings and cowbirds remained in the nest for 9–10 days, or a few days longer (up to 14 days) in cool weather. Female buntings bred in their first year, built the nest, incubated, and fed the nestlings; reproductive success was independent of female age (Payne, 1989). Males bred in their first year and many were successful, though the older adults were more successful. Males often fed the young after they fledged (Westneat, 1988) and also fed the fledged cowbirds (Sutton, 1959). Females frequently renested after the loss of an earlier nest and attempted as many as seven nests, and they often reared two broods and occasionally three broods in a season. Breeding pairs were active for as long as 14 weeks.

We captured the males in mist nets on their territories, then measured, weighed, and color banded them and aged them by plumage: the greater primary coverts were brown in yearlings (first-year males) and blue in older adult males. We found no plumage differences between yearling and older adult females, but we knew the ages of females that we had banded as nestlings and the minimum ages of females that we had banded in an earlier year. We banded nearly all territorial male buntings and about half the females with a U.S. Fish and Wildlife (USFWS) band and three color bands for individual recognition. Males were 12.5–17.5 g (n = 1,159, x = 14.96 ± 0.74 g). Females were 11.9–17.5 g (n = 398, x = 14.35 ± 0.96 g). Cowbird adults were larger than buntings (males, n = 32, x = 49.62 ± 4.07 g; females, n = 27, x = 39.14 ± 2.80 g), nestlings were as large as 53.1 g, and fledglings being fed by a host were as large as 38.0 g (cowbird specimens from southern Michigan in the University of Michigan Museum of Zoology).

We determined the immediate effect of cowbirds on reproductive success from the nesting and fledging success of buntings from 1980 through 1987. We censused each territory at least once a week throughout the breeding season. When we saw a male with nesting material in her bill or knew that she was mating or laying, we avoided the site so that we would not cause her to desert the nest. We compared breeding success for 1733 bunting nests which met the following criteria: (1) a bird (cowbird or bunting) laid at least one egg, (2) the male was born by 1984 (we did not follow all birds in later years, though the birds born from 1979 through 1984 we followed through 1991) or the male or its mate was banded as a nesting or was known to be the parent of a nesting that returned to its natal area, (3) we did not disturb the nest (that is, we did no apparent damage to the nest or its contents, such as when we accidentally trampled a few nests or spilled a nest and broke the eggs, or we netted the female within a few days after she laid and she deserted, or she deserted her young when she was biopsied; Westneat et al., 1986; n = 13, or 1% of all nests), and (4) we determined nesting and fledging success by visiting the nest until it failed or fledged. We compared the frequency of nest parasitism with age of the breeding adult to test whether parasitism decreased with age and breeding experience.

We identified the eggs and nestlings by their appearance. Cowbird eggs were large (20–23x15–17 mm) and pale blue with brown spots; indigo bunting eggs were small (17–20x13–15 mm), white and unspotted. Cowbird nestlings were large...
and had pink mouth linings, a white gape, and gray-white natal down; bunting nestlings were small and had orange mouth linings, a yellow gape, and a darker, more sparse coat of down.

We estimated the impact of egg removal by the female cowbird on clutch size of the buntings by comparing the number of eggs in nests with a cowbird egg and in the number of eggs unparasitized nests. We inferred that a lower clutch size of parasitized nests was due to egg removal or damage by the cowbird, as female cowbirds have been seen to remove and eat a host egg before they lay their own (Neudorf and Sealy, 1994; Scott et al., 1992), and they also may damage a host egg when they lay (Payne, 1997; Roskaft et al., 1990).

We determined fledging when the young survived to at least 7 days in the nest. We often heard and sometimes saw birds after they fledged, and in the other cases we confirmed fledging by the form of the nest, when it was stretched and flattened by the growing brood. We determined loss to weather when the nest was found tipped and empty or with abandoned eggs or dead young after a period of wind, cold or rain. We determined predation when the nest that had contained eggs or young was found empty before it could have fledged and the nest was torn or the nest lining was pulled up, much as we observed when we grasped large nestlings and lifted them from the nest (when we observed fledglings out of the nest, the nest was stretched and not torn or lining pulled), excluding loss to weather; we excluded nests (n = 15) for which we were uncertain whether the loss was at the egg or the nestling stage. We tested the effect of cowbird nestling competition by comparing the fledging success of buntings in parasitized nests and unparasitized nests when the nest was not predated and at least one young bird, whether bunting or cowbird, survived to fledge from the nest.

We determined postfledging survival by observing the buntings when they returned to their natal area in a later year. We banded nearly all nestlings from 1978 through 1990 (a longer period than the study of reproductive success) at day 4-5 when large enough to hold a metal USFWS band and color band (Holcomb, 1966). We did not regularly weigh or measure them to lessen our disturbance to the breeding birds (young 7 days or older sometimes fledged prematurely when an observer approached the nest). In the following years through 1991 we captured and re-marked the banded birds that returned to their natal area (Payne, 1991; Payne and Payne, 1993b). To estimate the effects of competition by fledgling cowbirds, we compared the proportion of nestling bunting that returned in the next year from nests where they fledged with a cowbird and nests where a cowbird did not fledge. Most surviving young apparently settled outside the study area (most new breeding birds in the study area were unbanded when first observed). Nevertheless, the difference in return of parasitized and unparasitized fledglings appeared to be due to survival and not to dispersal: insofar as bunting that fledged from a crowded nest (as with a cowbird) might settle at a distance and be undetected, the observed natal dispersal distances did not vary with brood size of the buntings, and there was no apparent effect of brood competition on natal dispersal distance (Payne, 1991).

We determined the long-term effects of parasitism through the season by comparing the proportion of marked birds that nested again and the success of the next nest when the earlier nest was parasitized and when it was not parasitized. We also compared the total number of buntings fledged for the marked females that were parasitized or were not parasitized in at least one nest.

We determined survival of adults and reproductive success of the adult females into the next year. We interpret whether a bird returned in terms of survival rather than breeding dis-

Statistical analyses

We compared the proportions of nests parasitized in different habitats and nest plants with log-likelihood G tests and the associations of breeding buntings' age and parasitism with 2 × 2 chi-square tests. For clutch size, we compared the distribution of numbers with log-likelihood tests, as the clutches were usually zero, three, or four bunting eggs. We used logistic regressions to test whether seasonal variation in clutch size or egg removal by the female cowbirds explained the lower clutch size in parasitized nests.

We used log-likelihood tests to compare the number of buntings fledged in parasitized nests when the cowbird egg failed to hatch, when it hatched but did not fledge, when it fledged, and when the nests were not parasitized. We used t tests to distinguish at which stages the cowbird affected the breeding success of the buntings, and we used the mean differences in success to compare the effects of parasitism at these stages. We determined whether the variances were equal; we report the uncorrected or adjusted t and p values according to the results. We used chi-square and t tests to compare nesting and the breeding success of later nests that followed a parasitized nest and an unparasitized nest. To test whether fledging cowbirds affect the postfledging survival of buntings, we used a chi-square test to compare the proportion of banded nestlings that we saw in a later year. We used one-way ANOVA to compare seasonal reproductive success of females in different categories of being parasitized and t tests to compare these groups pairwise. We used logistic regressions to compare the effects of age, number of buntings fledged, and whether a cowbird fledged on whether a breeding adult bird returned in the following season. We used t tests to compare reproductive success in the next season for females that returned after rearing a cowbird or rearing only their own brood.

Our sample sizes varied with the completeness of the data; for example, we did not always record the nest plant, and not all nests were observed from the time of laying to determine clutch size. We analyzed the two study areas separately because they differed in several features; the consistency in results indicated some generality to the conclusions.

We used the SAS System for Solaris, version 6.11 (Cary, North Carolina), for statistical analyses. All tests were two-tailed and conducted at the α = .05 significance level. Means are reported ± SD.
To test whether risk of being parasitized varied with nesting habitat, we compared the proportion of nests that were parasitized in different habitats (Table 1). The proportion did not differ significantly among these habitats (Niles, $n = 1,040$, $G = 1.52$, df = 4, $p = .82$; George Reserve, $n = 693$, $G = 4.59$, df = 4, $p = .35$).

Fewer than half the nests were parasitized in each kind of nest plant (Table 2). We found no significant differences among nest plants with at least 10 nests within an area at risk of cowbird parasitism (Niles, $n = 465$, $G = 4.17$, df = 5, $p = .53$; George Reserve, $n = 277$, $G = 6.55$, df = 4, $p = .16$).

Age of breeding adults

In the early years where eggs were laid by 10 July, yearling and older adult males at Niles were equally likely to be parasitized (yearlings, 39.0% of 215 nests; adults, 34.9% of 505 nests, $x^2 = 1.10$, $p = .29$), and at George Reserve the yearling males were more likely to be parasitized (yearlings, 27.5% of 189 nests; adults, 19.8% of 569 nests, $x^2 = 4.30$, $p = .04$). At Niles 50 female birds that we banded as nestlings returned in a later year; of these, 28 females that returned as yearlings also returned for a later year, 14 did not return, and 8 we found only in a later year. For these 50 females we found 192 nests. Nests of yearlings were no more likely to be parasitized than nests of older females (yearlings, 56 nests, 35.7% parasitized; older adults, 66 nests, 31.8% parasitized, $x^2 = 0.13$, $p > .5$). At George Reserve, where few birds returned to breed in their natal area, 44% of 9 nests were parasitized in the female's yearling year, and 0 of 3 nests in a later year. There was no difference in risk of being parasitized in yearling and older females.

Effects of cowbird parasitism on breeding success

Clutch size

Nests with cowbird eggs had fewer bunting eggs than nests with no cowbird eggs. In the 2 years with our most complete information (Payne, 1992), mean clutch size was significantly lower in the parasitized nests at Niles (unparasitized nests, $n = 174$, $x = 3.13$ ± 0.59 SD; parasitized nests, $n = 97$, $x = 2.96$ ± 0.75; $G = 87.3$, df = 3, $p < .001$) and at George Reserve (unparasitized nests, $n = 87$, $x = 3.41$ ± 0.8; parasitized nests, $n = 57$, $x = 2.35$ ± 0.82; $G = 49.7$, df = 3, $p < .001$).

The difference appears not to be due to female age, as clutch size did not differ between yearling and older females (individual females of each age laid three-egg and four-egg clutches within a season), and both yearling and older females nested through the season (Payne, 1989; our observations). The difference was not due to a larger clutch size after the cowbird season, as mean clutch size of the unparasitized nests (the nests unlikely to have been disturbed by a cowbird) did not increase, rather, it decreased through the first 3 months (Figure 2).

When we considered variables in logistic regressions, whether a nest was parasitized affected clutch size, but month did not at Niles ($n = 271$ nests, month Wald $x^2 = 0.22$, df = 4, $p = .64$; parasitism Wald $x^2 = 65.6$, $p < .0001$). Both month and parasitism affected clutch size at George Reserve; the effect of parasitism was greater ($n = 124$ nests, month Wald $x^2 = 22.4$, $p < .0001$; parasitism Wald $x^2 = 44.2$, $p < .0001$).

On the other hand, we observed nests from day to day that lost a bunting egg and gained a cowbird egg. Because age and season did not account for much of the variation in clutch size in the unparasitized nests or for the difference in clutch size between parasitized and unparasitized nests, the difference in clutch size was likely due to a cowbird removing a host egg before she laid her own egg.

Nesting success

Unparasitized nests were significantly more likely to fledge a bunting than were parasitized nests. The unparasitized nests
were nearly three times more likely to fledge a bunting in both areas (Table 3).

Production of young bunting
Fewer bunting fledged from parasitized nests, and the number fledged varied with the success of the cowbird (Table 4). Comparing all nests, the mean number of bunting fledged was 1.54 ± 1.46 from unparasitized nests and 0.57 ± 0.81 from parasitized nests (t = 12.5, p < .0001) at Niles, and 1.62 ± 1.51 versus 0.40 ± 0.90 (t = 16.3, p < .0001) at George Reserve. The cost of parasitism as indicated by the difference in the number of bunting fledged from the parasitized nests was 1.17 fledglings at Niles and 1.22 at George Reserve. The lower success of the unsuccessful nests was often due to loss of the entire clutch or brood to predators or to desertion of the eggs or young, and this affected the bunting as well as the cowbird. Nonetheless, most nests where a cowbird fledged also fledged one or more bunting.

Nest predation
Nests with cowbird eggs and nests with cowbird nestlings were more likely to be taken by a predator than were unparasitized. At Niles, 145 (19.3%) of 753 unparasitized clutches and 36 (31.1%) of 112 parasitized clutches were taken (x² = 16.3, df = 1, p < .001). At George Reserve, 96 (17.5%) of 556 unparasitized clutches and 39 (28.7%) of 136 clutches with a cowbird egg were taken (x² = 9.06, df = 1, p = .01). Broods with a nestling cowbird were more likely to be taken than were broods with no cowbird [Niles, 53 of 112 parasitized broods (47.3%), 143 of 626 unparasitized broods (22.8%), x² = 29.2, df = 1, p < .001; George Reserve, 16 of 44 parasitized broods (36.4%), 106 of 468 unparasitized broods (22.7%), x² = 4.17, df = 1, p < .05].

Nestling competition
We tested the competitive effect of cowbird young in nests where at least one nestling (a bunting or a cowbird) survived to fledge. When a cowbird fledged, fewer bunting fledged (Niles, nests that fledged a cowbird, n = 45, x = 1.27 ± 0.86 bunting fledged, other nests, n = 451, x = 2.71 ± 0.75 bunting fledged, t = 12.2, p < .0001; George Reserve, nests that fledged a cowbird, n = 29, x = 0.83 ± 0.89, other nests, n = 325, x = 2.85 ± 0.74, t = 13.8, p < .0001). In these nests that survived to fledge, the average cost of successful parasitism when a cowbird fledged was 1.44 fewer bunting fledged at Niles and 2.02 fewer at George Reserve.

The effect varied with the number of cowbirds. Three nests fledged two cowbirds, and in these no bunting fledged. No nests fledged three cowbirds; in the two nests with three cowbird eggs, no more than two cowbird eggs hatched. In the 52 nests that fledged both a cowbird and a bunting, most fledged only 1 or 2 bunting, in contrast to the 9 or 4 bunging fledged from nearly all the successful unparasitized nests. In four broods, 5 bunting fledged with a cowbird. In two of these the cowbird hatched after the bunting; hatching time was not determined in the other two. Occasionally (n = 4) the cowbird disappeared and the bunging survived to fledge.

Table 2
Proportion of nests parasitized in different nest plants

<table>
<thead>
<tr>
<th>Nest plant</th>
<th>Rubus</th>
<th>Cornus</th>
<th>Bracken</th>
<th>Goldenrod</th>
<th>Gooseberry</th>
<th>Suckle</th>
<th>Honeyrose</th>
<th>Multiflora</th>
<th>Sapling</th>
<th>Sumac</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niles</td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>2</td>
<td>9</td>
<td>2</td>
<td>62</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Yes</td>
<td>179</td>
<td>29</td>
<td>5</td>
<td>19</td>
<td>5</td>
<td>0</td>
<td>2</td>
<td>62</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>George Reserve</td>
<td>84</td>
<td>11</td>
<td>4</td>
<td>6</td>
<td>2</td>
<td>1</td>
<td>7</td>
<td>20</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>No</td>
<td>72</td>
<td>103</td>
<td>5</td>
<td>6</td>
<td>18</td>
<td>10</td>
<td>14</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Yes</td>
<td>21</td>
<td>23</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>10</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

* Nest plants where n > 10 for both study areas combined.
may be due to fledging at lower weight or to competition for parental care after fledging.

Although some buntings fledged from nests where a cowbird also fledged, these bouts were rarely recruited into the adult breeding population. The mean fledging success from a nest where a cowbird fledged when adjusted for survival in a later year (18% of the survival of bunting fledged from nests where a cowbird did not fledge at Niles) is 0.22 buntins at Niles and 0.14 buntins at George Reserve, or only 14% of the success of the unparasitized nests at Niles and 12% at George Reserve.

Reproductive success later in the breeding season
Cowbird parasitism is limited to the first half of the breeding season, so to compare the effect of parasitism on later nesting we considered the early nests where an egg was laid by 10 July. For all nests, we found no difference in the proportion of females that nested again (Niles, 63.6% of 632 unparasitized nests were followed by another nest, and 69.5% of 266 parasitized nests, \(q^2 = 2.92, \text{df} = 1, p = .09\); George Reserve, 44.7% of 530 unparasitized nests, and 44.1% of 136 parasitized nests, \(q^2 = 0.02, \text{df} = 1, p = .90\)). For females that nested after their earlier nest had fledged, we found no decrease when they fledged a cowbird (Niles, 59% of 41 nests that fledged a cowbird were followed by another nest, and 44.0% of 164 nests that fledged a bunting but no cowbird, \(q^2 = 3.05, \text{df} = 1, p = .08\); George Reserve, 27.6% of 29 nests that fledged a cowbird, and 26.7% of 303 nests that fledged only a bunting, \(q^2 = 0.01, \text{df} = 1, p = .92\)).

We tested whether the later nest of a female had a lower probability of success when her earlier nest was parasitized (1) in all nests, (2) in nests that fledged a cowbird, and (3) in nests that fledged at least one young, a bunting or a cowbird. If rearing a cowbird affects the ability of a female to rear another brood within the season, then we predict a lower fledging success in nests following a parasitized nest, in scenario 3 and perhaps also in scenario 2. If fledging success depends on whether the cowbird survives to fledge, then we expect a lower success in scenario 3; if it depends on desertion or other effects of being parasitized, then we expect a lower success in scenario 1 as well. There was no significant decrease in fledging success in later nests that followed a parasitized brood and the clutches and broods that were not parasitized in any of these tests (Table 6).

We also tested whether fewer buntings fledged after the female fledged a cowbird. When she had fledged a nestling of either species, the success of her later nest was slightly lower when a cowbird fledged, but the difference was not significant (Niles, bunting fledged from the early nest, \(n = 89, x = 1.49 \pm 1.45\), cowbird fledged, \(n = 14, x = 1.07 \pm 1.45, t = 1.02, p = .32\); George Reserve, bunting fledged, \(n = 52, x = 1.73 \pm 1.43\), cowbird fledged, \(n = 4, x = 1.25 \pm 1.50, t = 0.62, p = .57\)). In summary, we found no evidence of decreased fledging success in a later nest after an earlier nest was parasitized.

### Seasonal reproductive success
Females that were parasitized fledged fewer buntins than females that were not parasitized (Table 7). At Niles, females not parasitized had the highest reproductive success, but not significantly higher than females whose cowbird fledged (\(t = 0.65, p = .45\); they had higher success than females whose cowbird failed to hatch or fled高达 \(t = 4.56, p < .0001\)). At George Reserve, females not parasitized had higher success than parasitized females, which was significant for females whose cowbird failed and females that fledged a cowbird (\(t = 6.65, p < .0001; t = 2.65, p < .01\)).

### Survival and reproduction in the next season
We tested whether males that fledged a cowbird were as likely to return as were males that did not fledge a cowbird. In logistic regressions, neither male age (yearling or older adult), the number of buntings fledged from all nests on his territory, nor whether a cowbird fledged affected whether the male returned at Niles (\(n = 441, x^2 = 0.69, \text{df} = 3, p = .87\)). Age and number of buntings fledged affected return at George Reserve, but whether a cowbird fledged had no effect (\(n = 252, x^2 = 12.27, \text{df} = 3, p = .0065\); age Wald \(x^2 = 4.01, p < .05\); buntings fledged Wald \(x^2 = 4.45, p < .05\), cowbird fledged Wald \(x^2 = 0.38, p = .54\)).

Female reproductive success affected whether a female returned in the next season, but her minimum age and whether she fledged a cowbird did not (Niles, \(n = 433, x^2 = 20.21, \text{df} = 3, p = .0001\), bunting fledged Wald \(x^2 = 17.01, p < .0001\); George Reserve, \(n = 295, x^2 = 11.44, \text{df} = 3, p = .0069\), bunting fledged Wald \(x^2 = 9.75, p = .002\)). When the model also included whether a female had fledged any nesting, either bunting or cowbird, the number of buntings fledged was less significant (\(p = .06\) at Niles, \(p = .08\) at George Reserve) in predicting whether she returned than in the first test, and
Cowbird egg, cowbird egg did not hatch; cowbird nestling, cowbird nestling did not fledge; cowbird fledgling, a cowbird fledged.

The number of buntings fledged and whether a cowbird fledged had no significant effect.

Returning females that had fledged a cowbird fledged as many buntings in the next season as females that had fledged only their own brood (Niles, fledged a cowbird, n = 14, \( \bar{x} = 1.86 \pm 1.51 \); no cowbird, n = 146, \( \bar{x} = 2.10 \pm 2.09 \), t = 0.43, p = .67; George Reserve, fledged a cowbird, n = 6, \( \bar{x} = 4.00 \pm 2.00 \); no cowbird, n = 65, \( \bar{x} = 2.40 \pm 1.96 \), t = 1.95, p = .06). We found no decrease in adult survival or reproductive success when the breeding season had reared a cowbird in the previous year.

**DISCUSSION**

**Cowbird parasitism of indigo buntings**

Indigo buntings are parasitized by cowbirds through their breeding range, and there is no evidence of regional difference in the incidence of brood parasitism where samples were large (n > 15) and nests were checked through the breeding season (Table 4). A report of 80% parasitism in Illinois was based on observations in the first half of the breeding season (Robinson, 1992, personal communication; Robinson et al., 1995); later in the season indigo buntings are cowbird-free in Illinois (Twomey, 1945). In Michigan and other parts of the Midwest, parasitism is common early in the breeding season, but cowbirds cease laying by early July (Bent, 1968; Carey, 1982; Johnston, 1964; Lowther, 1993; Payne, 1965, 1976; Peck and James, 1987; Trautman, 1940; Wood, 1951), and the later nests in summer escape parasitism.

Over a longer scale of time, there is little information on the local incidence of cowbird parasitism. However, at George Reserve, from 1934 to 1946, four of nine nests (44%) of indigo buntings were parasitized by 10 July, and none of nine nests were parasitized after 10 July (Sutton, 1959), and the proportion of nests parasitized and the seasonal change in risk of parasitism were like our observations there 40 years later.

**Costs of brood parasitism and costs of defense**

Indigo buntings accept the cowbird egg and give care to the cowbird nestling even though cowbird parasitism decreases their own reproductive success. At least half the immediate cost of parasitism can be accounted for by the loss of a host egg when the cowbird lays. At Niles, egg removal accounted for the loss of 0.77 bunting eggs in a nest (the difference in clutch size of unparasitized nests and parasitized nests), and parasitized nests had 1.17 fewer bunting fledged (in all nests, not just those where a nestling fledged); egg removal thus accounted for 66% of the cost of parasitism. At George Reserve, 1.06 fewer bunting eggs were in parasitized nests and 1.22 fewer young fledged from parasitized nests. By this reasoning, egg removal accounted for 87% of the cost of parasitism.

Nestling competition also is a significant cost of parasitism. In broods that fledged, at Niles 1.44 fewer bunting fledged when a cowbird fledged (twice as many as accounted for by egg removal), and at George Reserve 2.02 fewer bunting fledged when a cowbird fledged (35% more than accounted for by egg removal), so rearing a cowbird to fledging lowered the success of the hosts more than only the losses incurred earlier in the nesting effort. Buntings sometimes starved and died a day or two after hatching when the cowbird was only a day or two older. Cowbirds hatch earlier, are larger at hatching, louder in begging, and grow more rapidly (Morgan, 1976; Ortega and Cruz, 1992; Scott, 1979). Cowbird nestlings were more than 20 g (twice as large as a feathered 10-12 g bunting) and would demand a considerable amount of parental care, as avian energy requirements vary directly with body size (Weathers, 1996). Occasionally a cowbird nestling pushes the bunting nestling from the nest, where it starves (Dearborn, 1996); we observed a few dead nestlings below the nest (one was a second nestling cowbird) while a live cowbird remained in the nest, but we did not directly observe nestling ejection. Buntings grow more slowly in broods with a cowbird nestling than in broods without a cowbird, and more slowly still in broods with two cowbirds, where the buntings starve and fail to fledge (Twomey, 1945). Also, in captive broods the cowbird covered the buntings, pushed them into the floor of the nest, climbed onto them, trampled them, and interfered with their access to feeding (Payne, 1999). The cost of parasitism also includes lower postfledging survival of young buntings, and the buntings that fledged with a cowbird were only 18% as likely to return as buntings from nests where a cowbird did not fledge.

Nests with cowbird eggs were more likely to be taken by a predator, and choice of certain nest sites may have led to discovery both by a cowbird and by a predator. The higher rate of predation of nests with cowbird nestlings may be due to

---

**Table 4**

<table>
<thead>
<tr>
<th>Area</th>
<th>Cowbird parasitism&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Number of nests where n buntings fledged</th>
<th>G</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Niles</td>
<td>None</td>
<td>354</td>
<td>23</td>
<td>111</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>Cowbird egg</td>
<td>141</td>
<td>5</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Cowbird nestling</td>
<td>69</td>
<td>9</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Cowbird fledged</td>
<td>9</td>
<td>18</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>George Reserve</td>
<td>None</td>
<td>241</td>
<td>13</td>
<td>72</td>
<td>178</td>
</tr>
<tr>
<td></td>
<td>Cowbird egg</td>
<td>69</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Cowbird nestling</td>
<td>29</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Cowbird fledged</td>
<td>13</td>
<td>9</td>
<td>6</td>
<td>1</td>
</tr>
</tbody>
</table>

<sup>a</sup> Cowbird egg, cowbird egg did not hatch; cowbird nestling, cowbird nestling did not fledge; cowbird fledgling, a cowbird fledged.

---

**Table 5**

<table>
<thead>
<tr>
<th>Area</th>
<th>Buntings fledged seen in later year?</th>
<th>Did a cowbird fledge from the nest?</th>
<th>( \chi^2 )</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yes</td>
<td>No</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Niles</td>
<td>63</td>
<td>1225</td>
<td>4.41</td>
<td>&lt;.05</td>
</tr>
<tr>
<td>George Reserve</td>
<td>1</td>
<td>124</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>32</td>
<td>1217</td>
<td>0.71</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>27</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
the fact that nestling cowbirds are loud, call persistently, and call when unattended. Experimental tests with recorded begging calls in other species indicate that nest predators cue to begging nestlings (Haskell, 1994).

Although cowbirds affect their breeding success, the adult buntings did not remove cowbird eggs nor did they discriminate against cowbird nestlings. The cost of rejecting a cowbird egg may be less than the cost of accepting it. When the host removes an odd egg from the nest, it risks removing its own egg in error or damaging its own eggs (Davies and Brooke, 1988; Davies et al., 1996; Lotem et al., 1995; Raskkaft et al., 1990). Many small acceptors such as indigo buntings have short bills and this limits their ability to grasp or pierce the large and hard cowbird egg and remove it from the nest (Robwer and Spaw, 1988). Also, when the cowbird egg is laid before her own, a bunting may desert at cost, and when it is laid after her own clutch is complete, the cowbird egg may fail to hatch (Payne, 1992). Perhaps a host would not regain the cost already paid when the cowbird removed or damaged a host egg so it will not hatch, and this may explain why most small hosts accept the cowbird egg (Raskkaft et al., 1990; Rothstein, 1990). Parental discrimination and rejection of the nestlings in their nest is rare in birds (Davies and Brooke, 1988; Dawkins and Krebs, 1979), and, as with eggs, this lack of discrimination may in part reflect a cost of removing their own young. When we grasped a nestling bunting, it often grasped another nestling or the nest lining, and the disturbance caused another young to leave the nest, either a small nestling that was accidentally removed or a larger one that prematurely fledged, so the removal of one may lead to the loss of another nestling. In addition, Davies and Brooke (1988) described the difference in removal of a parasitic egg and the removal of a nestling in terms of benefits, where removal of an egg results in the host saving its current brood, but removal of a nestling results in saving only a future brood. This is the argument in cuckoos, where the hatchling evicts the host eggs, and the same may apply to cowbirds where the nestling has already caused the host nestlings to starve.

In summary, the evolutionary response of bunting hosts to cowbird parasitism may be limited by the non-recoverable cost of removal of its egg by the female cowbird, the costs of discriminating eggs and nestlings, and the physical constraints in removing the cowbird egg, all as in some other parasitized songbirds (Davies and Brooke, 1988; Davies et al., 1996; Payne, 1997; Rohwer and Spaw, 1988; Raskkaft et al., 1990).

Long-term costs of cowbird parasitism on host survival and reproduction

In our study, cowbird parasitism was independent of the condition of the breeding birds insofar as the probability of being parasitized did not vary with female age or habitat, and cowbird parasitism approximated a natural experiment on the reproductive success of the breeding adults later in the season and in the next season. The subsequent survival and reproductive success of buntings was independent of whether they

Table 7
Seasonal reproductive success of female buntings that were parasitized and those that were not parasitized in at least one nest

<table>
<thead>
<tr>
<th>Area</th>
<th>Cowbird parasitism</th>
<th>Females</th>
<th>成功</th>
<th>Buntings fledged</th>
<th>( \bar{x} \pm SD )</th>
<th>F</th>
<th>( \rho )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niles</td>
<td>None</td>
<td>357</td>
<td>2.45 \pm 1.92</td>
<td>9.37</td>
<td>&lt;.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cowbird egg, not fledged</td>
<td>144</td>
<td>1.66 \pm 1.64</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cowbird fledged</td>
<td>35</td>
<td>2.23 \pm 1.57</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>George Reserve</td>
<td>None</td>
<td>258</td>
<td>2.58 \pm 1.85</td>
<td>17.40</td>
<td>&lt;.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cowbird egg, not fledged</td>
<td>57</td>
<td>1.16 \pm 1.36</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cowbird fledged</td>
<td>22</td>
<td>1.50 \pm 1.63</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
reared a cowbird. In this respect, the buntings suffered no
long-term cost of rearing a cowbird.

Our observations provide the most comprehensive data on
the effect of cowbird parasitism on fledging success for any
species of host. Cowbirds affect the breeding success of indigo
buntings by means of egg removal, nestling competition, in-
creased risk of nest predation, and decreased survival of
young buntings that fledge from a nest where a cowbird also
fledges. Because rearing a cowbird to fledging has no effect
on a later nest of the adults within a season or on their sur-
vival and reproductive success into a later year, the cost of
parasitism is mainly accounted for by the frequency of brood
parasitism through the breeding season, the difference in
fledging success of parasitized and unparasitized nests, and
the effect of cowbird fledging on the survival of buntings' fled-
glings. There is little long-term cost of brood parasitism on
the reproductive success of adult indigo buntings beyond the
impact on their current nest and brood.

We thank our research assistants, especially Chris Bowen, Jamie Black-
burn, Cynthia DeMeester, Scott Fogel, Kathy Groachup, Carola Haas,
Robin Jung, Susan Doehlert Kiclb, Chris Kurtz, Rebecca Irwin, Selma
Iait, Roy Smith, Mark Stanback, Paul Super, Dave Westneat, and Jean
Woods. Amtrak and landowners allowed access to lands at Niles. The
University of Michigan Museum of Zoology provided accommodations
and access to the George Reserve. Birds were banded under U.S. Fish
and Wildlife Service Bird Banding Laboratory permit 20080. For ad-
vice on statistics, we thank Ken Guire, Kathy Welch, and Jean Woods.

Table 8
Cowbird parasitism of indigo buntings in various regions

<table>
<thead>
<tr>
<th>Region</th>
<th>Parasitized nests/total nests checked</th>
<th>% Parasitized</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Michigan, Niles</td>
<td>277/1040</td>
<td>26.6</td>
<td>This study</td>
</tr>
<tr>
<td>Michigan, George Reserve</td>
<td>137/693</td>
<td>19.8</td>
<td>This study</td>
</tr>
<tr>
<td>Michigan, George Reserve</td>
<td>4/18</td>
<td>22</td>
<td>Sutton (1959)</td>
</tr>
<tr>
<td>Wisconsin</td>
<td>12/26</td>
<td>46</td>
<td>Young (1963)</td>
</tr>
<tr>
<td>Ontario</td>
<td>40/165</td>
<td>24</td>
<td>Peck and James (1987)</td>
</tr>
<tr>
<td>Quebec</td>
<td>6/50</td>
<td>20</td>
<td>Terrill (1981)</td>
</tr>
<tr>
<td>Ohio</td>
<td>5/16</td>
<td>31</td>
<td>Trautman (1940)</td>
</tr>
<tr>
<td>Ohio</td>
<td>17/45</td>
<td>40</td>
<td>Hicks (1994)</td>
</tr>
<tr>
<td>Indiana</td>
<td>22/63</td>
<td>35</td>
<td>Carey (1982)</td>
</tr>
<tr>
<td>Illinois</td>
<td>16/41</td>
<td>39</td>
<td>Twomey (1945)</td>
</tr>
</tbody>
</table>

REFERENCES

Bent AC (ed), 1968. Life histories of North American cardinals, gros-
beaks, buntings, towhees, finches, sparrows and allies. U.S. National
Museum Bulletin 237, Washington, DC.

Carey M, 1982. An analysis of factors governing pair-bonding period
and the onset of laying in indigo buntings. J Field Ornithol 55:240-
248.

Davies NB, Brooke MdeL, 1988. Cuckoos versus reed warblers: adap-
tations and counteradaptations. Anim Behav 36:262-284.

Davies NB, Brooke MdeL, Kacelnik A, 1996. Recognition errors and
probability of parasitism determine whether reed warblers should
accept or reject mimetic cuckoo eggs. Proc R Soc Lond B 263:925-
931.


Dearborn DC, 1996. Video documentation of a brown-headed cow-

bird nestling ejecting an indigo bunting nestling from the nest.
Condor 98:645-649.

Friedmann H, 1963. Host relations of the parasitic cowbirds. U.S. Na-
tional Museum Bulletin 253, Washington, DC.

Gustafsson L, Pärt T, 1990. Acceleration of senescence in the collared
flycatcher Ficedula albicollis by reproductive cost. Nature 347:279-
281.

Hicks LE, 1954. A summary of cowbird host species in Ohio. Auk 51:
585-586.

Högestedt G, 1981. Should there be a positive or negative correlation
between survival of adults in a bird population and their clutch

Holcomb LC, 1966. The development of grasping and balancing coordi-
nation in nestlings of seven species of altricial birds. Wilson Bull
88:57-63.

Johnston RF, 1964. The breeding birds of Kansas. Univ Kansas Publ
Mus Nat History 12:575-655.

32-68.

Lessells CM, 1993. The cost of reproduction: do experimental manip-
ulations measure the edge of the options set? Ecolography 3:95-111.

Lindén M, Måsler, AF, 1989. Costs of reproduction and covariance of

Lotem A, Nakamura H, Zahavi A, 1999. Constraints on egg discrimi-
nation and cuckoo-host co-evolution. Anim Behav 49:1185-1209.

Lowther PE, 1993. Brown-headed cowbird. The birds of North Amer-
ica, no. 47 (Poole A, Gill F, eds). Philadelphia: American Orni-
thologists' Union.


McGillivray WB, 1983. Intraseasonal reproductive costs for the house
sparrow (Passer domesticus). Auk 100:25-32.

Morgan FD, 1976. Nesting studies of the indigo bunting (Passerina


Nur N, 1988. The cost of reproduction in birds: an examination of

Brood-size manipulations within the natural range did not reveal
intragenetational cost of reproduction in the willow flycatcher Ficedula
albicollis. Ibis 138:530-537.

brown-headed cowbirds and yellow-headed blackbirds. Auk 109:
368-376.

Partridge L, 1989. Lifetime reproductive success and life-history evo-

Rohwer S, Spaw CD, 1988. Evolutionary lag versus bill-size constraints: 


Peck GK, James RD, 1987. Breeding birds of Ontario, nidiology and 


Raskin E, Orians GH, Beletsky LD, 1990. Why do red-winged black- birds accept the eggs of brown-headed cowbirds? Evol Ecol 4:35- 


122.