

BROWN-HEADED COWBIRD NESTLING VOCALIZATIONS AND RISK OF NEST PREDATION

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ABSTRACT.—Models concerning the evolution of avian begging behavior predict that nestlings of brood parasites should beg more loudly or frequently than nonparasitic nestlings and that the exaggeration of begging calls in general may be limited by the risk of nest predation. This study is the first to test experimentally for a link between brood parasitism, nestling vocalizations, and the risk of nest predation. Begging calls at Indigo Bunting (*Passerina cyanea*) nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) were louder and more frequent than those at nonparasitized nests. Predation rates at Indigo Bunting nests were significantly higher at parasitized nests than at nonparasitized nests during the incubation period and over the entire nesting cycle, and there was a trend for such a difference during the nestling period as well. I performed an artificial nest experiment to test for an effect of nestling vocalizations on the risk of nest predation. Nests broadcasting cowbird begging calls (300 calls/h at 80 dB) experienced the highest predation rates, followed by nests broadcasting bunting begging calls (60 calls/h at 74 dB), followed by silent nests. The overall difference among predation rates for the three treatments was significant, but follow-up pairwise comparisons detected a difference in predation rates only between nests broadcasting cowbird begging calls and silent nests. Thus, nestling vocalizations may be partly responsible for the observed difference in predation risk during the nestling period at parasitized and nonparasitized natural nests, but other factors such as nest site or parental behavior are likely to influence the risk of both parasitism and nest predation. *Received 2 September 1997, accepted 23 September 1998.*

A CRITICAL ISSUE in understanding the evolution of begging behavior is determining the selective forces that limit its exaggeration (see Kilner and Johnstone 1997). Because exaggerated begging can result in increased food acquisition for a nestling (Smith and Montgomerie 1991, Teather 1992, Price and Ydenberg 1995), selective forces must act to prevent runaway expression of begging. Four factors have the potential to limit the exaggeration of begging behavior. First, begging may be energetically costly. Second, if begging determines the distribution of food among nest mates (i.e. assuming total food delivery is fixed), then increased begging by one individual could cause a reduction in food received by that individual's nest mates, which typically are full or half siblings in most bird species. Third, if begging influences the rate of food delivery to the nest (i.e. assuming total food delivery is not fixed), then increased begging could cause a parent to

increase its investment in the current brood, potentially at the expense of its future reproductive success. Finally, begging may attract predators to the nest.

Most models of the evolution of begging have incorporated predation risk and/or energetic costs as factors that limit the exaggeration of begging (MacNair and Parker 1979; Harper 1986; Godfray 1991, 1995), but empirical evaluations of the importance of any of the four factors are few. Three studies have estimated the energetic cost of begging (Leech and Leonard 1996, McCarty 1996, Bachman and Chappell 1998). One comparative study has addressed begging intensity and relatedness among nest mates (Briskie et al. 1994), and numerous studies have shown that increased investment in the current brood reduces the future reproductive potential of the parents, although these experiments typically have been performed by altering brood size rather than begging behavior (Stearns 1992). Lastly, one study has examined the relationship between begging rate and predation risk (Haskell 1994). Haskell conducted an experiment with artificial nests in which he broadcast begging calls at different rates and

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from different nest sites, finding an effect of call rate on predation risk in one nest type. An alternative method for investigating the relationship between begging vocalizations and predation risk is studying a brood-parasite system. Such a system allows one to examine, both naturally and experimentally, the rate and loudness of begging vocalizations and the risk of predation at parasitized and nonparasitized nests of a single species.

Investigating the relationship between begging calls and predation risk in a brood-parasite system can provide insight into the evolutionary role of predation risk in limiting begging behavior because the evolutionarily stable intensity of begging is likely to be higher for a brood-parasitic nestling than for a nonparasitic nestling. Although energetic costs could limit begging behavior in a brood parasite, three additional factors that have the potential to limit begging in nonparasitic nestlings apply differently or not at all to brood parasites. First, brood-parasitic nestlings are not related to their nest mates and therefore would incur no inclusive fitness costs for outcompeting them for food. Second, brood-parasitic nestlings are not related to the adults that provision the nest and so would not pay an inclusive fitness cost for causing the adult to increase its rate of provisioning at the expense of its future reproductive success. Finally, the risk of nest predation has less potential to limit the expression of begging behavior by a brood-parasitic nestling because a brood parasite's nest mates are not conspecifics (Harper 1986, Motro 1989). The latter factor would operate under the assumption that the begging calls of individuals in a nest attract predators in at least an additive manner. Consequently, a nest with four loud chicks would be more likely to be depredated than a nest with one loud chick and three quiet chicks, and a nest with one loud cowbird chick and three quiet host chicks would be less likely to be depredated (all else being equal) than a nest with no cowbirds and four loud hosts. Under these conditions, an allele for "loud begging" in a population of hosts would result in more overall noise coming from nests and a higher risk of nest predation than would a comparable allele in a population of cowbirds parasitizing a normal "quiet" host. This difference in predation risk would allow a "loud begging" allele to spread in a cowbird population under

conditions in which it would not spread in a host population.

For this combination of reasons, cowbird begging calls should be more intense (i.e. louder or more frequent) than those of host chicks, and, within a particular host species, parasitized nests should experience higher rates of nest predation than nonparasitized nests as a result of the louder or more frequent begging calls emanating from parasitized nests. Several researchers have noted anecdotally that brood-parasitic nestlings beg louder or more often than their host nest mates (Friedmann 1929, Nice 1939, Payne 1991 for *Molothrus ater*; Carter 1986 for *M. aeneus*). A recent study found that one brood-parasitic Common Cuckoo chick (*Cuculus canorus*) begged as frequently as an entire brood of host chicks (Davies et al. 1998). Three additional studies have demonstrated that the begging calls of brood-parasitic nestlings are louder or more frequent than those of nonparasitic nestlings (Gochfeld 1979 for *M. bonariensis*; Redondo 1993 for *Clamator glandarius*; Briskie et al. 1994 for *M. ater*). The comparative work of Briskie et al. (1994) demonstrated that, across taxa, the loudness of begging calls was negatively correlated with average relatedness among nest mates, and in one of their phylogenetic contrasts, they found that Brown-headed Cowbirds (*Molothrus ater*) begged more loudly than Red-winged Blackbird (*Agelaius phoeniceus*) nestlings, a closely related nonparasitic species. However, only Gochfeld (1979) and Davies et al. (1998) have addressed whether parasitic nestlings increase the noise emanating from natural nests. This information is an important step in assessing the extent to which begging by brood-parasitic chicks may increase the risk of nest predation.

Several authors have hypothesized that the vocalizations of brood-parasitic nestlings increase the risk of predation at parasitized nests (Friedmann 1929, Gochfeld 1979, Payne 1991, Robinson et al. 1995), but no study has tested for a link between brood parasitism, nestling vocalizations, and the risk of nest predation. In this study, I tested for such a link in nests of Indigo Buntings (*Passerina cyanea*), a frequent cowbird host and a typical host in terms of body size and taxonomy (Friedmann and Kiff 1985). Indigo Buntings are shrub nesters that commonly occur in early successional habitat. They do not eject cowbird eggs or abandon par-

asitized nests, and they are usually capable of raising their own chicks when parasitized (Payne 1991, Dearborn et al. 1998). Here, I quantify the rate and loudness of begging vocalizations at parasitized and nonparasitized Indigo Bunting nests, compare nest-predation rates at parasitized and nonparasitized Indigo Bunting nests, and describe the results of an artificial nest experiment that directly tests the influence of cowbird nestling vocalizations on predation risk.

METHODS

Vocalizations at bunting nests.—I monitored Indigo Bunting nests daily in mixed old-field and wooded areas at the University of Missouri's Thomas Baskett Wildlife Research Area in Boone County, Missouri, in 1995 and 1996. On days 2, 4, and 6 of the 10-day nestling period, I measured two aspects of nestling vocalizations: (1) the sound pressure level (SPL) of begging calls (in decibels [dB] re 20 μ Pa), and (2) the rate of call production. I measured SPL with a Radio Shack sound-level meter mounted on a tripod and pointed down at the nest at angle of approximately 30°, with the meter's microphone placed 0.3 m from the outer edge of the nest rim. I set the meter to measure the maximum SPL peak in each 1-s interval, using the A-weighted setting, which responds mainly to frequencies between 0.5 to 10 kHz. I set up a video camera to record both the reading on the sound-level meter and the activity at the nest in order to obtain a measure of the SPL of begging calls when a parent arrived at the nest with food. For each nest, I recorded the highest clean (i.e. no background noise) SPL reading during the first feeding trip after the equipment was in place.

I measured the rate of begging calls by recording nest noise with a sound-activated tape recorder connected to a small lapel-style microphone mounted on vegetation approximately 0.1 m above the nest. Recordings were usually made for 4 h (range 1.75 to 4.75 h). Sonograms of bunting and cowbird begging calls made using a Kay 5500 sonograph exhibit too much intraspecific variation and too much interspecific overlap to distinguish one species from the other. Both types of calls have dominant frequencies of 7 to 8 kHz, upper and lower frequencies of approximately 10 and 6 kHz, and an approximately 20-dB change in amplitude between the dominant frequency and the upper or lower frequencies. Temporally, the peak amplitude occurs near the center of the call. Both types of calls exhibit rapid frequency oscillations over time but generally without the harmonic overtones and upward frequency sweep found in the calls of some of the younger Indigo Bunting chicks studied by Thompson and Rice (1970).

Because the begging calls of cowbirds and bun-

tings at my study site exhibit similarities in power spectra, oscillograms, and spectrograms, they cannot be consistently identified to species. Thus, all measurements of the rate of begging calls represent the combined calling of all nestlings in a given nest. Each nest contributed a single measure of the number of calls per hour.

In contrast to calls recorded at day-6 nests, many day-2 and day-4 begging calls were difficult to hear on the audio tape, and it is likely that additional calls were not loud enough to activate the tape recorder. The SPL threshold at which begging calls activated the tape recorder was approximately 56 dB, a higher SPL level than those recorded from many of the 2- and 4-day-old broods that I measured. Thus, data from tape recordings of day-2 and day-4 nests would underestimate the rate at which calls are produced at those nests. In addition, if cowbird nestlings are louder than bunting nestlings at these ages, analysis of these tapes could give the false impression that parasitized nests produced more frequent begging calls than did nonparasitized nests. Thus, I do not present the data on the rate of begging calls by 2-day-old and 4-day-old nestlings.

Artificial nest experiment.—Data collected in the above manner in 1995 suggested that begging calls at parasitized nests were louder and more frequent than those at nonparasitized nests. To test for an effect of louder and more frequent calls on predation risk, I performed an artificial nest experiment in 1996. I mounted small speakers in the bottom of wicker basket nests (10 cm in diameter and ca. 7 cm tall with speaker attached) and connected them to tape players via a 1.5-m brown speaker wire. Nests were baited with two plasticine eggs of similar size (21 \times 15 mm) and appearance (white, immaculate) as Indigo Bunting eggs. The use of plasticine eggs prevented a predator from receiving a reward and thus may have reduced the likelihood of individual predators forming a search image for artificial nests or becoming "artificial nest specialists." Nests were arranged in trios along the forest-field edge, which is where we found most of the natural bunting nests. Nests in a given trio were placed in a line parallel to the forest edge, with nests spaced 20 m apart and connected to a single battery via 18-gauge black wire concealed in the vegetation. This distance between nests was within the range found for natural nests at these sites. Nests were placed 0.2 to 0.5 m above the ground in plants commonly used by locally nesting buntings (i.e. coralberry [*Symphoricarpos orbiculatus*], box elder [*Acer negundo*], blackberry [*Rubus allegheniensis*]). Nest heights were similar to those of natural bunting nests along the forest-field edge at the study sites (\bar{x} = 0.47 \pm SE of 0.02 m; Burhans 1997). Tape players were concealed in green plastic on the ground beneath the nests. After the three nests in a replicate were mounted in the plants, each nest was randomly assigned to one of the three treatments: (1)

TABLE 1. Rate and loudness ($\bar{x} \pm SE$) of begging calls at natural Indigo Bunting nests on day 6, 1995 to 1996, and as broadcast from artificial nests during nest-predation experiment in 1996. Data from natural nests are least-squares marginal means that account for variation in brood size based on a two-way ANOVA. Sample sizes in parentheses refer to number of nests.

Nest type	Begging rate (calls per h)		Begging loudness (dB)	
	Natural	Experimental	Natural	Experimental
Parasitized nests	398.7 \pm 53.2 (8)	300	78.8 \pm 63.8 (6)	80
Nonparasitized nests	93.2 \pm 33.5 (22)	60	70.0 \pm 59.4 (18)	74

cowbird calls, in which five begging calls of a 6-day-old cowbird were broadcast once per minute (300 calls/h) at an SPL of 80 dB; (2) bunting calls, in which three begging calls of a 6-day-old Indigo Bunting were broadcast once every 3 min (60 calls/h) at an SPL of 74 dB; and (3) silent, in which no calls were broadcast but tape players were turned on and produced the same slight static hiss that was audible between calls in the other treatments. Because begging calls of the two species could not be reliably distinguished, the bunting calls used in the experiment were recorded at a nonparasitized nest, and the cowbird calls were recorded at a parasitized nest in which the bunting eggs had failed to hatch (i.e. the cowbird nestling was the only nest occupant). Owing to logistical problems with timer switches, tapes were played constantly (day and night).

My choice of the rate and loudness of calls was based on data collected at natural bunting nests in 1995, which were similar to the combined data for 1995 and 1996 (see Table 1). Because the tape recorders that I used to record begging calls at natural nests were sound activated, calls were recorded in episodes that were interrupted by the slight sound of the tape player starting and stopping. In analyzing call-rate data, I found that parasitized nests differed from nonparasitized nests in both episodes per hour and calls per episode. A recording episode cannot be directly equated to a feeding trip by a parent because adult buntings at parasitized nests made more feeding trips per hour than those at nonparasitized nests (Dearborn et al. 1998), but cowbirds were more likely than buntings to beg at inappropriate stimuli, potentially leading to more vocalizations in the interval between parental visits at parasitized nests than at nonparasitized nests (Dearborn 1998). Although the meaning of a recording episode is somewhat unclear, I incorporated these data into the design of the nest-predation experiment (temporal spacing of calls in the experiment was also constrained by the maximum length of available audio loop tape). Thus, nests in the parasitized treatment (i.e. five cowbird calls followed by roughly 55 s of silence) differed from those in the nonparasitized treatment (i.e. three bunting calls followed by roughly 2 min 57 s of silence) in both episodes per hour and calls per episode.

The set of three nests was replicated 15 times in locations at least 150 m apart; this low density of artificial nests reduced the likelihood of multiple replicates being encountered by the same individual predator. Artificial nests and bunting nests were checked daily. Because the three nests within a replicate may not be independent, a replicate was discontinued once the first nest was depredated. If no nests in a replicate were depredated after seven days, the replicate was terminated in order to recharge the battery for the tape players. The exposure days for all nests were included in the analysis regardless of whether a predation event occurred at that particular replicate. When possible, nest predators were identified to species based on tooth or beak impressions made in the plasticine eggs.

Statistical analyses.—I analyzed predation data for both natural and artificial nests using the Mayfield method (Mayfield 1975). I calculated daily predation rates (DPR) for the incubation and nestling periods based on the number of predation events relative to the number of exposure days in each period. I calculated interval predation rates as $1 - (1 - DPR)^t$, where t = the number of days within the interval (12 days for incubation and 10 days for the nestling period). The interval length for the full nesting cycle was 24 days including two days for egg laying (females usually began incubating after laying the third egg). Predation rates at artificial nests are expressed as interval rates for a 10-day interval to facilitate comparison with predation rates from the nestling period of natural nests. I used program MICRO-MORT (Heisey and Fuller 1985) to estimate the variance for each predation rate and program CONTRAST (Sauer and Williams 1989, Hines and Sauer 1990) to compare predation rates. Program CONTRAST generates a chi-square statistic that is based on a linear contrast of the rates. Tests were one-tailed because I predicted that parasitized nests would exhibit the highest predation rates, followed by nonparasitized nests, and finally, in the case of the nest experiment, silent nests.

SPL measurements were originally made in decibels (a logarithmic scale). For measurements made on day 6 of the nestling period, I transformed these values to microbars (a linear scale) and then used an ANOVA to test for effects of parasitism on the max-

imum sound pressure of begging calls. On days 2 and 4, the SPL of begging calls often was lower than the lower threshold of the sound-level meter. For analysis of calls at these ages, I used Fisher's exact test to compare the proportion of parasitized and nonparasitized nests at which calls registered on the meter. For data on begging-call rates from day-6 nests, I used an ANOVA to test for an effect of parasitism on the number of begging calls per hour.

All ANOVAs were computed using SAS (SAS 1989). Brood size was included as a predictor variable only to remove variation associated with this factor. Significant overall *F*-tests were followed by Tukey HSD pairwise comparisons. I obtained data from only one multiply parasitized nest; thus, during analyses I make no distinction between nests with one cowbird and the nest with two cowbirds. To prevent possible seasonal changes in predation risk or predator identity from affecting my comparisons between parasitized and nonparasitized nests, I studied only the nonparasitized nests that were initiated between early May and mid-July, which is the portion of the breeding season when other nests were being parasitized by cowbirds. I also conducted the nest-predation experiment during this portion of the breeding season. Estimates of predation rates for natural Indigo Bunting nests are based on 280 nests, 123 from my study and 157 monitored in the same manner at the same study sites in 1992 to 1994 (Burhans 1996).

RESULTS

Nestling vocalizations.—On day 6 of the nestling period, begging calls were louder at parasitized Indigo Bunting nests than at nonparasitized nests ($F = 9.62$, $df = 1$ and 16 , $P < 0.01$; Table 1). There was a weaker effect of brood size on SPL ($F = 2.88$, $df = 3$ and 16 , $P < 0.1$) and no interaction ($F = 2.02$, $df = 3$ and 16 , $P > 0.15$). SPL did not appear to increase with brood size, and none of the pairwise comparisons of different brood sizes was significant. On day 4, begging calls were audible at 3 of 3 parasitized nests and at 5 of 10 nonparasitized nests (Fisher's exact test, $P = 0.23$). Power for a comparable chi-square test based on Cohen's (1988) medium effect size ($w = 0.30$) was low ($1 - \beta = 0.191$; Buchner et al. 1996). On day 2, begging calls were audible at three of four parasitized nests and at two of five nonparasitized nests (Fisher's exact test, $P = 0.52$), but power was again low ($1 - \beta = 0.147$ for a comparable chi-square test with $w = 0.30$).

On day 6, begging calls were more frequent at parasitized than at nonparasitized nests ($F =$

TABLE 2. Number of exposure days, daily predation rate, and interval predation rate for parasitized and nonparasitized Indigo Bunting nests, 1992 to 1996. Interval rates represent the probability of a nest being depredated during the entire period of interest; incubation = 12 days, nestling period = 10 days, full nesting cycle = 24 days (including two days of egg laying). Predation rates of parasitized and nonparasitized nests were compared using linear contrasts. *P*-values are one-tailed based on a *prior* predictions of higher predation at parasitized nests.

Variable	Parasitized nests	Nonparasitized nests	<i>P</i>
Incubation period			
No. of exposure days	752	818	
Daily predation rate	0.0705	0.0501	0.045
Interval predation rate	0.5840	0.4605	0.044
Nestling period			
No. of exposure days	320	705	
Daily predation rate	0.0936	0.0667	0.076
Interval predation rate	0.6257	0.4984	0.065
Full nesting cycle			
No. of exposure days	1,090	1,578	
Daily predation rate	0.0798	0.0577	0.014
Interval predation rate	0.8641	0.7596	0.012

23.63, $df = 1$ and 22 , $P < 0.0001$; Table 1). Brood size ($F = 7.95$, $df = 3$ and 22 , $P < 0.01$) and the brood size \times parasitism interaction term ($F = 11.10$, $df = 3$ and 22 , $P < 0.001$) were both significant in explaining variation in call rate. Although larger broods appeared to exhibit higher call rates, none of the Tukey pairwise comparisons was significant.

Predation risk at natural and experimental nests.—At natural bunting nests, predation rates were significantly higher at parasitized nests than at nonparasitized nests during incubation and over the course of the entire nesting cycle. There was also a trend for predation rates to be higher at parasitized nests (relative to nonparasitized nests) during the nestling period (Table 2).

In the artificial nest experiment, experimental nests broadcasting cowbird begging calls experienced the highest predation rates, followed by nests broadcasting Indigo Bunting calls, and then silent nests (Fig. 1). The overall contrast comparing the interval predation rates of the three treatments was significant (linear contrast, $\chi^2 = 4.75$, $df = 2$, $P < 0.05$). Planned pairwise comparisons among the three treatments detected a significant difference between

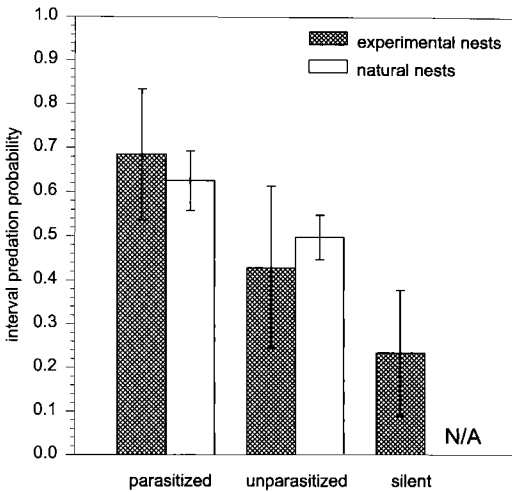


FIG. 1. Probability of predation ($\bar{x} \pm SD$) during the 10-day nestling period at 45 experimental and 280 natural Indigo Bunting nests. Experimental nests were of three treatments: (1) nests broadcasting cowbird begging calls, (2) nests broadcasting Indigo Bunting begging calls, and (3) silent nests. See text for tests of significance.

the parasitized treatment and silent nests ($\chi^2 = 4.73$, $df = 1$, $P < 0.02$), but not between the parasitized and nonparasitized treatments ($\chi^2 = 1.16$, $df = 1$, $P > 0.15$) or between the nonparasitized and silent treatments ($\chi^2 = 0.69$, $df = 1$, $P > 0.25$). Nest predation occurred at 11 nests from 10 of the 15 replicates. The nest broadcasting cowbird calls was the first nest depredated at five replicates, the nest broadcasting bunting calls was the first nest depredated at two replicates, and the silent nest was the first nest depredated at two replicates. At one additional replicate, the nest broadcasting cowbird calls and the nest broadcasting bunting calls were both depredated on the same day. Based on bill or tooth impressions in the plasticine eggs, three of the predators of artificial nests were raccoons; three were raccoons or foxes; one was a skunk, opossum, raccoon, or fox; one was a chipmunk or mouse; one was a bird; one was a snake; and one was unknown.

DISCUSSION

Nestling vocalizations.—Measurements of sound pressure level and call rate indicated that at day 6, Indigo Bunting nests containing Brown-headed Cowbird nestlings produced louder

and more frequent begging calls than did nests without cowbirds when statistically controlling for the effect of brood size. On days 2 and 4, I did not detect a significant difference in sound pressure level between parasitized and nonparasitized nests, but power was low. Thus, the differences seen between day-6 parasitized and nonparasitized nests may also exist at days 2 and 4 of the nestling period, or such differences may arise as the nestlings develop.

The calls at parasitized nests could have been louder and more frequent due to a direct effect of the begging calls of the cowbird or an indirect effect of the cowbird on the host chicks (i.e. host chicks intensify their begging in the presence of a cowbird). Data on nonvocal begging behavior (as transcribed from videotapes, where it is difficult to assign vocalizations to particular nestlings) suggest that both factors are important. First, in parasitized bunting nests, cowbird chicks begged on a higher proportion of trips and for more seconds per hour than did their bunting nest mates (Dearborn 1998). Second, bunting chicks in parasitized nests spent more time begging per hour than did buntings in nonparasitized nests (Dearborn et al. 1998). This may have been because they were hungrier; adults brought more food to parasitized nests than to nonparasitized nests, but cowbirds received a disproportionate share of the food. As a result, buntings in parasitized nests received less food and gained mass more slowly than buntings in nonparasitized nests (Dearborn 1998, Dearborn et al. 1998). However, it is also possible that buntings in parasitized nests increased their begging simply because the cowbird was begging so frequently; at least one study has shown that increasing a target chick's begging calls (by depriving it of food) can cause increased begging by unmanipulated nest mates (Smith and Montgomerie 1991; but see Kacelnik et al. 1995). In summary, it seems likely that the higher rate of begging calls at parasitized nests resulted from a combination of high begging rates by cowbird chicks and increased begging rates by bunting chicks when raised with a cowbird nest mate. The higher SPL values at parasitized nests likewise may have resulted from a combination of direct and indirect effects of the cowbird, although this hypothesis is more difficult to evaluate with the available data.

Predation risk at natural and experimental nests.—During the nestling period at natural Indigo Bunting nests, there was a trend (albeit nonsignificant) for a higher risk of predation at parasitized nests than at nonparasitized nests. The results of the artificial nest experiment suggested that the louder, more frequent begging vocalizations produced at parasitized natural nests contributed to this difference in predation risk. In this experiment, artificial nests broadcasting cowbird calls (300 calls/h at 80 dB) experienced the highest predation rate, followed by artificial nests broadcasting bunting calls (60 calls/h at 74 dB), and then by silent artificial nests. Although the pairwise comparison between predation rates at artificial nests broadcasting cowbird calls and artificial nests broadcasting bunting calls was not significant, the fact that the cowbird treatment differed from the control, whereas the bunting treatment did not differ from the control, was strongly suggestive of an effect of cowbird begging calls on predation risk.

The reliability of the results of the nest-predation experiment depends on the extent to which the experimental setup was realistic (Major and Kendal 1996). The audio tapes of begging calls used in the experiment were similar to calls produced at natural nests, both in terms of call rate and call loudness (Table 1). The experiment was also subjectively similar to natural conditions in terms of nest habitat, vegetation features (e.g. plant species, size), nest height, and nest concealment. All artificial nests and natural nests were visited daily, so any effects of human visitation should have been equal for both types of nest. The similarity of predation rates at experimental nests and corresponding natural nests (Fig. 1) suggested that in some ways the experimental setup was realistic.

However, several critical differences existed between natural and artificial nests. First, artificial nests did not contain nestlings and were not visited by adult birds. If predators cue in on the scent of nestlings or the traffic of adults at the nest, the experiment would underestimate the rate of nest predation. This is potentially important because adult buntings provisioned parasitized nests more frequently than nonparasitized nests (Dearborn et al. 1998). Second, wicker nests may have been easier for visually oriented predators to locate because

these nests were not as cryptic as natural nests (Major and Kendal 1996), or they may have been more difficult to locate because they do not match the predators' search image (Martin 1987). Third, use of a single exemplar of begging calls in each treatment of the experiment may limit generalization of the results (Kroodsma 1989, 1990). Finally, I played the tapes of begging calls constantly (day and night); nestlings presumably beg very little (if at all) at night, and mammals, which are likely to cue in on sound, may be more active at night than during the day when nestlings are normally begging (Schaub et al. 1992, Thompson et al. 1999). However, all of the mammalian predators at the experimental nests were observed at my study sites during the day. An ongoing research project at these study sites is using video cameras to document nest predators at natural nests of Indigo Buntings and Field Sparrows (*Spizella pusilla*). Most of the predators have been snakes, but mammals and birds, which are more likely to respond to nestling vocalizations, were responsible for 36% of the predation events (Thompson et al. 1999). In this study, cameras were placed at nests in successional fields, rather than along the forest-field edges where I conducted the artificial nest experiment. Thompson et al.'s (1999) work is being expanded to include nests under the forest canopy, and preliminary results suggest that predation by mammals is more prevalent in the woods (F. R. Thompson unpubl. data). Overall, video documentation of nest predators suggests that my broadcasting of begging calls for 24 h in the artificial nest experiment exaggerated the effect of noise on predation risk, but it probably did not create this effect.

Additional factors are likely to contribute to the difference in predation risk between parasitized and nonparasitized natural Indigo Bunting nests. If nestling noise had been the only factor increasing predation risk at parasitized nests during the nestling stage, the risk of nest predation should have increased as nestlings got older and louder. Analysis of a larger data set of bunting nests at these sites suggests that this was not the case (D. E. Burhans unpubl. data). The higher frequency of parental provisioning trips to parasitized nests (Dearborn et al. 1998) may attract more predators to nestling-stage parasitized nests than to nonparasitized nests. During the incubation period, when

parasitized nests also experienced higher predation rates than nonparasitized nests, parental behavior could be important in other respects. For example, some adults may travel to and from the nest in a conspicuous manner that attracts both cowbirds and predators. It is also possible that nest-site characteristics contributed to the likelihood of parasitism (see Robinson et al. 1995) and nest predation (Westmoreland and Best 1985, Martin and Roper 1988, Martin 1993). However, although certain nest-site features appear to be linked to the risk of parasitism for Indigo Buntings at these study sites (Burhans 1997), there is no indication of such an effect on the risk of nest predation (D. E. Burhans unpubl. data). Studies have shown that the risk of nest predation and the identity of nest predators vary with nest placement (e.g. ground vs. canopy; Martin 1993, Major and Kendal 1996, Porneluzi 1996), and typical hosts of cowbirds consist of ground-, shrub-, and canopy-nesting species (Friedmann and Kiff 1985). The only other study that has experimentally tested for an effect of nestling vocalizations on predation risk found that nests broadcasting very frequent calls (1,500 per h) were more likely to be depredated than silent nests when nests were placed on the ground, but not when nests were placed in understory trees (Haskell 1994). Thus, the effect of brood parasitism on predation risk may interact with effects of nest placement, nest microhabitat, and parental behavior in a manner that varies across host species.

In conclusion, I found support for the prediction that begging calls were louder and more frequent at Indigo Bunting nests parasitized by Brown-headed Cowbirds than at nonparasitized nests; this difference may have resulted from a combination of cowbird vocalizations and the response of buntings to being raised with cowbirds. Support was more equivocal for the prediction that the louder, more frequent begging calls at parasitized nests caused an increase in the risk of nest predation. My artificial nest experiment suggested that cowbird calls increased the risk of predation in forest-edge shrub nests. However, data from natural nests were less clear. Although parasitized nests had higher predation rates during both the incubation and nestling stages, the difference was statistically significant only during the incubation stage. Thus, it is unclear

from these data whether the presence of a cowbird nestling increases the likelihood of predation. Nevertheless, my overall results suggest that the upper limit of begging intensity is higher for cowbirds than for Indigo Buntings, and that the risk of nest predation may play a role in limiting the exaggeration of begging signals in nonparasitic species.

ACKNOWLEDGMENTS

I thank John Faaborg, Angela Anders, and other members of the MU Avian Ecology Lab for helpful advice and comments. Additional improvements to the manuscript were suggested by Carl Gerhardt, Mark Ryan, David Haskell, Steve Rothstein, and three anonymous reviewers. Rafael Herrera, Rafael Brito, Erin Drennan, and Angela Anders provided assistance with field work; Carl Freiling kindly allowed access to his property. I thank Dirk Burhans and Frank Thompson for helpful discussions and for access to unpublished data. This work was funded by the U.S. Forest Service North Central Forest Experiment Station and the U.S. Fish and Wildlife Service.

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Associate Editor: S. I. Rothstein