

VIDEO DOCUMENTATION OF A BROWN-HEADED COWBIRD
 NESTLING EJECTING AN INDIGO BUNTING
 NESTLING FROM THE NEST¹

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Obligate interspecific brood parasitism is known to occur in approximately 87 species of birds, which represent seven distinct groups: the cowbirds (Icterinae), two subfamilies of cuckoos (Cuculinae and Neomorphinae), the cuckoo-finch (*Anomalospiza imberbis*), the whydahs (Viduiinae), the honeyguides (Indicatorinae), and the Black-headed Duck (*Heteronetta atricapilla*) (Rothstein 1990, Lyon and Eadie 1991). In several of these taxa, newly hatched parasitic nestlings commonly kill or eject from the nest all of the host nestlings and eggs, thus eliminating competition within the nest and simultaneously imposing a large fitness cost on the host. Nestlings of most cuckoo species push eggs and chicks from the nest, while nestling honeyguides and at least one cuckoo species kill host nestlings with hooked bills (reviewed in Payne 1977, Rothstein 1990). Direct killing of host nestlings by parasitic nestlings has not been documented in cowbirds, the Black-headed Duck, or the parasitic finches. This paper presents the first documented case of a Brown-headed Cowbird nestling (*Molothrus ater*) ejecting a host nestling from the nest. A 25-second video segment of this activity can be viewed at <http://server1.biosci.missouri.edu/dearborn/cowbird.html> on the World Wide Web.

METHODS

I located and performed daily monitoring of nests of Indigo Buntings (*Passerina cyanea*) in old-field habitat at the University of Missouri's Thomas Baskett Wildlife Research Area near Ashland, Missouri, during May-August 1995. As part of a broader study of host-cowbird interactions, I made 2-hour video recordings of Indigo Bunting nests on day six of the 10-day nestling period (day of hatching = day zero) and weighed nestlings daily from day zero through day seven. Of 17 videotaped nests, five contained both Indigo Bunting and cowbird nestlings. One of these video recordings documented the ejection of an Indigo Bunting nestling by a cowbird nestling.

I performed two analyses of nest data in order to

address the question of how frequently cowbird nestlings may eject host nestlings. For the first analysis, I counted the number of instances of partial brood loss (i.e., one or more chicks disappeared before fledging but at least one chick remained in the nest) and expressed this as a rate by dividing it by the total number of nestling-period exposure days from all nests. Since this measure is a rate of loss relative to exposure days, I compared parasitized nests and unparasitized nests using an analysis developed for survival rate data. I used the program MICROMORT (Heisey and Fuller 1985) to estimate the variance of these rates and the program CONTRAST (Sauer and Williams 1989, Hines and Sauer 1990) to create a linear contrast for comparing the rate of loss at parasitized nests to the rate of loss at unparasitized nests.

Since several nests contributed multiple observations of partial brood loss, I performed a second analysis in which I measured the frequency of partial brood loss as the number of nests in which partial loss occurred at least once divided by the total number of nests which survived to the nestling period. I used a Fisher exact test to compare the proportion of parasitized and unparasitized nests which experienced partial loss.

For both analyses, nests with one or two cowbird nestlings were pooled because only two multiply parasitized nests survived to the nestling period. All unparasitized nests included in these analyses were initiated during the two-month period of cowbird parasitism at my study sites and thus do not differ in any seasonal respects from parasitized nests. One incident of partial brood loss was clearly due to the nest tilting and partially falling from the nest plant, dumping a nestling onto the ground; this incident was excluded from analysis.

RESULTS

VIDEO RECORDING

The nest in which I documented the ejection behavior was found during incubation and initially contained three Indigo Bunting eggs and one Brown-headed Cowbird egg. All four eggs hatched on 9 July 1995. On 13 July (day four of the nestling period), the smallest Indigo Bunting nestling was found on the ground 2 m beneath the nest and was placed back in the nest by one of my field assistants. The next day (day five), the same nestling was missing again and could not be located on the ground. On day six, I made a video re-

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FIGURE 1. The Indigo Bunting nestling being pushed from the nest by a cowbird nestling. Both birds are facing away from the camera. The Indigo Bunting is partially out of the nest and is on the back of the cowbird. The time, as indicated in the frame, is measured in CDT.

cording of nest activity from 06:30–08:30 CST. At the start of that period, the nest contained two Indigo Bunting nestlings and one cowbird nestling, which had weighed 7.6, 6.9, and 18.2 g, respectively, on the previous day. When I returned at approximately 10:30 to retrieve the video camera, the larger Indigo Bunting chick was gone.

The following description is a summary, based on the video recording, of the events leading up to the loss of the Indigo Bunting nestling. At 06:53 CST, the adult female Indigo Bunting arrived at the nest rim on the side opposite from the direction that the three chicks were facing. The nestlings reached up and back to beg; the adult fed the cowbird chick and then departed. After she left, all nestlings slowly turned around to face the area of the nest where she had arrived. This re-shuffling continued until 06:55, at which point one Indigo Bunting, the eventual victim, had been bumped upwards and was positioned partially on the nest rim behind the other two nestlings. At 06:56, the displaced bunting tried briefly to settle back down into the nest, but quickly gave up and remained in its position partway up on the rim. At 06:58, the bunting tried again to return to the central portion of the nest, chipping twice as it wiggled down into the nest and partway onto the back of the cowbird. The cowbird then slowly stood up, backing towards the nest rim as it straightened up (Fig. 1). The pushing/standing action appeared to be quite deliberate, and lasted for roughly 10 seconds. Once the bunting was off the cowbird and completely out of the nest, the cowbird slowly lowered itself, taking approximately 4 sec to return to a resting position in the bottom of the nest cup with its head down. Meanwhile, the ejected bunting clung to the outside of the

nest with one foot for approximately 6 sec before falling 2 m to the ground (Fig. 2).

NEST DATA

One measure of partial brood loss is the number of incidents of partial loss divided by the total number of nest exposure days during the nestling period (Table 1). Based on this measure, the rate of partial brood loss was significantly higher at parasitized nests than at unparasitized nests (linear contrast of rates, $\chi^2 = 8.17$, $df = 1$, $P = 0.004$). I also quantified the frequency of partial brood loss as the proportion of nestling-stage nests that experienced at least one incident of partial loss. Parasitized nests suffered a significantly higher frequency of loss by this measure as well: four of 12 (33.3%) parasitized nests experienced partial loss while only one of 31 (3.2%) unparasitized nests did so (Fisher exact test, $P = 0.017$).

DISCUSSION

An important question to consider about this ejection behavior is the extent to which it is deliberate. The protracted nature of the pushing/lifting action (10-sec duration) would suggest an intentional effort on the part of the cowbird, as would the fact that the cowbird appeared to back towards the edge of the nest while pushing the bunting chick. The cowbird's actions may have been solely in response to the bunting contacting the cowbird's back in its attempt to regain a central position in the nest. Of course, the cowbird's actual intentions must remain the subject of speculation. However, even if a cowbird ejects a host opportunistically or unintentionally, the net result is the same as if the ejection were premeditated. In order to predict



FIGURE 2. The Indigo Bunting nestling, facing to the right, is hanging from the side of the nest by its foot, shortly before falling to its death. The cowbird nestling has settled back down into the nest.

whether or not this behavior will become more common, we need additional data on whether or not it confers a fitness advantage to the cowbird and whether or not it is genetically based.

Furthermore, we need to know how rare this behavior currently is. We might presume it to be uncommon, since it has not been previously documented. However, several factors may make detection of such an event unlikely, regardless of how often it occurs: (1) if a human observer is close enough to the nest to notice such an event, the nestlings will probably be crouched down, inactive, in the bottom of the nest; (2) there are, to my knowledge, no published studies in which video recordings were made at nests with Brown-headed Cowbird chicks in them; (3) previous researchers may have assumed (as I have done) that partial brood loss was due to predation or to starvation and subsequent removal by the parent, and thus not looked for "ejected" nestlings on the ground near a nest (but see Nolan 1978, p. 387). Thus, it is conceivable that the ejection of host nestlings is not rare, but only rarely observed.

My nest data are consistent with this hypothesis. Partial brood loss, whether measured in terms of either number of incidents or number of nests where it occurred, occurred at a higher rate in nests with cowbirds in them. It could be argued that parasitized nests experience increased predation rates and thus the rate of partial predation increases also. However, two lines of evidence do not support this interpretation. First, predation rates on Indigo Bunting nests at these sites from 1992–1995 did not differ significantly between parasitized and unparasitized nests (unpubl. data; Burhans 1996). Second, of the eight nestlings that disappeared from parasitized nests, none was a cowbird. These two observations are consistent with the hypothesis that

the higher rate of partial brood loss at parasitized nests is due to host nestling ejection by cowbird nestlings.

However, partial brood loss could also be due to the host parent removing a host nestling that had starved. In some host species, the host chicks in parasitized nests gain weight normally (Yellow Warbler [*Dendroica petechia*] and Red-winged Blackbird [*Agelaius phoeniceus*], Weatherhead 1989; Prothonotary Warbler [*Protonotaria citrea*], Petit 1991); but in other species, host nestlings suffer reduced growth rates or starve to death (Prairie Warbler [*Dendroica discolor*], Nolan 1978, p. 287; Solitary Vireo [*Vireo solitarius*], Marvil and Cruz 1989; Eastern Phoebe [*Sayornis phoebe*], Weeks 1994).

At my study site, preliminary data indicate that Indigo Buntings in parasitized nests often exhibit somewhat depressed growth rates during the middle portion of the nestling period, but undergo rapid weight gain

TABLE 1. Rate (\pm SD) of partial brood loss in parasitized and unparasitized nests. Rate is expressed as number of incidents of partial loss divided by total number of exposure days for nests during the nestling period.

	n incidents of partial loss	n exposure days	Rate of loss
Parasitized nests:	8	65	0.1231 \pm 0.04075
Unparasitized nests:	1	180	0.0055 \pm 0.00554

during the last few days in the nest and frequently attain a fledging weight that is similar to chicks from unparasitized nests (unpubl. data). Although Indigo Bunting chicks raised with cowbirds do occasionally starve, the death of a chick is routinely preceded by two to four days of weight loss (Dearborn and Burhans unpubl. data). All of the partial brood loss incidents included in the analyses presented in this paper were of normalized chicks that were not exhibiting the drastic weight loss characteristic of Indigo Buntings that eventually starve to death. Starvation of host young may frequently be responsible for partial brood loss in some host species, but nestling mass measurements suggest that this is not the case here.

A previous study also implicates cowbirds in the loss of Indigo Bunting nestlings. Twomey (1945) indicated that three Indigo Bunting nestlings were "pushed out" or "ejected" from a single parasitized nest and one Indigo Bunting was "pushed out" from an additional nest. However, he does not state that the ejections were performed by the cowbirds, he does not mention finding any nestlings on the ground, and it is not clear whether or not he witnessed any of the ejections. He may have only noticed that host nestlings were disappearing between nest checks.

There has been at least one additional case in which a researcher observed cowbird behavior that was suggestive of the ejection of a host nestling. L. Petit (pers. comm.) was monitoring a Hooded Warbler (*Wilsonia citrina*) nest that contained one cowbird chick and one Hooded Warbler chick. When she checked the nest on the third day post-hatch, the host nestling was on the back of the cowbird nestling, although the events leading to that situation had not been witnessed. The following day, the host nestling was gone.

It is not surprising that the evidence for ejection behavior comes from cowbirds found in the nests of relatively small host species. A cowbird nestling may be unable to push a larger nestling from the nest. Weatherhead (1989) found that parasitized nests of Yellow Warblers experienced a greater decline in brood size over the nestling period than did unparasitized nests, but no such trend was detected for Red-winged Blackbirds. One explanation for this observation is that the difference in body size of the two host species creates a difference in their susceptibility to ejection by cowbird nestlings (adult male and female body masses: Yellow Warbler, 9.8 g and 9.2 g; Red-winged Blackbird, 63.6 g and 41.5 g; Brown-headed Cowbird, 49.0 g and 38.8 g; Dunning 1993). However, the high frequency of brood loss in parasitized Yellow Warbler nests could also be due to more frequent starvation of host nestlings as a result of competitive asymmetries with the much larger cowbird nestlings.

A last point to consider about the ejection behavior of the Brown-headed Cowbird is the age at which the behavior was performed. If this age is much greater than the age typical of corresponding behavior in cuckoos, it could be viewed as evidence that the cowbird's ejection behavior was opportunistic or unintentional. The ejection that I recorded occurred at 6 d post-hatch, and additional ejections may have been performed at the ages of 4 days and 5 days by the same cowbird and at the age of 3 days by the cowbird noted by L. Petit.

Although these ages are greater than the age at which European Cuckoos (*Cuculus canorus*) eject host eggs (8–36 hr post-hatch, Wyllie 1981), they are within the range of ages reported for ejection of host eggs and nestlings by the Shining Cuckoo (*Chrysococcyx lucidus*; 3–7 days post-hatch, Gill 1983).

In conclusion, I have documented that cowbird nestlings are capable of ejecting host nestlings from the nest, although it remains unclear how frequent this behavior is and whether or not a cowbird nestling could eject the nestling of a larger host species. I would encourage researchers with appropriate nest data sets to perform analyses similar to mine in order to obtain a broader perspective on the rate of partial brood loss in parasitized and unparasitized nests.

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SATELLITE TRACKING OF SOUTHERN BULLER'S ALBATROSSES FROM THE SNARES, NEW ZEALAND¹

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Pelagic seabirds spend most of their time foraging at sea far from their breeding grounds. Yet most information on their ecology comes from land-based studies, and the need for studies on their foraging ecology has been recognised as of prime importance to an understanding of their extreme life history traits (Ricklefs 1990). Recently, such studies have been made possible for large seabirds such as albatrosses with the development of satellite telemetry (Jouventin and Weimerskirch 1990). However, most studies have concentrated on the largest of the albatross species (e.g., Prince et al. 1992, Weimerskirch et al. 1993, Nicholls et al. 1994), with only one on a smaller species, the Light-mantled Sooty Albatross *Phoebastria palpebrata* (Weimerskirch and Robertson 1994). No studies have been published on mollymawks, the subfamily with the greatest number of species.

Buller's Albatrosses (*Diomedea bulleri*) are endemic to New Zealand, where the Southern subspecies (*D. b. bulleri*) breeds at The Snares and the Solander Islands, and the Northern subspecies (*D. b. platei*) at the Chatham and Three Kings Islands (Turbott 1990). Their distribution at sea is poorly known, although the pelagic range is across the Southern Pacific Ocean, north of the Antarctic Convergence from southeastern Australia to Chile and Peru (Marchant and Higgins 1990). Movements of adults are also poorly known, and Mar-

chant and Higgins (1990) suggested that they may move only locally. An examination of 27 regurgitations from adults and chicks collected on The Snares and the Chatham Islands (West and Imber 1986) indicated that the diet comprised mainly species which occur within the New Zealand region. However, Richdale (1949) showed that incubation spans of birds on The Snares ranged up to 21 days, indicating that these birds could forage long distances from the breeding colonies.

Substantial mortality of Southern Buller's Albatrosses has been reported to occur as a result of commercial fisheries southwest of New Zealand (Bartle 1991, Murray et al. 1993), so knowledge of the foraging zones of the subspecies has important implications for conservation. We used satellite telemetry to determine the foraging movements during late incubation of Southern Buller's Albatrosses breeding at The Snares.

STUDY AREA AND METHODS

The Snares (48°02'S, 166°36'E) consist of North East Island (280 ha), Broughton Island (90 ha) and numerous islets and rock stacks. In 1992, an estimated 8,460 pairs of Southern Buller's Albatrosses bred on these islands (Sagar et al. 1994). Six Southern Buller's Albatrosses breeding within the same colony on North East Island were fitted with four Toyocom 2038C and two Toyocom 2050 Platform Transmitter Terminals (PTTs): four on 25 February 1995, and two on 26 February 1995. The six PTTs deployed were packaged in epoxy resin and weighed 58 g (T2038) and 46 g (T2050), which corresponded to 1.5–2.0% of the body masses of the birds. They were attached directly to the back feathers using adhesive tape. The PTTs were fitted to birds immediately after they had completed incu-

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