Starvation and nestling ejection as sources of mortality in parasitized Lazuli Bunting nests

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Many studies have documented a reduction in host nestling growth and the number of fledglings produced from nests of small hosts parasitized by Brown-headed Cowbirds (Molothrus ater; Nolan 1978, Scott 1979, Hatch 1983, reviewed in May and Robinson 1985, Marvil and Cruz 1989, Weatherhead 1989). A short incubation period (Nice 1953, Nolan 1978, Lowther 1993), loud begging calls (Friedmann 1929, Dearborn 1997), and larger relative mouth sizes (Ortega and Cruz 1991), coupled with a rapid growth rate (Norris 1947, Scott 1979, Hatch 1983, Lowther 1993), typically give the cowbird nestling a head start over host young. As a result, the larger cowbird nestling gapes higher than most host nestlings, which increases the probability of the cowbird being fed by host parents (Smith and Montgomery 1991, Teather 1992, Leonard and Horn 1996). Thus, one potential cause of reduced reproductive success in parasitized nests of small host species could be a disproportionate provisioning of food to the young cowbird, resulting in starvation of host nestlings. However, I know of only a single study (Dearborn 1997) documenting the distribution of food among nestlings in parasitized nests.

In addition, several studies have implicated cowbird nestling ejection behavior as a source of host nestling mortality (Twomey 1945, Dearborn 1996). Cowbird nestlings ejecting host young have been video taped once (Dearborn 1996) and suggested by at least 2 other researchers (reviewed in Dearborn 1996). The extent to which this behavior occurs is not known, since most researchers assume missing host young are taken by predators or removed from the nest by parents after starving.

In this study I recorded feeding rates, size of food items delivered, distribution of food, and growth rates in parasitized and unparasitized nests of Lazuli Buntings (Passerina amoena). I specifically examined whether bunting nestlings in parasitized nests die due to starvation or to physical aggression from the cowbird nestling.

The primary study area is in western Montana in Missoula County on the western side of Mount Sentinel and Mount Jumbo. These mountains are part of the Sapphire Range and are located on the eastern edge of the city of Missoula. Elevations range from 1070 to 1719 m. Primary habitat is Palouse prairie, consisting of native bunchgrasses interspersed with shrubs.

From late May to August 1995, I monitored 2 parasitized and 16 unparasitized nests on Mount Jumbo and Mount Sentinel and weighed daily (to the nearest 0.1 g) cowbird and bunting chicks using a Pesola scale. I conducted 2-h behavioral observations of parasitized and unparasitized nests from a distance of 20–30 m using a variable-power spotting scope to record nestling behavior and the proportion of food delivered to cowbird and/or bunting nestlings. The size of food items delivered to each nestling was placed into 1 of 5 categories based upon the following criteria: 1 = hard to see, 2 = equal to bill length, 3 = just longer than bill, 4 = twice bill length, 5 = more than twice bill length. Volume of food per hour delivered to nestlings was calculated by multiplying the number of feeding trips per hour by average load size. Observation times were selected to ensure that parasitized and unparasitized nests were observed during the same times of day and under similar weather conditions.
I used a Mann-Whitney U test (Zar 1996) to compare (1) day 3 weights of bunting nestlings in parasitized and unparasitized nests, (2) average nesting weights per nest on day 3 in parasitized and unparasitized nests, (3) volume of food per hour delivered to nestling cowbirds and buntings, and (4) average number of feeding trips per hour for parasitized and unparasitized nests. A binomial test was performed to compare the proportion of feeding trips in which only the cowbird was fed to the proportion of feeding trips in which just bunting nestlings were fed.

The day 3 weight of Lazuli Bunting nestlings in parasitized nests (n = 5 nestlings) was significantly lighter than the day 3 weight of Lazuli Bunting nestlings in unparasitized nests (n = 16 nestlings; Mann-Whitney U test, P = 0.0009). Recognizing that within-nest variation may confound this analysis, I then averaged the day 3 weights for each nest. The average day 3 weight of Lazuli Bunting nestlings differed between parasitized and unparasitized nests (X̄ = 1.84 ± 1.15 g and 4.28 ± 0.34 g, respectively; Mann-Whitney U test, P < 0.10). Small sample size prevents significance; however, each of the 3-d-old bunting nestlings in parasitized nests weighed less than the lightest 3-d-old bunting nestlings in unparasitized nests. By day 4 all 5 bunting nestlings in parasitized nests were dead. A graph of nestling mass over time shows a steady decline in weight of host nestlings in parasitized nests (Greene et al. 1996).

I observed 57 feeding trips at 2 parasitized nests. In the 1st nest, the cowbird hatched the same day as 1 bunting nestling and the day before the other bunting nestling. In the 2nd nest, the cowbird nestling hatched 1 d before 3 bunting nestlings. All observed feeding trips occurred 1–3 d after hatching. Of 57 feeding trips observed at 2 parasitized nests, 32 of 46 resulted in only the cowbird being fed at 1 nest (binomial test, P = 0.02), and 11 of 11 resulted in only the cowbird being fed at the 2nd nest (binomial test, P < 0.001).

I observed an average of 6.75 (s = 0.992) feeding trips per hour for 6 unparasitized nests (n = 87 feeding trips to 18 nestlings) where bunting nestlings were 1–3 d old. This did not differ significantly from the average 6.14 (s = 1.86) feeding trips per hour in 2 parasitized nests (n = 36 feeding trips to 5 nestlings) where bunting nestlings were 1–3 d old (Mann-Whitney U test, P = 0.39). These results should be interpreted with caution since the power of this test is low. There was a trend toward cowbird nestlings (18.46 per hour) receiving a larger volume of food per hour than bunting nestlings (11.64 per hour; Mann-Whitney U test, P = 0.06).

The relative strength of the provisioning stimulus provided by bunting nestlings did differ between parasitized and unparasitized nests. Lazuli Bunting eggs in the same nest usually hatch on the same day (Greene et al. 1996). Consequently, the degree of development and corresponding height of the gape of bunting nestlings between 1 and 4 d of age in unparasitized nests were relatively even. However, I observed that at every feeding trip to parasitized nests, the gape of the cowbird nestling was at least 2.5 cm higher than the gape of the bunting nestlings. For all 36 observed feeding trips to parasitized nests during days 1 and 2, at least 1 bunting nestling could be seen begging. But after day 2 of receiving less than 20% of the food delivered to the nest, the bunting nestlings in parasitized nests often did not gape when an adult arrived with food. By day 4, both bunting nestlings in 1 parasitized nest died of starvation and were found flattened in the bottom of the nest. Two bunting nestlings in the 2nd parasitized nest also died of starvation on day 4. The third 4-d-old bunting nestling was found dead on the ground below the 2nd parasitized nest.

My observations reveal that gaping and jostling for position by the much larger cowbird nestling often move the bunting nestlings around inside the nest. Most of these interactions appear to be nonaggressive; however, on 2 occasions I witnessed what appeared to be aggressive head pecking by cowbird nestlings. On 4 separate occasions I witnessed a single 3-d-old bunting nestling settle onto the back of a 4-d-old cowbird nestling. In every instance, the cowbird raised up on its legs within 1–3 sec and moved backwards or to the side for 3–12 sec until the bunting nestling was no longer touching its back. Over 2 occasions this resulted in the 3-d-old bunting nestling lying on its side perpendicular to the rim of the nest with its head outside the nest and the rest of its body directly on the rim. In both instances the bunting nestlings raised their heads and fell back into the nest within 3–5 sec. Upon returning to this nest the next day, I found 2
bunting nestlings dead inside the nest and the 3rd bunting nestling lying on the ground directly below the nest.

In addition to mortality from inclement weather, nestling predation, physical aggression from cowbird chicks, and ectoparasites, my results suggest that another cause of reduced nestling survival in parasitized Lazuli Bunting nests is starvation, which results from cowbird nestlings receiving most of the food delivered to parasitized nests. While this appears to be the primary factor responsible for reduced reproductive success in parasitized Lazuli Bunting nests, my observations of nestling activity also reveal that host young may be indirectly ejected from the nest as the cowbird nestling attempts to maintain its position.

The relative importance of ejection as a source of mortality and the ability of cowbirds to eject host species larger than Indigo or Lazuli Bunting remains unknown (Dearborn 1996). Given that nestlings of many small host starve in parasitized nests (Mayfield 1977, Payne 1977, Nolan 1978, Marvil and Cruz 1989), ejecting them would seem to do little to increase cowbird nestling fitness. However, many host species nestlings gain weight normally (Field sparrow [Spizella pusilla], Carey et al. 1994; Common Grackle [Quiscalus quiscula], Peer and Bollinger 1997; Prothonotary Warbler [Protonotaria citrea], Petit 1991; Red-winged Blackbird [Agelaius phoeniceus] and Yellow Warbler [Dendroica petechia], Weatherhead 1989; Dickcissel [Spiza americana], Hatch 1983) in parasitized nests, and ejecting them would likely increase the fitness of cowbird nestlings.

Another possible factor influencing ejection of host young could be nest shape. Nest shape varies both within and among species. Twenty-six Lazuli Bunting nests from my study site varied in depth from 3 to 5.5 cm, averaging 3.5 cm (Greene et al. 1996). A nest depth of 3–4 cm is typical of many cowbird host species; however, there is considerable variation in nest depth of cowbird hosts (Harrison 1975). Species with shallow nest cups may lose proportionally more young due to ejection than species with deep nest cups. Given the recent evidence in support of cowbird nestling ejection behavior, I would encourage researchers to consider this behavior and its potential impacts on cowbird fitness in future studies of nest parasitism.

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