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EGG-EATING BY FEMALE BROWN-HEADED COWBIRDS[1]

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Abstract. We estimated the proportions of eggs and nestlings, removed from hosts' nests, that were eaten by female Brown-headed Cowbirds (*Molothrus ater*) from (1) a compilation of published and unpublished observations (n = 36) of egg or nestling removal and egg-eating by female cowbirds and (2) the proportion of removed eggs that were found uneaten below parasitized nests (n = 69) of Northern Cardinals (*Cardinalis cardinalis*). Female cowbirds were seen removing eggs only before midday or in late afternoon and early evening. Eggs were removed from both parasitized and unparasitized nests and at any nesting stage from laying to late incubation. Although eggs, contents and shell, were frequently eaten, removed nestlings were not observed to be eaten. However, as many as 40% of removed eggs were not eaten, despite the apparent energetic benefits of egg-eating. We offer six explanations to account for the failure of cowbirds to eat many eggs, and suggest experiments to elucidate this puzzling behavior of cowbirds. We conclude that the use of eggs as food may not be the primary cause of egg removal by Brown-headed Cowbirds.

Key words: Brood parasitism; Brown-headed Cowbird; Molothrus ater; *egg removal; egg-eating.*

INTRODUCTION

More than a century ago Hudson (1870, 1874) noted that female Shiny Cowbirds (*Molothrus bonariensis*) frequently took, and sometimes ate, eggs from host's nests. Subsequent studies showed that all other species of *Molothrus* take eggs (Burroughs 1871, 1887; Bucher and Orueta 1977; Carter 1986; Fraga 1986) and that at least Brown-headed Cowbirds (*M. ater*) and Bay-winged Cowbirds (*M. badius*), eat them. There are few data on this behavior, although the proportions of parasitized nests from which eggs have been removed, apparently by female *M. ater,* have been documented (e.g., Hann 1937, Nolan 1978). Although *M. ater* often eats a host's egg, the frequency of eating eggs has not been determined. The primary purpose of this note is twofold: (1) to report the fate of eggs that were seen being removed by Brown-headed Cowbirds and (2) to estimate the proportion of removed eggs that are eaten. We compare this behavior of Brown-headed Cowbirds with that of Common Cuckoos (*Cuculus canorus*). Finally, we speculate on the role of egg-eating in the energetics of egg production by Brown-headed Cowbirds, and on the failure of Brown-headed Cowbirds to eat many removed eggs.

METHODS

The proportion of removed eggs that was eaten was estimated in two ways. (1) We collected published records, unpublished records sent to us in response to a request for information published in the OSNA Newsletter, records extracted from the Ontario Nest Records Scheme, and personal observations of cowbirds removing eggs. We used only records where the fate of the egg could be assigned to one of three categories: abandoned, eaten, or carried away out of sight. Recognizing bias in these records, we separated observations (n = 25) in which a cowbird was seen removing an egg from a nest from those (n = 8) in which a cowbird was first seen, usually flying, carrying an egg, after it had presumably removed the egg from a nest. This latter group is biased towards birds that had carried an egg some distance from a nest and excludes birds that removed and disposed of an egg from a nest before being observed. That is, cowbirds seen carrying an egg are noteworthy, literally, unlike cowbirds seen

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TABLE 1. Records of female Brown-headed Cowbirds seen removing eggs or nestlings or seen first carrying eggs, arranged by fate of eggs and nestlings and by authority. Standard Time of observation follows the citation (n.t. indicates that no time was recorded).

Abandoned	Eaten	Carried away
A. Eggs or nestlings seen being removed from nests		
Roberts (1932) n.t.	Hann (1937) n.t.	Hann (1937) 09:01
Blincoe (1935) 17:30[a]	Benson (1939) 08:40	Harrison (1952) 04:34
Hann (1941) 09:10[a]	Johnstone (1949) 12:00	DuBois (1956) n.t.[b]
Tate (1967) 10:15[b]	Enstrom (pers. comm.) 05:55, 07:45	Mitchell (unpubl.) 12:36
Potter (1985) 12:36[a]	Fleischer (pers. comm.) 11:00	Prescott (1965) 04:58[c]
Beane and Alford (1990) 10:15[b]	Weatherhead (pers. observ.) 09:00	Kinser (1973) 08:30
Earley (1991) 18:14		Rothstein (1975) n.t.[d]
Beane (pers. comm.) 19:11		Nolan (1978) 05:22[c]
Enstrom (pers. comm.) 06:15, 07:17, 08:00		
Middleton (pers. comm.) 18:00		
Scott (pers. observ.) 04:53		
B. Eggs first seen being carried		
Kus (pers. comm.) 05:53[a]	Nice (1937) 09:15	Burroughs (1887) a.m.
Newsome (pers. comm.) 06:40[a]	Olson (1943) 17:15	Nice (1937) 08:45
	Norris (1944) 09:45	Zimmerman (pers. comm.) 06:15

[a] Probably frightened by observer, dog, or host.
[b] Nestlings.
[c] A cowbird appeared again at nest a few seconds later.
[d] Egg taken from nest artificially placed on feeder.

without an egg. The second group, however, provides an estimate of the fate of those eggs from the first group that were carried away from the observer. (2) Although many observers (e.g., Hess 1910, Brandt 1947) have seen uneaten eggs, presumably removed from nests by cowbirds, lying on the ground close to unparasitized nests, no attempt has been made until now to determine the number of these observed eggs as a proportion of the total number of eggs that were removed. Scott (unpubl. data) recorded the number of marked eggs that disappeared from 69 parasitized nests of Northern Cardinals (*Cardinalis cardinalis*) and the number of these eggs that were found uneaten near the nest. The proportion of the found eggs is a minimal estimate of the real proportion of uneaten eggs as searches below the nest were not intensive and may not always have been made. No record was kept of searches that did not find an egg. Moreover, some eggs that were carried away may not have been eaten. We assumed that cowbirds had removed most of the eggs that were found because cardinals do not apparently eject eggs (Rothstein 1971) and predators, other than cowbirds, would not likely have left uneaten eggs. Scott (1977) concluded from a comparison of rates of egg loss from parasitized and unparasitized cardinal nests that cowbirds caused most egg loss from parasitized nests. Estimates derived by this method, unlike those derived from method 1, should be free from the effect of disturbances caused by human observers. Thus, the estimate from Method 2 should be more accurate than that from Method 1.

Unless otherwise specified, we use the names "cowbird" and "cuckoo" to refer respectively to female Brown-headed Cowbirds and Common Cuckoos.

Standard Time is used exclusively throughout the paper.

RESULTS AND DISCUSSION

We compiled 25 observations of female cowbirds seen removing eggs (Table 1A); of these eggs, 7 were carried out of sight, 7 were eaten, and 11 were abandoned uneaten, 9 by dropping and 2 by placement on the ground. Three eggs were abandoned, probably because the cowbirds were disturbed by a dog (Blincoe 1935), by a photoflash at the host's nest (Hann 1941), and by a returning host (Potter 1985). If these eggs had been eaten, cowbirds would have eaten 10 of the 18 eggs in Table 1A whose fates were known. Of the 8 eggs referred to in Table 1B, 3 were carried out of sight, 3 were seen to be eaten,

and 2 were dropped and abandoned, possibly because the observers (Kus, pers. comm., Newsome, pers. comm.) were nearby and probably in full view of the cowbirds. If these 2 eggs had been eaten, it would suggest that eggs carried out of sight are eventually eaten. If true, then the 7 eggs in Table 1A that were carried away should be added to the 10 eggs in Table 1A that were considered to be eaten to estimate that the proportion eaten was about 70% (17/25). Therefore, cowbirds did not eat about 30% of the removed eggs.

Thirty-nine eggs, usually punctured or otherwise broken, were found below 28 cardinal nests; 58 eggs, missing from 41 cardinal nests, were not found. Thus, at least 40% of this sample of eggs was uneaten and at most only 60% might have been eaten. We conclude that female cowbirds fail to eat a large proportion, perhaps more than 40%, of the eggs that they remove.

Male cowbirds occasionally take eggs (Sealy, pers. comm.) but this is rare. King (1979) studied captive cowbirds and never saw males visiting nests, but females made frequent visits and removed and ate many more eggs than they laid.

Cowbirds removed eggs in the forenoon and in late afternoon and early evening; the earliest removal occurred at 04:35 (Harrison 1952), the latest at 19:11 (Beane, pers. comm.). We found no records of cowbirds removing or eating eggs between 12:36 and 17:15, a period when cowbirds usually are foraging outside nesting habitat (Rothstein et al. 1986). This lack of records may also reflect observers' inactivity. A substantial proportion of eggs was taken around sunrise, the normal laying time of cowbirds (Hann 1941, Scott 1991). On four of 24 occasions (references in Scott 1991) when a female cowbird was seen visiting a nest around sunrise, an egg was removed before any cowbird laid in that nest on that day (it is assumed that the cowbirds that took the eggs were the same birds that in three cases returned shortly to lay—one bird did not return to lay [Harrison 1952]). The fate of only one egg was known certainly; it was found below the host's nest (Scott, pers. observ.). The interval in the other two cases was so short (Prescott 1965, Nolan 1978) that it seems unlikely that the eggs could have been eaten. Thus, there is no evidence that eggs removed just before laying were eaten.

Eggs were eaten on the ground, either close to the nest (about 2 m away, Weatherhead, pers. observ.) or at distances more than 10 m away (Olson 1943, Norris 1944). Cowbirds eat most of the contents, but not always the shell, which was not eaten in two of eight cases. The time required to eat an egg has been reported only twice. Benson (1939) noted that an episode, lasting 3 min, began with a female cowbird appearing near a nest and ended with her departure after carrying a cowbird's egg to the ground and eating it. Weatherhead (pers. observ.) watched a female cowbird eat the contents and most of the shell of an Eastern Phoebe's (*Sayornis phoebe*) egg in about 30 sec.

Cowbirds ate eggs regardless of the state of incubation. Benson (1939) and Weatherhead (this study) saw unincubated eggs being eaten, and Johnstone (1949) saw a cowbird eating an egg (presumably fertile) removed on the ninth day of incubation. A student of Sealy (pers. comm.) saw a cowbird eating an egg of a Yellow Warbler (*Dendroica petechia*) and, when alarmed, it flew off carrying a small embryo. Not only do cowbirds eat incubated eggs, but they also take incubated eggs from apparently unparasitized nests (Blincoe 1935, Johnstone 1949, Potter 1985). These observations may represent more common behavior than their frequency indicates, because many records in Table 1 were made when observers were deliberately watching nests in prelaying or laying stages to record cowbird or host activities (e.g., Hann 1937, Harrison 1952, Prescott 1965, Enstrom, pers. comm.).

Although nestlings may be removed (Table 1), evidence suggests that they are not eaten. In one of the three reported cases of nestling removal, all four nestlings were removed and dropped from the nest (Beane and Alford 1990). In another case, three nestlings were found to one side of a ground nest and a fourth nestling was carried away by a female cowbird (DuBois 1956). In the third case, Tate (1967) saw a cowbird fly away with a three-day-old warbler nestling and drop it in an open area.

Most estimates indicate that, for each cowbird egg laid, at least 0.80 eggs (host or cowbird) are apparently removed by cowbirds (Hann 1937, Hofslund 1957, Mayfield 1960, Scott 1977 for Northern Cardinal nests, Nolan 1978, Weatherhead 1989). Values much less than 0.80 have been reported by Nice (1937) for Song Sparrows (*Melospiza melodia*) and by Scott (1977) for Gray Catbirds (*Dumetella carolinensis*).

Although both female cowbirds and Common Cuckoos remove many host eggs from parasit-

ized nests (Chance 1940, Wyllie 1981), the time of removal and fate of the eggs differ between the two species. A cuckoo typically picks up an egg while she is on a nest preparing to lay, unlike a cowbird which is not known to remove an egg while she lays. Thus, a cowbird must make two trips to a nest to accomplish both laying and egg-removal (or alternatively a trip to each of two nests) (Chance and Hann 1942). Moreover, a cowbird risks removing her own egg on a return visit. Besides removing eggs from parasitized nests, both species remove eggs (and nestlings) from unparasitized nests (Chance 1940, Potter 1985, Wyllie 1981, Beane and Alford 1990). Cuckoos eat more eggs relative to the number they lay than do cowbirds, because they apparently do not often drop eggs that they remove. Thus, cuckoos typically eat at least one egg for each they lay, unlike cowbirds, which likely eat only one egg for every two that they lay. Because cuckoos and cowbirds lay eggs of similar mass (about 3 g; Nice 1937), egg-eating by cuckoos contributes more energy to egg production.

King (1973) estimated that the maximum daily cost of egg production for passerines could be met by about a 15% increase in daily energy intake. Using King's estimates of an energy equivalent of 4.4 kJ/g of egg and 70% efficiency of conversion of food to eggs, we calculated that a cowbird could gain about one-half of the energy content of her own egg (3 g) by eating a host's egg of 2 g. This could be doubled if female cowbirds ate eggs at the same rate as cuckoos do. Moreover, this concentrated energy could be obtained rapidly, and does not necessarily require a return trip to a nest in which a female had laid because cowbirds also remove eggs from unparasitized, incubated clutches. Thus, Rothstein et al.'s (1986) estimate that female cowbirds must increase foraging time by 15% to meet the energy demands of laying an egg will be too high for females that eat eggs.

Eating the contents and the shell of an egg not only reduces time spent on energy acquisition, but also gains ideal nutrients for egg formation. As cowbirds eat, often incompletely, only about 50% of the removed eggs, the overall gain in energy requirement is likely less than 25% of the energy content of a cowbird's egg. This gain is modest, when it could easily be much greater. Furthermore, if Rothstein et al. (1986) were correct that the higher mortality rate of adult female Brown-headed Cowbirds compared to adult males is due to cost of egg production, then it is necessary to explain why cowbirds do not eat more eggs.

All of the following possible explanations that we suggest seem inadequate to account for the incomplete use of eggs as food by Brown-headed Cowbirds. (1) Recency of the habit of egg-eating cannot explain the failure of cowbirds to eat many removed eggs, as it is widespread in *Molothrus* and has been known, at least in *M. bonariensis,* for more than a century. Thus, there has been sufficient time for the habit to have become more common. (2) An egg is a large source of nutrients, which could be rapidly acquired through eating and which would supplement other foods and would save foraging time. This saving in time could be important, given the time that female cowbirds must devote to searching for nests. That removed eggs frequently are not eaten suggests, however, that egg-eating is often superfluous to using other foods. It is, however, difficult to imagine the conditions under which egg-eating is superfluous. Regardless of the degree of abundance of food, egg-eating would probably be beneficial because the acquisition of large amounts of appropriate nutrients is so quick. Therefore, we reject the explanation that egg-eating is nonadaptive. (3) Methods of carrying eggs differ between cowbirds and cuckoos (Chance and Hann 1942). Cowbirds drop more eggs than do cuckoos. Chance (1922, 1940) recorded 30 eggs being removed by his Cuckoo A; of these eggs only two were dropped at the nest, two were eaten at the nest, and the rest were apparently eaten elsewhere. Although eggs dropped by cowbirds are usually abandoned, sometimes cowbirds land and eat them (Enstrom, pers. comm.). Some portion of a dropped egg, particularly the shell, should be salvageable so, even if cowbirds are less efficient at carrying eggs than are cuckoos, this inefficiency does not explain why they do not eat more removed eggs. (4) Cowbirds removing eggs are more solitary than when they are foraging normally in open fields (Rothstein et al. 1986: 159). They are probably at a greater risk of predation when solitary, but it seems unlikely that the slight amount of time involved in eating an egg increases the probability of predation sufficiently to deter cowbirds from eating eggs. (5) Some passerine eggs may be sufficiently distasteful to be rejected as food by cowbirds. Experiments using carnivorous mammals showed that eggs of some passerines were shunned, presum-

ably on the basis of chemical stimuli (Cott 1953–1954). This explanation seems unlikely because many birds, including close relatives of cowbirds (e.g., Common Grackle, *Quiscalus quiscula*), eat passerine eggs. (6) Contrary to our reasoning, the contents of host eggs may not be a useful food for cowbirds. We assumed that host eggs are an ideal food for a laying cowbird, as the nutrients of host and cowbird eggs should be nearly identical. However, a cowbird may have difficulty digesting them. The cowbird's normal diet of seeds and invertebrates may not predispose them to digest passerine eggs efficiently. If improved efficiency digesting eggs can only be achieved at the expense of reduced efficiency digesting the normal diet, selection may not have favored an increase in egg consumption. This could be tested by experimenting with the diets of captive breeding cowbirds. If such experimentation reveals that female cowbirds can produce eggs on a diet of passerine eggs, then their failure to eat many passerine eggs in nature will require other explanations.

To aid in understanding the incomplete use of removed eggs, we need to know variation in the frequency of egg-eating by individual female cowbirds. Do some never eat eggs despite experience with broken eggs, which should provide a gustatory stimulus? That is, does the population show a balanced polymorphism, and, if so, what are its offsetting features? Alternatively, all females may sometimes eat eggs, either irregularly or invariably once they have begun. To what extent is egg-eating learned or do naive cowbirds recognize eggs as food before they remove their first egg? Finally, further studies are needed to refine our estimates of the proportion of uneaten eggs.

Several hypotheses, including the use of eggs as food, have been suggested to explain the significance of host-egg removal by some brood parasites (Davies and Brooke 1988). Our study suggests that the use of eggs as food is not the primary cause of egg removal by Brown-headed Cowbirds.

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LITERATURE CITED

Beane, J. C., and S. L. Alford. 1990. Destruction of a Pine Warbler brood by an adult cowbird. Chat 54:85–86.

Benson, M. H. 1939. A study of the American Redstart (*Setophaga ruticilla* Swainson). M.Sc.thesis, Cornell Univ., Ithaca, NY.

Blincoe, B. J. 1935. A cowbird removes a robin's egg. Wilson Bull. 47:158.

Brandt, A. E. 1947. The rearing of a cowbird by Acadian Flycatchers. Wilson Bull. 59:79–82.

Bucher, E. H., and Orueta, A. 1977. Ecologia de la reproduccion de la paloma *Zenaida auriculata* II. Epoca de cria, suceso y productividad en las colonias de nidificacion de Cordoba. Ecosur 4:157–185.

Burroughs, J. 1871. Wake-robin. Riverside Press, Cambridge, MA.

Burroughs, J. 1887. Birds and bees. Riverside Press, Cambridge, MA.

Carter, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88:11–25.

Chance, E. P. 1922. The cuckoo's secret. Sidgwick and Jackson, London.

Chance, E. P. 1940. The truth about the cuckoo. Country Life. London.

Chance, E. P., and H. W. Hann. 1942. The European Cuckoo and the cowbird. Bird-Banding 13: 99–103.

Cott, H. B. 1953–1954. The palatability of the eggs of birds. Proc. Zool. Soc. Lond. 123:123–141.

Davies, N. B., and M. de L. Brooke. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. Anim. Behav. 36:262–284.

DuBois, A. D. 1956. A cowbird incident. Auk 73: 286.

Earley, C. G. 1991. Brown-headed Cowbird, *Molothrus ater,* seen removing a Chipping Sparrow, *Spizella passerina,* egg. Can. Field Nat. 105:281–282.

Fraga, R. M. 1986. The Bay-winged Cowbird (*Molothrus badius*) and its brood parasites: interactions, coevolution and comparative efficiency. Ph.D.diss., Univ. of California, Santa Barbara, CA.

Hann, H. W. 1937. Life history of the Oven-bird in southern Michigan. Wilson Bull. 49:145–237.

Hann, H. W. 1941. The cowbird at the nest. Wilson Bull. 53:210–221.

Harrison, H. H. 1952. Notes on a cowbird removing an egg at dawn. Redstart 19:46–48.

Hess, I. E. 1910. One hundred breeding birds of an Illinois ten-mile radius. Auk 27:19–32.

Hofslund, P. B. 1957. Cowbird parasitism of the Northern Yellow-throat. Auk 74:42–48.

Hudson, W. H. 1870. Sixth letter on the ornithology of Buenos Ayres. Proc. Zool. Soc. Lond. 1870: 548–550.

Hudson, W. H. 1874. Notes on the procreant instincts of the three species of *Molothrus* found in

Buenos Ayres. Proc. Zool. Soc. Lond. 1874:153–174.

JOHNSTONE, W. B. 1949. An annotated list of the birds of the East Kootenay British Columbia. Occ. papers of B.C. Prov. Mus. No. 7, Victoria, B.C.

KING, A. P. 1979. Variables affecting parasitism in the North American cowbird. Ph.D.diss., Cornell Univ., Ithaca, NY.

KING, J. R. 1973. Energetics of reproduction in birds, p. 78–107. *In* D. S. Farner [ed.], Breeding biology of birds. Natl. Acad. Sci., Washington, DC.

KINSER, G. W., JR. 1973. Ecology and behavior of the cardinal, *Richmondena cardinalis* (L.), in southern Indiana. Ph.D.diss., Indiana Univ., Bloomington, IN.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci. Bull. 40:1–242.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, part 1. Trans. Linn. Soc. No. 4.

NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler, *Dendroica discolor*. Ornithol. Monogr. No. 26. American Ornithologists' Union, Washington, DC.

NORRIS, R. T. 1944. Notes on a cowbird parasitizing a Song Sparrow. Wilson Bull. 56:129–132.

OLSON, A. L. 1943. Cowbird carrying away and eating a bird's egg in the evening. Wilson Bull. 55:195.

POTTER, E. F. 1985. Breeding habits, nestling development, and vocalizations in the Summer Tanager. Chat 49:57–65.

PRESCOTT, K. W. 1965. Studies in the life history of the Scarlet Tanager *Piranga olivacea*. Investigations No. 2, New Jersey State Museum, Trenton, NJ.

ROBERTS, T. S. 1932. The birds of Minnesota, vol. 2. Univ. of Minnesota Press, Minneapolis.

ROTHSTEIN, S. I. 1971. Observation and experiment in the analysis of interactions between brood parasites and their hosts. Am. Nat. 105:71–74.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1986. Social dominance, mating and spacing systems, female fecundity, and vocal dialects in captive and free-ranging Brown-headed Cowbirds, p. 127–185. *In* R. F. Johnston [ed.], Current ornithology, vol. 3.

SCOTT, D. M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. Auk 94:18–27.

SCOTT, D. M. 1991. The time of day of egg laying by the Brown-headed Cowbird and other icterines. Can. J. Zool. 69:2093–2099.

TATE, J., JR. 1967. Cowbird removes warbler nestling from nest. Auk 84:422.

WEATHERHEAD, P. J. 1989. Sex-ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358–366.

WYLLIE, I. 1981. The cuckoo. Universe Books, New York.