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REMOVAL OF YELLOW WARBLER EGGS IN ASSOCIATION WITH COWBIRD PARASITISM[1]

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Abstract. In this study, I quantified the removal of eggs by the Brown-headed Cowbird (*Molothrus ater*) from parasitized Yellow Warbler (*Dendroica petechia*) nests. Laying cowbirds removed one warbler egg from about one in three parasitized nests. Assuming the same individual was involved in both acts, cowbirds removed host eggs on a day before or the same day they laid their own eggs (33.3%, $n = 8$ nests), on the same day (20.8%, $n = 5$) but after they laid, or on the same or subsequent days (46%, $n = 11$). As almost half (41%) of the parasitized nests received cowbird eggs before host eggs appeared, many cowbirds that removed eggs had to return to the nest to do so, although burial precluded that at some nests. Return trips increased the chances that a cowbird might mistakenly remove its own egg, especially if it was the only egg in the nest, and that interactions might occur between host and parasite. Explanations for the removal of eggs at the time of parasitism are summarized and two hypotheses are tested. The likelihood of warblers accepting a cowbird egg experimentally introduced into their nests was not influenced by the removal of a host egg at the time of parasitism, as predicted by the "host deception" hypothesis. Yellow Warblers tolerated five- and four-egg clutches being reduced to three eggs (36/37 nests), but abandoned nearly one-third of clutches reduced to two eggs (13/42) and most clutches reduced to one egg (20/22). Only one control nest was deserted ($n = 41$ and 59 clutches of five and four eggs, respectively). Only four of 13 (31%) clutches reduced to one egg of each of the warbler and cowbird were abandoned, but 11 of 14 (79%) clutches reduced to only one cowbird egg were deserted. None of the 10 clutches reduced to two cowbird eggs was deserted. These results suggest that cowbirds can remove at least two eggs without risking desertion by the warblers. It is not clear why only one egg is removed, when removal occurs in the first place. Cowbirds that manage to ingest eggs they remove undoubtedly gain nourishment.

Key words: Brood parasitism; egg laying; egg removal; clutch reduction; nest desertion; Brown-headed Cowbird; Yellow Warbler.

INTRODUCTION

Avian brood parasites manipulate the clutches and broods of their hosts. Parasitic eggs increase the volume of host clutches unless the parasites remove one or more host eggs when they parasitize nests (e.g., Lombardo et al. 1989) or if the hosts respond to the parasitic egg(s) by laying fewer eggs (e.g., Kendra et al. 1988). Parasitic nestlings of some parasites may kill their host "siblings" (e.g., Friedmann 1955, Morton and Farabaugh 1979), physically oust them or the unhatched host eggs from the nest (e.g., Jensen and Jensen 1969, Wyllie 1975, Gill 1983), or outcompete host young by monopolizing the food brought by the foster parents, eventually crowding their undernourished nest mates until they starve and are removed by the hosts or fall from the nests (e.g., Gaston 1976, Carter 1986, Briskie and Sealy 1987, Marvil and Cruz 1989).

Some of these manipulations occur early in the nesting cycle of the hosts, while others take place much later. Ejection of host young and unhatched eggs clearly eliminates any competitive advantage host nestlings might have, maximizing the survival of the parasitic young to fledging (e.g., Blankespoor et al. 1982, Carey 1986). However, it is not obvious why many brood parasites steal eggs from nests they parasitize. Few studies have quantified the extent of removal or identified the circumstances under which it occurs (but see Davies and Brooke 1988, Lombardo et al. 1989). Some species of parasitic cuckoos almost always remove one or more eggs from host nests (e.g., Jensen and Jensen 1969, Wyllie 1975, Brooker et al. 1988), while other species usually do not remove any (e.g., Liversidge 1971, Gaston 1976). Among the parasitic cowbirds, females remove or damage host eggs with considerable variability, possibly depending upon the particular host species parasitized (e.g., Friedmann 1963, Post and Wiley 1977, Smith 1981, Zimmerman 1983, Carter 1986).

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habit of removing eggs from parasitized nests has been suspected for over 100 years (e.g., Burroughs 1887, Savage 1897). Since then, anecdotal observations and studies of closely watched nests of a few host species have revealed that if a female cowbird removes an egg at all, she may do so either a day before, later on the same day, or a day after she laid her own egg (assuming the same female is involved in both acts). Because egg removal by female Brown-headed Cowbirds apparently requires extra visits to host nests, opportunities increase for interactions to occur between cowbirds and hosts. As Yellow Warblers (*Dendroica petechia*) recognize female cowbirds as a threat (e.g., Hobson and Sealy 1989), they may reject parasitized clutches after intercepting a cowbird at their nests. Indeed, cowbirds and other brood parasites lay their eggs within seconds (e.g., Seel 1973, Nolan 1978:371, Brooker et al. 1988), presumably to avoid being detected by hosts. Davies and Brooke (1988) and Moksnes and Røskaft (1989) demonstrated experimentally that some hosts of the Common Cuckoo (*Cuculus canorus*) presented at their nests with a model of the cuckoo plus its egg, were more likely to reject the egg than hosts in whose nests only a cuckoo egg had been introduced.

Several hypotheses have been proposed to explain the function of host-egg stealing. Few have been tested (see Payne 1977, Davies and Brooke 1988, Rothstein 1990). This behavior has received relatively little attention in the literature, despite its likely importance in the dynamics of parasite-host interactions. In the present study, I examined the removal of Yellow Warbler eggs by Brown-headed Cowbirds (hereafter cowbirds). My objectives were (1) to measure the rate at which cowbirds removed warbler eggs in relation to laying by the cowbird and warbler, (2) to quantify the frequency of removal over several breeding seasons, and (3) to summarize explanations for why laying brood parasites remove (usually one) host egg. In addition, I describe two experiments designed (1) to ascertain whether Yellow Warblers are more likely to accept cowbird eggs experimentally introduced into their nests, if switched with a host egg, and (2) to reduce warbler clutches to ascertain the extent to which warblers tolerate lowered clutch sizes.

EXPLANATIONS FOR HOST-EGG REMOVAL

In my treatment of egg removal, I address only the removal of eggs by parasites in association with the act of parasitism. Below, I summarize explanations for this behavior. I exclude from consideration behavior of many other brood parasites, which may also remove eggs when they parasitize nests, but are known also to destroy host or potential host clutches or broods at other stages of the breeding cycle, possibly to create new opportunities for parasitism (e.g., Payne 1977), to prevent other females from gaining access to nests to parasitize (Wyllie 1975), or to revisit parasitized nests after hatching and, if the parasite chick is not in the nest, prey upon host nestlings to force them to renest (Zahavi 1979). Lastly, I do not consider the destruction of host eggs in nests parasitized by some of the other species of cowbirds (e.g., Post and Wiley 1977, Carter 1986).

Host deception. Egg removal may dupe a host that counts eggs into accepting a parasite egg (e.g., Hamilton and Orians 1965, Moksnes and Røskaft 1987). This hypothesis predicts that parasitic eggs laid in nests where a host egg is not removed are more likely to be rejected than those laid in nests where a host egg is removed.

Food for the parasite. Typically, brood parasites remove a single egg from each host nest, if they remove any at all (e.g., Jensen and Jensen 1969, Gill 1983, Wyllie 1975, Brooker et al. 1988, Lombardo et al. 1989). Although early workers debated whether female Common Cuckoos ate the eggs they removed from host nests (e.g., Gurney 1897), this behavior has since been confirmed for this and many other species of parasitic cuckoo (e.g., Livesey 1936, Friedmann 1968, Jensen and Jensen 1969, Wyllie 1975, Brooker and Brooker 1989), and other brood parasites, including cowbirds (see below). Löhrl (1979) established from observations of captive Common Cuckoos that only females remove eggs and that they swallow them whole. Because parasites undoubtedly gain nourishment from this behavior (see Payne 1974, Becking 1979, Löhrl 1979), Davies and Brooke (1988) wondered why they do not remove more eggs and suggested that hosts are prone to desert greatly reduced clutches.

Do Brown-headed Cowbirds eat eggs they remove from host nests? Females have been reported carrying eggs away from nests in flight (Nice 1937, Mitchell 1956, Earley 1991), dropping them while flying from nests (Roberts 1932), and carrying eggs to the ground where, in cases where females were not immediately flushed, ate them piecemeal, sometimes shell and all (Nice

1929; Blincoe 1935; Hann 1937, 1941; Olson 1943; Norris 1944; Nolan 1978:371). On our study area, we have thrice observed females eating eggs on the ground and once observed a cowbird carrying an egg away from a nest (Sealy, unpubl. observ.). Benson (1939:122) watched a female cowbird remove one of two cowbird eggs (the only eggs in the nest) from an American Redstart (*Setophaga ruticilla*) nest and eat it, shell and all, on the ground a few meters away. Captive females noted by King (1979:13) either ate or "disregarded" eggs they removed from artificial nests. Thus, ingestion of eggs removed by cowbirds from naturally parasitized nests appears to be a regular behavior associated with the act of parasitism. If cowbirds remove eggs to obtain food, but are limited by the risk of host desertion if too many eggs are stolen, I would predict that clutches reduced more than those induced naturally (see below) should lead to more desertions by hosts and should be selected against.

Ankney and Scott (1980) demonstrated that egg-laying female cowbirds, which lay an estimated 40 eggs in an eight-week breeding season in southern Ontario (Scott and Ankney 1980), rely on exogenous nutrients for egg production. Cowbirds obtained these nutrients by increasing their intake of protein. Stomachs of females they examined often contained pieces of mollusc shell, which are sources of calcium. Although leg-bone calcium reserves were also used by female cowbirds for egg production (Ankney and Scott 1980), eggshells may supplement their calcium uptake. This would be another benefit to ingesting eggs removed from host nests. Löhrl (1979) reported that one captive female Common Cuckoo swallowed 65 passerine eggs in one breeding season. Wyllie (1975) reported a wild female cuckoo parasitizing Reed Warblers (*Acrocephalus scirpaceus*) that took at least 19 fresh eggs and two nestlings in one season.

Test incubation status of hosts. Livesey (1936) suggested that cuckoos might remove an egg to determine whether host clutches are fresh or incubated, thus ascertaining whether or not they are suitable for parasitism. Predicted here is that brood parasites should eat, or at least break, a host egg before they commit their own egg to the nest.

Reduction of crowding and competition. For parasites such as cowbirds, whose newly hatched young do not eject host eggs or nestlings, egg removal probably reduces nestling competition (e.g., Scott 1977, Blankespoor et al. 1982). Gaston (1976) detected egg removal in populations of the Pied Crested Cuckoo (*Clamator jacobinus*), which normally does not remove host eggs when laying. In these populations, multiple layings by the parasite were common and Gaston (1976) suggested that it is imperative under these circumstances that some eggs are removed to ensure the brood does not become too large.

Enhancement of host incubation efficiency. Davies and Brooke (1988) pointed out that in some species larger clutches have a higher frequency of unhatched eggs (e.g., Yom-Tov 1980, Wiklund 1985). Thus, it might benefit a brood parasite to remove a host egg if the addition of its own egg to the host clutch results in less efficient incubation, because the parasitic egg also would be less likely to hatch. The incubation limit hypothesis predicts that the incidence of unhatched eggs in nests from which a host egg is removed to make room for the parasitic egg will be less than that in nests where no host egg is removed.

Parasitism of smaller hosts. This explanation involves two quite different behaviors—the eviction of host nestlings by newly hatched parasites, and the removal of host eggs at laying. Gaston (1976) suggested that eviction of eggs and nestlings may be an adaptation for parasitizing hosts that are much smaller than the parasite, where the rearing of a single nestling is the equivalent to rearing a whole brood of host offspring. In the genus *Clamator,* most species parasitize hosts similar to, or larger than themselves in size, and hence eviction is not necessary if the female cuckoo removes or destroys one of the host's eggs while laying (see also Lack 1954). Supportive of this hypothesis is Friedmann's (1960) observation that viduines, which parasitize estrildine hosts similar to themselves in size and mass, frequently remove a host egg at laying. Friedmann noted, however, that other parasites that are hardly larger than their usual hosts, such as honeyguides and the Didric Cuckoo (*Cu. caprius*), usually replace the entire host brood with a single individual of their own.

METHODS

STUDY AREA

Natural parasitism on the Yellow Warbler by the Brown-headed Cowbird was studied from 1974–1987 (except 1977) on the forested dune ridge that separates Lake Manitoba and Delta Marsh, Manitoba (see MacKenzie 1982). The study area (50°11'N, 98°19'W) is a 3-km portion of the ridge forest that averages 80 m in width as it runs westward from the Portage Diversion to Cram Creek (see map in Sealy 1980), on the adjoining properties of the University of Manitoba Field Station and Portage Country Club.

EGG LAYING BY HOST AND PARASITE

Nests at all heights over the entire ridge forest were checked before 12:00 (Central Daylight Time) each day before and throughout egg laying, and intermittently during incubation. Nests were numbered with flagging tape placed nearby and individual eggs, including cowbird eggs, were marked in 1974–1976, and 1987 with waterproof markers in the order they were laid. Unparasitized and parasitized clutches were considered complete when the number of eggs remained the same for at least two consecutive days.

REMOVAL OF YELLOW WARBLER EGGS

Daily visits to warbler nests in which each egg was marked on the day it was laid showed that one egg, rarely more, sometimes disappeared with the nests remaining active. Because predators and strong winds could account for these losses (Goossen and Sealy 1982), the relative effects of these influences were estimated by comparing egg-loss rates in parasitized and unparasitized nests. Data for this analysis were from nests examined in 1974–1976 and 1987. I determined the proportion of nests that lost at least one egg without the nest being abandoned, in the five days following laying of the first host egg and also during the incubation period. I used only nests that were visited daily from at least the day before the first host eggs were laid. A nest that lost eggs without being abandoned was counted as having a loss. One that survived to the morning of Day 6 without egg-loss was scored as a no-loss.

The timing of egg removal relative to stage of the host's reproductive cycle was determined to the nearest day in some nests, to within two days in others. Thus, a warbler egg that disappeared between inspections could have been removed either later that day or before I checked the nest the next morning. As a typical example of the latter kind of data, egg B sometimes disappeared between mid-morning inspections on the second and third days of laying. I subdivided the data according to their two degrees of precision but did not distinguish between nests that lost one egg or more than one egg.

Cowbird eggs disappeared from some parasitized nests, but in all cases host clutches were completed and otherwise remained active. Warblers might have ejected them (see Weatherhead 1989), although other authors either did not record the disappearance of cowbird eggs or stated explicitly that Yellow Warblers cannot eject them (e.g., Rothstein 1975a, Clark and Robertson 1981, Graham 1988, Rohwer and Spaw 1988). On the other hand, cowbirds or predators might have removed them (see Rothstein 1975b). Cowbirds have been suspected of occasionally removing cowbird eggs from nests, usually those parasitized more than once or where host eggs were larger or similar in appearance to cowbird eggs (e.g., Hann 1937, Benson 1939:122, Klaas 1975, Elliott 1977, Scott 1977).

CLUTCH MANIPULATIONS

Experimental parasitism. I experimentally parasitized Yellow Warbler nests in 1988, 1989 and 1990 using real cowbird eggs collected from nests of several host species, including the Yellow Warbler, in and near the Delta Marsh. I parasitized most nests between 07:00 and 10:00, so as not to interfere with normal laying by the warblers (see below). I experimentally parasitized two groups of nests with single cowbird eggs on LD1 (= Laying Day 1, i.e., day on which the A-egg was laid) or LD2, without removing a host egg from nests in one group, and switching the cowbird egg and one host egg in the other group. I considered cowbird eggs accepted when egg laying was not interrupted and clutches were completed, or incubation continued for at least six days. I considered desertion to have occurred when all activity at the nest ceased after parasitism and the eggs were cold to the touch, or, if the female laid after the interference, but never incubated.

Clutch reduction. I reduced clutch size in three groups of nests to determine the tolerance of Yellow Warblers to lowered clutch volumes. In the first group, I removed the first-laid eggs, i.e., A-eggs, within 1–2 hours of their being laid, leaving the nests empty. B-eggs followed by C-, D-, and E-eggs (when laid) were removed as they were laid in the second group, leaving only the A-egg in nests. In the third group, nests with four or five eggs, the most common clutch sizes in the population (Goossen and Sealy 1982), were assigned to one of six treatments, plus a control group, i.e., nests with eggs numbered but only visited each day. Seven or eight days after the A-egg was laid, clutches in four treatments were reduced to one, two, three, or four warbler eggs. Nests in two other treatments were reduced to one cowbird egg only, and one egg each of the warbler and cowbird. All nests were checked daily for at least six days, or until they were abandoned, i.e., not incubated for three consecutive nights, or depredated. Ten nests were also reduced to two cowbird eggs, three by experimental reduction and seven as a result of parasitism by cowbirds.

MEASUREMENTS OF COWBIRD AND WARBLER EGGS

Cowbird eggs are fairly consistent in appearance and do not mimic eggs of host species (see Rothstein 1974). Nevertheless, Yellow Warbler eggs (see photo in Harrison 1975:183) and cowbird eggs are similar in appearance, although the latter averages 47.2% larger in volume and is 45.5% heavier. The mean length and breadth (measured with dial calipers) of 77 cowbird eggs laid in 73 warbler nests was 21.07 (SE = 0.12 mm) and 16.36 (SE = 0.09 mm), respectively. Mean mass (measured on an electronic balance) was 3.14 (SE = 0.04 g) and volume (calculated using the formula $V = 0.498LB^2$, where V is interior volume, L is length, and B is breadth; from Spaw and Rohwer 1987) was 2.82 (SE = 0.33 ml). The mean length and breadth of 85 Yellow Warbler eggs (irrespective of laying order) was 16.80 (SE = 0.08 mm) and 12.60 (SE = 0.04 mm). Mean mass was 1.43 (SE = 0.01 g) and volume was 1.33 (SE = 0.11 ml).

RESULTS

EGG LAYING BY HOST AND PARASITE

Frequency of parasitism. Of the 1,885 Yellow Warbler nests studied, 396 (21%) were parasitized by cowbirds. Of the 396 parasitized nests, 354 (89.4%) were parasitized once, 38 (9.6%) were parasitized twice, and 4 (1.0%) were parasitized three times. The following intervals were observed between successive cowbird eggs laid in the same nest: 0 day (n = 1), 1 day (n = 34), 2 days (n = 3), 3 days (n = 1), and 4, 5, and 8 days (n = 1 each). The preponderance of 1-day, over 0-day intervals, at multiply parasitized nests suggests that the same females were usually involved (see Gaston 1976), as cowbirds are known to lay their eggs on successive days (Ankney and Johnson 1985). In these cases, cowbirds that stole an egg from nests almost certainly had to distinguish between host eggs and their own egg.

Time of day of laying. Cowbirds usually lay shortly before sunrise (Scott 1991). Time of day of laying by 10 Yellow Warblers, determined between 2 and 10 June 1989 (sunrise times 05:23 and 05:19, respectively) using Muma's (1986) observational procedure, ranged from 05:15 to 06:15, with a mean time of 05:52.

Laying by individual cowbirds relative to laying by host warblers. In 255 cases, I knew the day on which a cowbird laid in a warbler nest and the day on which the host female laid its first egg, i.e., LD1. I assumed that when a cowbird and a warbler laid on the same day, the cowbird laid earlier (see above). All nests were observed before any eggs were deposited, but some cowbirds may have removed warbler eggs from nests they parasitized before I recorded them. If egg A had been removed before my inspection on the day it was laid, I might have thought laying began the following day. However, because cowbirds generally removed host eggs after mid-morning (see later), after I had checked most nests, I am confident that this bias was small. Of the 255 cowbird eggs in the sample, 105 (41.2%) were laid before the day on which warblers laid their first eggs, i.e., during the pre-laying period (Fig. 1). Most of these cowbird eggs (62.9%) were buried or the nests were deserted. The remaining 150 eggs (58.8%) were laid during the laying period and in some cases after host clutches were complete (Fig. 1).

REMOVAL OF YELLOW WARBLER EGGS

Number of eggs removed. Totals of 1,005 and 216 unparasitized and parasitized nests contained means of 4.47 (SE = 0.0006) and 4.15 (SE = 0.003) warbler eggs, respectively (Table 1), which differed significantly (Kruskal-Wallis test, adjusted for ties, $H = 50.516$, df = 1, $P < 0.001$). Thus, the number of Yellow Warbler eggs in naturally parasitized nests was 0.32 eggs less than in unparasitized ones, which indicates that female cowbirds typically removed an egg from about one-third of the warbler nests parasitized. I assumed this difference was due to cowbirds stealing host eggs from nests they parasitized (see Rothstein 1975b for discussion of the legitimacy of this assumption). The following analysis supports this assumption, as does the summary be-

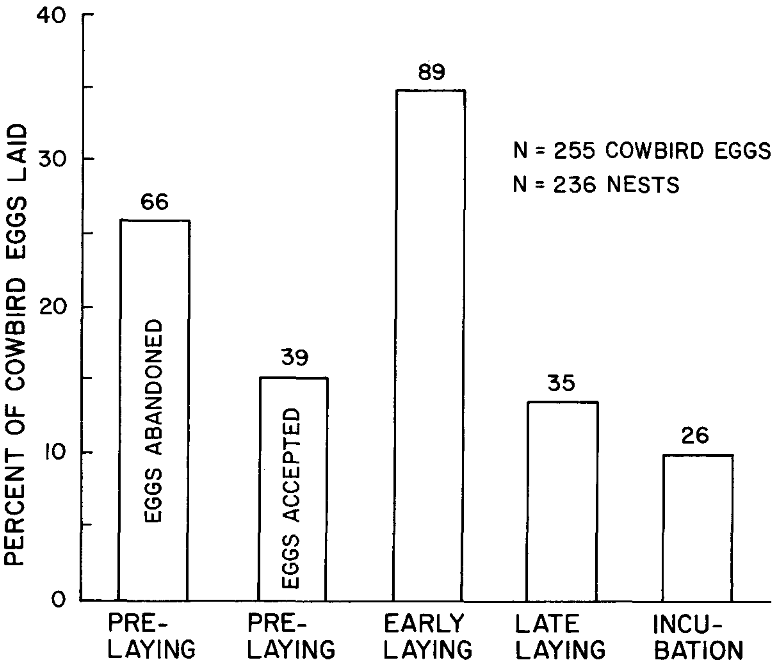

FIGURE 1. Frequency of cowbird laying in relation to laying stage of the Yellow Warbler. PRE-LAYING STAGE: cowbird eggs laid before LD1. EARLY LAYING STAGE: cowbird eggs laid on LD1 and LD2. LATE LAYING STAGE: cowbird eggs laid on LD3–LD5. INCUBATION STAGE: cowbird eggs laid after LD5. The values on top of the bars are the number of cowbird eggs laid.

low of observations of cowbirds removing and eating host eggs, including those of the Yellow Warbler.

Thirty-eight of 231 unparasitized warbler nests lost eggs during the laying period, a rate significantly lower than for parasitized nests (38:193 vs. 29:33; $G = 11.419$, $df = 1$, $P < 0.001$). Losses during incubation in unparasitized and parasitized nests, however, did not differ (23:117 vs. 5: 18, $G = 0.052$, $df = 1$, $P > 0.20$). The results confirm that cowbirds removed most of the eggs lost from parasitized nests during laying, but not during incubation.

Although the number of warbler eggs laid in unparasitized and parasitized nests varied among years (Kruskal-Wallis ANOVAS, adjusted for ties, $H = 19.392$, $df = 9$, $0.05 > P > 0.02$ (unparasitized); $H = 19.49$, $df = 9$, $0.05 > P > 0.02$ (parasitized)), there was no correlation between the number of host eggs in unparasitized and parasitized nests between years (Spearman rank correlation coefficient, $p = 0.258$, $P > 0.05$). Over the breeding season, egg removal was estimated by calculating the percentage difference between each parasitized clutch and the mean for all unparasitized clutches for the same week. A Kruskal-Wallis ANOVA showed a significant difference in egg removal among weeks ($T = 24.91$, $df = 5$, $P < 0.001$). Multiple comparisons following this test suggest that egg removal was greater in weeks two, four, and six than in week three, and greater in week two than in week one.

Hour of removal. On the study area, female cowbirds were twice observed eating Yellow Warbler eggs away from nests, at 10:00 and 10:47, and an American Robin (*Turdus migratorius*) egg near the nest, at 16:07. At 09:47 on 2 June 1991, I watched a female cowbird carrying an egg from a warbler nest. Elsewhere, female cowbirds have been observed removing eggs from just before sunrise through the evening (e.g., Hann 1937, Nice 1937, Olson 1943, Nolan 1978:374–378, Wolf 1987, Earley 1991).

Stage of host nesting effort. At least 80% (24/30) of all laying-interval removals were on LD1 or LD2 of the warbler laying cycle. Three removals were known for sure to have left the nests empty (Table 2).

Removal relative to cowbird laying. Treating each removal separately, I determined the inter-

TABLE 1. Number of host eggs in unparasitized and parasitized Yellow Warbler nests.

	No. of clutches										
	Unparasitized						Parasitized				
Year	2 eggs	3 eggs	4 eggs	5 eggs	Total nests	$\bar{x}$ ± SE	3 eggs	4 eggs	5 eggs	Total nests	$\bar{x}$ ± SE
1974		1	15	17	33	4.5 ± 0.02	0	11	6	17	4.4 ± 0.03
1975		0	27	25	52	4.5 ± 0.009	3	7	6	16	4.2 ± 0.05
1976		4	25	30	59	4.4 ± 0.01	1	9	9	19	4.4 ± 0.03
1980		1	20	28	49	4.6 ± 0.01	0	5	0	5	4.0 ± 0.00
1981		4	34	39	77	4.5 ± 0.008	3	11	10	24	4.3 ± 0.03
1982		5	52	45	102	4.4 ± 0.006	4	20	4	28	4.0 ± 0.02
1983		7	67	63	137	4.4 ± 0.004	7	7	2	16	3.7 ± 0.05
1984	1	12	67	103	183	4.5 ± 0.004	2	18	8	28	4.2 ± 0.02
1985		10	59	56	125	4.4 ± 0.005	5	27	7	39	4.1 ± 0.01
1986	2	7	57	122	188	4.6 ± 0.003	1	17	6	24	4.2 ± 0.02
Totals	3	51	423	528	1,005	4.5 ± 0.0006	26	132	58	216	4.1 ± 0.003

val between a cowbird's laying and removal to within one to two days (Table 3). I assumed that the cowbird that laid in the nest was the same one that removed the egg. Between 21% and 54% of 24 removals were on the day the parasite laid. At least 33% (8/24) of the host eggs were taken one or more days after the cowbird laid (Table 3). Finally, about 13% (3/24) of the warbler eggs were removed on a day before the cowbird egg was laid. Burial of cowbird eggs by Yellow Warblers precluded subsequent host-egg removal, which may bias the data in favor of early records of removal.

Warbler eggs were sometimes removed from "new" clutches initiated after the cowbird egg had been buried. At 28 such superimposed nests, host clutches were initiated 24 hr (1 nest, 3.6%), 48 hr (2, 7.1%), 72 hr (5, 17.9%), 96 hr (11, 39.3%), and 120 hr (9, 32.1%) after parasitism occurred. "New" clutches averaged 4.2 eggs (SE = 0.02, n = 25), compared with an average of 4.7 eggs (SE = 0.05, n = 144) per unparasitized nest (Mann-Whitney U-test, $z = 2.059$, $P < 0.02$).

Cowbird discrimination between cowbird and warbler eggs. Because cowbirds lay so early, they must rarely have removed an egg in the brief daylight interval before laying, although Nolan (1978:371) observed this once, within a few seconds of laying. For this reason, when a cowbird laid and a host egg disappeared on the same day, I assumed laying preceded removal. This scenario required the cowbird to return to the nest and to choose whether to remove a cowbird or warbler egg. Of the 30 nests in Table 2, at least seven contained only warbler egg(s) at the time of removal. In at least 19 parasitized nests, only host eggs were removed. In one case, a cowbird egg was removed, possibly the only egg present, from a nest that otherwise remained active. Finally, in three cases, Yellow Warbler eggs were taken, but I did not know whether a choice had to be made. Thus, most warbler eggs removed were from among the first three eggs in the laying order. Cowbird eggs disappeared from one other nest that otherwise remained active.

CLUTCH MANIPULATIONS

Experimental parasitism. The introduced cowbird egg was buried at only one of 47 nests (2.1%) parasitized on LD1 or LD2, from which one host egg was removed. In 54 nests similarly parasitized but with no host eggs removed, two cowbird eggs were buried (3.7%) and five were deserted (9.3%). Combining burials and desertions in these experimental groups, the results are not significantly different ($\chi^2 = 2.31$, df = 1, ns). Thus, Yellow Warblers were no more likely to reject an experimentally introduced cowbird egg, whether or not a host egg was removed.

Clutch reduction. Females at all nine nests from which I removed first-laid eggs as they were laid continued to lay. Seven females completed their clutches (four of four eggs, three of five eggs) and one nest was depredated after egg C was laid. A cowbird removed egg B later the day it was laid in the ninth nest after having parasitized the nest earlier in the day. Egg C was laid the next day, but the nest was eventually deserted.

All six females tolerated the reduction of their clutches to one egg, when egg B and all subsequent eggs were quickly removed as they were laid, which always left only egg A in the nest.

TABLE 2. Day of removal of Yellow Warbler eggs relative to the stage of breeding cycle at host nest.[a]

Host stage at removal	Number of nests	(%)
Laying		
Day 1	3[b]	10.0
Day 1 or 2	8	26.7
Day 2	10[c]	33.3
Day 2 or 3	3	10.0
Day 3	1	3.3
Day 3 or 4	1	3.3
Day 4	1	3.3
Day 4 or 5	1	3.3
Incubation		
Day 2	2	6.7
Total	30	99.9

[a] A possible source of error is that if the first warbler egg disappeared before I found it, I might have mistakenly concluded that no egg had been laid that day and underestimated the frequency of removal. The day on which the warbler laid the last egg of its clutch, whether the 4th or 5th day in 4- or 5-egg clutches, respectively, was also day 1 of the incubation period.

[b] One cowbird egg disappeared from another nest on this day.

[c] Two cowbird eggs disappeared from two other nests on this day.

TABLE 3. Day of removal of Yellow Warbler eggs relative to the stage of laying of cowbird egg.

Removal	Number of nests	(%)
Before laying		
2 days	1	4.2
1 day	2	8.3
1 day before or day of laying	5	20.8
Day of laying	5	20.8
Day of laying or 1 day after	3	12.5
After laying		
1 day	4	16.7
2 days	1	4.2
3 or 4 days	1	4.2
4 or 5 days	1	4.2
5 or 6 days	1	4.2
Total	24	100.1

Four nests failed between three and nine days of incubation; two nests fledged the single young. These results indicate Yellow Warblers are determinate layers (see also Sealy et al. 1989, Kennedy 1991) and tolerated clutch reduction while laying. During laying, all females seemed to tolerate zero or one egg, after reduction, but most deserted if their complete clutches were reduced this much after laying ceased.

Yellow Warblers abandoned reduced clutches more often than those from which eggs were not removed. Desertion rates for five-egg clutches reduced to one egg ($n = 9$ nests), two eggs ($n = 17$), three eggs ($n = 5$), four eggs ($n = 12$), and controls ($n = 41$) were 100%, 41%, 0%, 0%, and 0%, respectively. Reducing these clutches to one or two eggs increased the chances of their being abandoned when compared with controls ($\chi^2 = 34.89$, df = 1, $P < 0.001$). Desertion rates for four-egg clutches reduced to one egg ($n = 13$ nests), two eggs ($n = 25$), three eggs ($n = 20$), and controls ($n = 59$) were 85%, 24%, 5%, and 2%, respectively. Reducing four-egg clutches to one or two eggs also increased the likelihood of desertion ($\chi^2 = 28.69$, df = 1, $P < 0.001$). Abandonment usually occurred within 24 hr of the manipulation. However, two of the clutches reduced to single eggs were incubated for one and three days before being deserted, and at one nest in which the single egg was accepted, a young fledged. These results suggest female cowbirds can reduce Yellow Warbler clutches to two eggs without penalty at nests where they added one of their own eggs, but risk certain desertion by the host if they reduce them to one egg, even when the nest also contains a cowbird egg. The maximum number of eggs the cowbird can safely take from a clutch of three is one (she replaces it with her own egg so the final clutch is three), and from a clutch of four the maximum is two (two removed then her own egg added giving a clutch of three). The cowbird could remove three eggs from five-egg clutches (three removed then her own egg added to give a clutch of three). Of 14 clutches reduced to a single cowbird egg, 11 (79%) were deserted, while four of 13 nests (31%) reduced to one warbler plus one cowbird egg were deserted ($\chi^2 = 2.48$, df = 1, ns). None of the 10 nests reduced to only two cowbird eggs was deserted.

DISCUSSION

VARIATION IN HOST-EGG REMOVAL

Although early naturalists (e.g., Burroughs 1887: 29–30, Savage 1897, Hess 1910) were convinced that every cowbird egg laid was at the expense of one or two host eggs, Friedmann (1929:185–186) was unable to identify a pattern of egg-removal behavior in cowbirds. Recent studies of naturally parasitized host species, however, have confirmed that this behavior is a regular component of the breeding biology of cowbirds (e.g., Hann 1937, 1941; Nice 1937; Mayfield 1960: 160–164; Nolan 1978:374–378; Smith 1981; Zimmerman 1983; Wolf 1987). The results of the present study, and those of Nolan's (1978:

377), revealed that if female cowbirds remove an egg at all, they may do so either on a day before, later on the day they laid their own eggs, or on a subsequent day (see Table 3). Host-egg removal by cowbirds at the moment of parasitism has been reported only twice (e.g., Prescott 1965, Nolan 1978:371), and the (same?) females returned to lay within seconds of removing the egg. Cuckoos, on the other hand, seem to monitor potential host nests more closely and parasitize them when they contain one or two eggs, removing the egg when the nest is parasitized.

In the present study, cowbirds removed an egg from about one in three Yellow Warbler nests parasitized, over the entire breeding season. Although the percentage of egg removals from nests differed statistically over the season, this apparently resulted from differences among the first four weeks of the season, rather than a decline in the number of eggs removed per nest, as Zimmerman (1983) reported for the Dickcissel (*Spiza americana*). Also, the number of warbler eggs present in parasitized and unparasitized nests varied discordantly among the years, which suggests that there were annual differences in the rate of egg removal. Why such variation in egg-removal rates exists is not known. Perhaps some females always remove eggs, while others do not. As cowbirds do not remove eggs at the same time they parasitize nests, they may not always be able to return to remove an egg, or nest defense (Hobson and Sealy 1989) sometimes may be effective.

In populations of the Yellow Warbler in Ontario, Clark and Robertson (1981) estimated that host eggs were removed from about one-half of all parasitized nests, whereas Burgham and Picman (1989) recorded egg removal from only two of the 15 (13.3%) parasitized nests they studied. In Michigan, more than one egg was removed from each parasitized Yellow Warbler nest (DellaSala 1985). It is not known whether the geographic differences in egg-removal rates are real, or whether they reflect year-to-year differences within the populations.

Estimates of egg removal from nests of several other cowbird host species have ranged from 46% to 85% of parasitized nests (e.g., Hann 1937, Nice 1937, Smith 1981). Interestingly, cowbirds almost always remove one egg from Red-winged Blackbird nests, a larger host (Blankespoor et al. 1982, Røskaft et al. 1990). Cuckoos that parasitize hosts much larger than themselves, on the other hand, do not remove host eggs, possibly because they cannot lift them (see Soler 1990).

REMOVAL OF COWBIRD EGGS

Cowbirds should be expected to remove cowbird eggs at already-parasitized nests, as long as they are not their own, because this would maximize the care their own young would receive from the foster parents. Brooker and Brooker (1989) argued that single-egg parasitism among cuckoos allows a parasite to remove a host egg at laying without inadvertently removing one of its own eggs. This behavior is adaptive because cuckoo eggs often mimic those of the host eggs. In the Brown-headed Cowbird, Elliott (1977) suggested that the first cowbird eggs laid in multiply parasitized nests were deliberately placed in certain nests, while subsequent eggs were placed less discriminately. He reasoned that this distribution should result from females avoiding nests they had already parasitized, and should reduce the possibility of a female cowbird mistakenly removing one of her own eggs, when attempting to remove a host egg. Elliott (1978) interpreted the high frequency of mistaken removals of cowbird eggs in his study as evidence in support of this contention. This explanation, however, is not entirely consistent with what is known about the laying and egg-removal patterns of cowbirds. Because cowbirds usually do not lay their own eggs and remove host eggs at the same time, females that return to steal a host egg must often choose between it and their own egg.

COWBIRD NEST VISITS AND TIME OF DAY

Cowbirds that parasitize nests before they contain host eggs must return to the nest to remove an egg. This not only forces the cowbird to choose between its own egg and the host's, but the nest must be visited at least once more, which increases the chances of encountering hosts. Even cowbirds that remove host eggs before they parasitize nests must make additional trips to the nest (see also Mayfield 1961). Again, this behavior seems paradoxical because cowbirds lay earlier in the day than their hosts (Scott 1991) and lay within only a few seconds (e.g., Nolan 1978: 371), which suggests cowbirds attempt to minimize the chances they will be detected by hosts at their nests. The undetermined odds that a female cowbird will find a Yellow Warbler nest unattended again are probably small. This may be another reason why cowbirds do not remove an egg from every Yellow Warbler nest they parasitize. Interactions between other hosts and parasites have been shown to increase the likelihood of rejection by hosts (e.g., Davies and Brooke 1988), hence cowbirds may limit egg stealing to situations where the benefits accrued through consumption of the egg(s) outweigh the risk of encountering the host.

Chance and Hann (1942) regarded the early-morning laying of the Brown-headed Cowbird as a specialization for brood parasitism, which implies that this behavior evolved in the context of parasitism. These authors suggested that cowbirds lay around sunrise so as not to disturb host females, which they believed would be away foraging before laying their own eggs, and hence inattentive. However, Scott (1991) compared the time of day of laying of the Brown-headed Cowbird and several non-parasitic icterines, and concluded that the cowbird's early laying time may simply be a primitive icterine trait, which probably did not arise as an adaptation for parasitism. Nevertheless, Scott (1991) believed that laying very early allowed female cowbirds to parasitize nests before the hosts arrived to lay. That cowbirds do not parasitize nests on a particular day of the host's laying cycle frees them to parasitize nests earlier in the morning.

Laying earlier in the day, however, may not necessarily allow cowbirds to sneak into Yellow Warbler nests unseen, even though the warblers have not yet laid. This is because some females roost overnight in their nests, starting in some cases before they have laid their first eggs, with the frequency increasing through egg laying (Sealy et al., unpubl. data). Because roosting females usually do not leave their nests until after sunrise, presumably they would be confronted by the cowbird when it arrives to lay. Yellow Warblers are known to respond to the threat of cowbird parasitism by rushing to their nests and sitting tightly in them (Hobson and Sealy 1989), but I do not know whether warblers can actually deter cowbirds bent on parasitizing their nests. At nests in which female warblers did not roost, laying early may allow cowbirds to avoid flushing ovipositing females, although it is not likely that females flushed under such circumstances would desert their nests. Once I inadvertently flushed a female Yellow Warbler from her nest before she had laid. She did not lay in the nest that day, although she resumed laying the next morning and eventually completed her clutch. Common Cuckoos, on the other hand, may have evolved away from morning laying (Davies and Brooke 1988). Results of these authors' experiments suggest that this species parasitizes Reed Warblers in the afternoon, when they are likely inattentive, because to do so in the morning would lead to rejection of the cuckoo's egg.

ADAPTIVE VALUE OF EGG REMOVAL

Above, I have discussed risks that cowbirds might take when they steal eggs from host nests, i.e., mobbing by hosts, rejection of parasitism, and mistakenly removing their own eggs. However, parasites, and perhaps even hosts in some cases, presumably benefit from this behavior. Nevertheless, results of experiments conducted in the present study did not support two hypotheses proposed to explain this behavior. Firstly, experimentally parasitized Yellow Warblers were no more likely to reject a cowbird egg, whether or not a warbler egg was removed at the time of parasitism. This result, and those of other studies that have tested the host deception hypothesis, involving both cowbird and cuckoo hosts (Rothstein 1975a, Davies and Brooke 1978, Moksnes and Røskaft 1989), demonstrates that host-egg removal does not deceive hosts into accepting parasitic eggs. Secondly, the removal of only one egg from some Yellow Warbler nests, when they apparently can safely remove more than one without causing nests to be deserted, suggests that cowbirds remove one egg for a reason other than nourishment, and simply take advantage of a free meal. This behavior may enhance the cowbirds' own egg production over the season (see Payne 1974; Löhrl 1979).

The responses to experimentally reduced Yellow Warbler clutches revealed that nest abandonment was not simply a result of disturbance by potential predators or parasites (cf. Hamilton and Orians 1965) because only one control nest was deserted despite control nests being disturbed repeatedly. Nor was nest desertion simply a response to partial clutch losses because warblers abandoned one- and two-egg clutches only when eggs were removed from complete clutches but not during laying (see also Rothstein 1986, Armstrong and Robertson 1988). The results, however, may relate to the magnitude of egg loss in the two situations, rather than to nesting stage. During laying, one-egg clutches were tolerated, but the initial clutch size was never more than two, and one of these eggs was removed quickly. Three- and four-egg clutches (still in the laying stage) might be abandoned if they were suddenly reduced to one egg, as resulted from manipulations during incubation. Warblers possibly do not assess the overall value of their clutches until after they are complete.

If cowbirds removed eggs primarily for nourishment, they should be expected to remove more of them, possibly returning each day to remove the next-laid egg. However, this behavior would increase the chances of female cowbirds being intercepted at host nests, although waiting until the clutch is complete before returning to take the eggs all at once may not be an option. This is because cowbirds cannot carry off more than one egg at a time because they impale them on the tips of their mandibles. Either way several trips would be necessary to remove more eggs. Such disturbances at the nests might cause hosts to desert, although observations in the present study suggest that abandonment was a response to something other than, or in addition to, disturbance, assuming that warblers view in the same way visits to their nests by humans and cowbirds. Perhaps egg-removing cowbirds show restraint because they apparently could remove more eggs without causing hosts to desert. However, it is not known whether cowbirds have the time and ability to remove more eggs but do not do so.

Davies and Brooke (1988) concluded that the pattern of removal, and replacement, accurately predicted the observed behavior of the Common Cuckoo, which is usually to remove one host egg from each parasitized nest. These authors noted that Reed Warblers nearly always deserted clutches reduced to one egg, but never deserted a single warbler chick in naturally reduced broods. Thus, while the adult cuckoo is limited by the number of eggs it can remove, later when the cuckoo chick hatches it can eject all host eggs and nestlings without penalty. Davies and Brooke's (1988) results, and those of the present study, may not prove that cuckoos and cowbirds, respectively, remove host eggs to gain extra nourishment, but in the case of the Common Cuckoo, they nicely resolve the dilemma of why both adult and nestling cuckoos remove them.

Rothstein (1982) found that most passerine birds deserted their nests and laid new clutches in new nests if all, or all but one, of their eggs were removed. Experiments on accepter species (Common Grackle, *Quiscalus quiscula,* and Eastern Phoebe, *Sayornis phoebe*) revealed that birds do not count their eggs but instead "assess" their volume collectively (Rothstein 1982, 1986; see also Holcomb 1970). Interestingly, this assessment produces the paradoxical finding that phoebes are less likely to desert their four- to six-egg clutches if they are reduced to two cowbird eggs than to two of their own eggs. This may be because the two cowbird eggs represent a larger proportion of the original clutch volume (Rothstein 1982, 1986). Similarly, Yellow Warblers in the present study tended to desert clutches reduced to only one of their own eggs or to one cowbird egg, but incubated most clutches reduced to one warbler plus one cowbird egg and all clutches reduced to two cowbird eggs. Perhaps parental investment and its payoffs are important for hosts such as the Yellow Warbler. That Reed Warblers abandon a single egg but not a single chick strongly suggests that the schedule of parental investment is an important consideration in the "decision" to abandon nests.

Hann (1941) argued that if cowbirds removed eggs to obtain extra nourishment, unrelated to egg laying, we should expect both males and females to remove eggs from parasitized and unparasitized nests. This has not been observed (e.g., Scott 1977, this study). If the extra meal was tied to the need for calcium, we might expect only females to remove eggs. Indeed, evidence that free-ranging male cowbirds eat eggs is scarce and equivocal (e.g., Friedmann 1963:26; Sealy, unpubl. data), although experiments on captive cowbirds revealed males do have egg-pecking tendencies (Burgham and Picman 1989).

Despite the advantages gained from eating host eggs, we must still reconcile why usually only one egg is removed from a host nest. Livesey (1936) suggested that cuckoos remove an egg to test whether the clutch is fresh or incubated, thus ascertaining whether or not the nest is suitable for parasitizing. He noted that ingesting the eggs may simply be a convenient way of disposing of them. If the function of egg removal was to test the incubation status of host clutches, the parasite would be expected to eat a host egg *before* it commits its own egg to the nest. However, this is not the normal sequence of events in parasitic cuckoos. Cuckoos usually parasitize nests when they contain one or two host eggs, and normally remove and hold the egg in their bill while they lay their own egg (e.g., Wyllie 1975, Gärtner 1981). Thus, the egg is not eaten, i.e., "tested," until after they have laid their own and left the host's nest. In fact, cuckoos usually swallow host eggs whole (Wyllie 1975). As cowbirds often parasitize nests before the hosts have started to lay (e.g., Nolan 1978:372, Clark and Robertson 1981, this study), they appear not to be concerned with the incubation status of host clutches. If cowbirds tested nests randomly, we should expect more well-incubated eggs to be removed without being replaced, but they seldom remove eggs from incubated nests (e.g., Friedmann 1963, Nolan 1978: 377, this study).

Although the results of the present study (see also Rothstein 1986, Davies and Brooke 1988) reveal that cowbirds can remove more than one host egg without penalty, removing extra host eggs actually may be costly to the parasite. Davies and Brooke (1988) suggested that the more eggs that remain in a host nest, the less likely a second cuckoo will remove the first cuckoo's egg by chance. This is because cuckoo eggs usually mimic host eggs. But cowbird eggs do not mimic host eggs. Thus, they are "the odd ones out" in many host clutches and, as such, may be subject to selective predation (see Verbeek 1990). Although such an outcome would be disadvantageous for the cowbird, it might be advantageous for hosts that accept cowbird eggs, especially species whose productivity is not severely reduced by raising parasitic young. This hypothesis has not been tested (but see Mason and Rothstein 1987).

Lack (1954:42–43) argued that egg removal by laying female Great Spotted Cuckoos (*Clamator glandarius*) is adaptive because it reduces nestling competition. However, Hamilton and Orians (1965) pointed out that this argument fails to explain why laying female parasites remove eggs even though their nestlings evict their nestmates. These authors believed that because the young of some parasites resolve the competitive aspects of nest life by promptly evicting nestmates, the advantage of egg removal at the time of laying is not in reducing competition or crowding. Friedmann (1960:31) stated that "it is true that egg removal by the laying parasite sometimes eases the ensuing crowding and competition, but only to the extent of obviating what would otherwise be excessive crowding. In this connection, we cannot assume such a 'goal' as the original cause of the development of the egg removing habit, which merely seems to have been favored by natural selection by virtue of the result."

Enhanced incubation efficiency in parasitized clutches is the only explanation for host-egg removal that has received support (see Davies and Brooke 1988). This explanation indeed resolves the dilemma of parasites removing an egg when they parasitize nests, and when they hatch still evicting or outcompeting host eggs and young. In this context, without egg removal incubation might be prolonged in enlarged clutches, thus exposing nests to predation for a longer time, and possibly decreasing the survival rates of the young (Zimmerman 1983). As many parasitized nests, from which no host eggs were removed, have increased total clutch sizes and hence volume, incubation times could be increased because of the female's inability to maintain an adequately high egg temperature over all the eggs or the need for the female to be off her nest for longer inattentive periods of feeding in response to increased energy demands (Biebach 1981). This hypothesis provides a fruitful avenue for future investigation into the adaptive value of host-egg removal by brood parasites.

SUMMARY

Observations presented in this paper reveal that Brown-headed Cowbirds sometimes remove Yellow Warbler eggs in association with the act of parasitism, and although the stolen eggs are often eaten, the behavior seems to be a breeding strategy rather than a form of predation. However, whatever the function of host-egg stealing, present knowledge suggests that it is not a response to evolved host defenses, and hence does not represent an example of coevolution (Rothstein 1990).

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