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MALE NORTHERN ORIOLES EJECT COWBIRD EGGS: IMPLICATIONS FOR THE EVOLUTION OF REJECTION BEHAVIOR[1]

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Abstract. We experimentally parasitized 16 nests of the Northern Oriole (*Icterus galbula*) to determine the method of rejection of Brown-headed Cowbird (*Molothrus ater*) eggs, i.e., removal by spiking or by breaking the egg into pieces, and whether males remove cowbird eggs. Cowbird eggs were ejected from all 16 nests. We observed egg ejection at 14 of the parasitized nests. At six nests, cowbird eggs were ejected by breakage. Egg breakage did not result in more damage to Northern Oriole eggs than removal by spiking. For every cowbird egg ejected 0.38 Northern Oriole eggs disappeared or were damaged. Males removed the cowbird egg at two nests, females removed the cowbird egg at 11 nests, and at one nest both the male and female participated in the removal of the cowbird egg. At 13 nests, ejection was carried out by the bird that first inspected the nest after experimental parasitism. Damage to Northern Oriole eggs occurred proportionately more often during male ejections, which suggests males are less experienced egg ejecters, but this requires further testing. Because males can eject cowbird eggs the evolution of the rejecter trait may occur at an even faster rate than previously modeled.

Key words: Northern Oriole; Icterus galbula; *brood parasitism; egg ejection; puncture ejection; egg breakage; parasitism frequency.*

INTRODUCTION

Through experimentation, investigators of host defenses against parasitism by the Brown-headed Cowbird (*Molothrus ater*) have shown that most species tested respond uniformly to cowbird eggs placed into their nests (Rothstein 1975a, 1975b, 1977, 1982; Rich and Rothstein 1985; Hill and Sealy 1994; Sealy, unpubl. data). Most host species either "accept" or "reject" the cowbird's egg, although the responses of a few species vary according to nest stage (Rothstein 1976; Clark and Robertson 1981; Sealy, in press; see also Mason 1986). Most of the dozen or so known rejecter species (Rohwer and Spaw 1988; see also Rich and Rothstein 1985) carry cowbird eggs away from their nests held in their mandibles (grasp-ejection), whereas Cedar Waxwings (*Bombycilla cedrorum*), Northern Orioles (*Icterus galbula*) and Warbling Vireos (*Vireo gilvus*) remove the eggs by puncture-ejection, i.e., spiking or breaking the egg into pieces (Rothstein 1976, 1977; Rohwer et al. 1989; Sealy, unpubl. data).

In a study of the evolution of host defenses against brood parasitism, Rothstein (1975b) assumed that only females practice rejection behavior. He noted that whether males totally lack rejection behavior is an important question that remains critical to understanding the population genetics of the rejection trait. Nevertheless, Rothstein (1970) argued that because males of the known ejecter species play little or no role in incubation, ejection by males is unlikely. Other workers have also assumed or implied that only female hosts eject parasitic eggs (e.g., Davies and Brooke 1988, Lotem et al. 1992). Pinxten et al. (1991), however, recorded male European Starlings (*Sturnus vulgaris*) removing eggs laid parasitically by conspecifics but only before their own females had initiated their clutches.

In previous observations of Northern Orioles ejecting cowbird eggs, females carried out the ejections in all cases (Rothstein 1977, Rohwer et al. 1989). In this paper, we present observations of male Northern Orioles ejecting experimentally introduced cowbird eggs from their nests, describe the methods of ejection, i.e., spiking or breakage, used by males and females, quantify visitation frequencies of male Northern Orioles to their nests, and discuss the implications of egg ejection by males for the evolution of rejection behavior.

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METHODS

We located Northern Oriole nests in the forested dune ridge (see Sealy 1980, MacKenzie et al. 1982) that separates Lake Manitoba and Delta Marsh (50°11'N, 98°19'W), Manitoba. We experimentally parasitized 16 Northern Oriole nests (two nests in 1991, five in 1992, nine in 1993) by introducing one fresh Brown-headed Cowbird (hereafter cowbird) egg into each nest between 06:30 and 11:00 (Central Standard Time) during the egg-laying (four nests) and incubation (12 nests) stages. Female Northern Orioles were flushed from 12 nests at the time of parasitism. We did not remove an oriole egg from the manipulated nests because cowbirds do not always remove a host egg from nests they parasitize (Sealy 1992).

After parasitizing each nest, we watched it for one hour using a 20 power telescope positioned in a blind or concealed vantage point more than 20 m away from the nest tree. During the observation bouts, we recorded the birds' responses to the cowbird egg, distinguishing the sexes on the basis of plumage differences (Sealy 1979). We recorded the amount of time Northern Orioles were inside the nest before they ejected the cowbird egg. Upon ejection, we recorded the time and method of ejection (see below), the sex of the ejecter, and then observed the nest for an additional 15 min. Ejections were classified as either spiking (the egg was impaled on the tip of one or both mandibles) or breakage (the egg was spiked and broken into pieces and the fragments were removed one by one). We examined each nest after the observation bout to detect damaged Northern Oriole eggs (eggs with membranes pierced; see Røskaft et al. 1993) and for the next two days we visited the nest to record any Northern Oriole eggs removed after the cowbird egg had been ejected. If cowbird eggs were not ejected within the hour observation period, the nest was checked again after five hours to determine if the eggs were removed. We continued to inspect nests parasitized during egg laying to determine final clutch sizes.

We recorded visits male Northern Orioles made to their nests during three nest stages. This information was obtained from watches conducted during this and previous studies: nest building (22 May–2 June 1980; Sealy, unpubl. data), egg laying (Neudorf and Sealy 1994, this study) and incubation (this study). We calculated the number of visits (during which males looked into nests) per hour of observation.

TABLE 1. Northern Oriole nests (n = 16) subjected to experiments simulating cowbird parasitism at Delta Marsh, Manitoba.

Year and nest stage when parasitized[1,2]	Method of ejection[3] by male (M) or female (F)	Minutes to ejection[4]	Oriole eggs missing (M) or damaged (D)[5]
1991 I	S (F)	13	None
I	S (F)	36	None
1992 I	B (F&M)	25	None
L	S (F)	1	None
I	?	?	None
L	?	?	None
I	S (M)	2	2 M
1993 I	S (M)	1	1 D
L	B (F)	35	1 D
L	S (F)	3	None
I	S (F)	8	1 D
I	B (F)	2	None
I	S (F)	2	1 M
I	B (F)	4	None
I	B (F)	18	None
I	B (F)	5	None

[1] Experiments were conducted between 4 and 29 June. All experimental eggs used were real cowbird eggs.
[2] Nest stage: L = laying; I = incubation.
[3] Method of ejection of cowbird egg: S = spiked on open bill; B = breakage with successive removal of egg fragments. All cowbird eggs were ejected.
[4] Time from moment Northern Oriole started to peck cowbird egg until the egg or last piece of shell was removed. Ejection was not observed in two cases but the cowbird eggs were removed within 5 hr. At these nests, sex and method of ejection are unknown.
[5] A damaged Northern Oriole egg was removed from one nest. The other damaged eggs remained in the nests.

RESULTS

RESPONSES TO EXPERIMENTAL PARASITISM

Northern Orioles ejected the cowbird eggs at all 16 "parasitized" nests and 14 ejections occurred within one hour of parasitism (Table 1). Females ejected the cowbird egg at 11 nests, males at two nests and at one nest the male and female both participated in egg removal (see description below). The sex of the ejecter was undetermined at two nests where ejection occurred after the one-hour observation bout. Cowbird eggs were spiked with open beaks and removed from eight nests and at six nests the eggs were broken into pieces that were removed one by one. Except for one ejected cowbird egg that was dropped immediately beneath the nest, Northern Orioles carried the eggs 15–35 m away (Table 2).

In most (13/14) cases where ejection was observed, the first individual to return to the nest ejected the cowbird egg. In two of three instances where the male returned to the nest first after

TABLE 2. Methods used by host species to eject cowbird eggs.[1]

Host species	No. of observed[2] ejections by		Ejection by		Distance (m) ejected egg carried		References
	Grasping	Puncturing	Female	Male	<5	>5	
Eastern Kingbird *Tyrannus tyrannus*	23	0	23	0	0	23	Bazin (1991)
American Robin *Turdus migratorius*	1	3	4	0	1	3	Friedmann (1929:185), Nice (1944), Briskie et al. (1992), J.V. Briskie (pers. comm.)
Gray Catbird[3] *Dumetella carolinensis*	3	0	u	2	0	3	A. Wilson *in* Brewer (1840:242), Berger (1951)
Crissal Thrasher *Toxostoma dorsale*	2	0	u	u	0	2	Finch (1982, pers. comm.)
Brown Thrasher *T. rufum*	1	0	u	u	0	1	Rothstein (1970:67–70, 106)
Chalk-browed Mockingbird *Mimus saturninus*	2	0	u	u	0	2	Fraga (1982:30)
Warbling Vireo[4] *Vireo gilvus*	0	4	4	0	1	3	Sealy (unpubl. data)
Northern Oriole	0	20	18	2	1	15[5]	Rothstein (1977), Rohwer et al. (1989), S. Rohwer (pers. comm.), this study

[1] Eggs ejected from Chalk-browed Mockingbird nests were Shiny Cowbird eggs; eggs ejected from the other nests were Brown-headed Cowbird eggs.
[2] We considered egg breakage as a form of puncture-ejection.
[3] Alexander Wilson observed the ejection of two Brown Thrasher eggs that he had placed in a Gray Catbird nest. He observed that the male catbird "carried [the thrasher eggs] singly about thirty yards, and dropped them among the bushes." Wilson did not indicate how he was able to distinguish between the male and female catbird in this monomorphic species.
[4] At two nests, male Warbling Vireos attempted to eject the cowbird eggs. The vireos eventually ejected the cowbird eggs but the sex of the ejecter was not determined (Sealy, unpubl. data).
[5] Sample sizes differ in this category because observers could not always determine where the ejected egg was carried.

parasitism he ejected the cowbird egg whereas in all cases where females were first at the nest they ejected the egg. At the 14 nests where ejection occurred within one hour of parasitism, all birds began ejecting the cowbird egg within 12 min of returning to the nest and most (11/14) began to eject the egg within seconds.

Northern Orioles ate some of the eggs they broke before carrying away the eggshell. At one nest at least two pieces of eggshell fell over the edge of the nest and adhered to foliage whereby the female Northern Oriole sidled down and ate them. Other individuals carried the cowbird eggs to a branch or the ground and ate them there.

The mean time (±SE) of ejection from the moment a Northern Oriole started "working" at the cowbird egg until it removed the egg or last piece of eggshell was 11.0 ± 3.4 min (median = 4.5 min; $n = 14$). There was no significant difference in the amount of time taken to eject an egg by spiking ($\bar{x} = 8.3 \pm 4.2$ min; median = 2.5 min; $n = 8$) compared with breakage ($\bar{x} = 14.8 \pm 5.5$ min; median = 11.5 min; $n = 6$) (Wilcoxon two-sample test, $Z = -1.30$, $P = 0.19$). At five of the 16 nests, Northern Oriole eggs were damaged, or the egg(s) disappeared, presumably ejected by the Northern Oriole after they were damaged during ejection of the cowbird egg. Although not significant, loss or damage to eggs occurred more often during male ejections (2/2) than female ejections (3/11; Fisher exact test, $P = 0.13$; Table 1). Considering all 16 ejections of cowbird eggs, 0.38 Northern Oriole eggs were lost or damaged for every cowbird egg ejected. Removal of the cowbird egg by breakage did not result in more damage to Northern Oriole eggs than ejection by spiking (Fisher exact test, $P = 0.21$; Table 1).

OBSERVATIONS OF EJECTION BEHAVIOR

Rothstein (1977) presented observations of female Northern Orioles puncture-ejecting cowbird eggs. Below we describe the behavior of male Northern Orioles ejecting cowbird eggs from two nests and one instance where both a male and female removed an egg.

Males ejecting cowbird eggs. (1) We added a cowbird egg at 07:30 on 22 June 1992 to a nest containing five Northern Oriole eggs. One minute later, the male landed on the edge of the nest, peered into it for a few seconds, and left. At 07:37, the male returned and clung to the side of the nest and pecked at an object 6–7 times. He pierced an eggshell because he lifted his head four times, each time mandibulating and swallowing something. One minute later, the male was back in the nest and after 3–4 sec spiked the cowbird egg on its open beak and carried it more than 15 m from the nest and out of sight. Two Northern Oriole eggs eventually disappeared from this nest.

(2) At 07:50 on 14 June, we added a cowbird egg to a nest that contained four Northern Oriole eggs. Five minutes after the parasitism, the male went to the nest, clung to its edge, and pecked vigorously for 45 sec before changing positions. Back in the nest for about 30 sec, the male then left carrying the cowbird egg impaled on his open beak and dropped it more than 35 m into a marsh. One Northern Oriole egg that was punctured during the ejection process was gone by the next day.

Female and male removing a cowbird egg. At 06:40 on 19 June, we parasitized a nest containing four Northern Oriole eggs. Four minutes later the female entered the nest and pecked vigorously, leaving three minutes later carrying a piece of the eggshell. We inspected the nest and found the female had removed a piece of cowbird eggshell, leaving the egg with albumen spilling on to the nest lining. Two minutes later, the male entered the nest and immediately grasped the broken egg and carried it to a perch about 25 m away where he ate contents before dropping the shell. Two Northern Oriole eggs were slightly coated with albumen, but they and the others eventually hatched.

MALE NORTHERN ORIOLE VISITATION TO NESTS

Males inspected nest contents during nest-building, egg-laying and incubation stages (Table 3). Males visited nests most frequently per observation hour during the incubation stage. During visits males usually perched on the edge of the nest and peered in at the contents for less than one minute. Males occasionally brought food for females at all three nest stages. Twice males inspected nests immediately after they were checked by an observer.

TABLE 3. Visits to nests by male Northern Orioles.

Nest stage	No. of nests	Hours watched	Total visits by males	Visits per hour
Building	6	39.1	5	0.1
Laying	15	35.6	6	0.2
Incubation	12	8.9	8	0.9

DISCUSSION

EVOLUTION OF REJECTION BEHAVIOR

Ejection behavior characterizes all populations of the Northern Oriole that have been tested experimentally (Friedmann et al. 1977, Rothstein 1977, Rohwer et al. 1989, this study). Because the frequency of natural parasitism on Northern Orioles may be fairly high (Friedmann et al. 1977, Neudorf and Sealy 1994), selection for ejection behavior probably remains strong.

Rothstein (1975b) modeled the rate of increase of the rejecter trait assuming that a single autosomal gene was responsible for rejection behavior and that only females eject cowbird eggs. As a result he halved the selection coefficients for rejection because rejecter and accepter alleles would have the same fitness in males if they did not eject cowbird eggs. However, because males do eject, the selection coefficients will be twice as large as those used by Rothstein. The rejecter allele, therefore, should spread even more rapidly than previously calculated. This finding provides further support for the lack of species known to be at intermediate stages of rejection (Rothstein, pers. comm.).

Another consequence of males ejecting cowbird eggs is density-dependent selection (see Rothstein 1975b). As rejecters become more common the rate of replacement of accepter alleles declines because in situations in which only one mate is a rejecter and the other is an accepter, acceptance is not selected against. Thus the frequency of the accepter allele should decline at an increasingly slower rate until it eventually reaches zero. As cowbird eggs are accepted at some Northern Oriole nests (e.g., Nauman 1930, Friedmann 1963, Hobson and Sealy 1987), the rejecter allele may not yet have reached fixation in Northern Orioles.

Alternatively, acceptance could indicate that birds have misimprinted on cowbird eggs (Rothstein, pers comm.; also see Lotem et al. 1992). If female Northern Orioles learn the appearance of their own egg-type (see Rothstein 1978), and

if some naive females are parasitized early during their first nesting attempt, these females may learn to accept both cowbird and Northern Oriole eggs, and become accepters. Males must also learn to recognize the Northern Oriole egg-type in order to eject a cowbird egg. This would require males to visit the nest when the females are laying. Male Northern Orioles visited nests from building through incubation (Table 3), which would give them the opportunity to learn the oriole egg-type and also to eject foreign eggs.

Female Northern Orioles ejected more eggs than males (Table 1), but they are likely more familiar with cowbird eggs as they have a stronger asssociation with the nest. The low incidence of male ejections and the high proportion of Northern Oriole eggs damaged during ejection suggests males may be less experienced in ejecting cowbird eggs than females but this requires further testing. When first to arrive at the nest, male European Starlings ejected parasitic eggs 61% of the time compared with 98% by females. However, male ejections were related to nest stage, i.e., the closer females were to egg laying the less likely males ejected an egg and thus risked removing their own female's egg (Pinxten et al. 1991). Male European Starlings likely do not learn to recognize eggs but rather remove all eggs before their mates begin laying.

Most observed ejections of Brown-headed Cowbird and Shiny Cowbird (*M. bonariensis*) eggs have been of females removing the eggs (Table 2). Almost all known ejecter species are sexually monochromatic, which makes it difficult or impossible to identify the sex of unmarked individuals on the basis of plumage alone. Bazin (1991) determined that only female Eastern Kingbirds (*Tyrannus tyrannus*) removed experimentally introduced cowbird eggs, based on the birds' singing and incubation behavior.

Males must visit nests during egg laying and incubation if they are to eject cowbird eggs. In addition to Northern Orioles (Table 3), males of some other ejecter species are known to visit their nests at these times: American Robins (*Turdus migratorius*; pers. observ.), Gray Catbirds (*Dumetella carolinensis*; Slack 1976) and Warbling Vireos (Howes-Jones 1985; Sealy, unpubl. data). Males of these species might be expected to eject cowbird eggs. Indeed, Sealy (unpubl. data) watched a male Warbling Vireo attempt to puncture a cowbird egg that had been experimentally introduced into its nest. The cowbird egg was later ejected but which sex ejected it was not known. We expect that species in which males incubate or feed the female on the nest will be the most likely to have evolved male egg ejection.

METHODS OF EJECTION

All Northern Orioles observed removed cowbird eggs by puncturing them (as opposed to grasping) and almost half of these eggs were removed after they had been broken into pieces. Breakage of Northern Oriole eggs likely occurs when an individual fails to spike the egg on the tip of its bill. Rensch (1924) was apparently the first to provide evidence that some hosts break parasitic eggs in the nest and then remove them piecemeal. He found yolk on some eggs that remained in the nest after an experimentally introduced egg had been ejected.

Rothstein (1970) believed that breaking apart an egg in a nest would be dangerous to the host's own eggs, as the contents might coat the host's eggs and cause them to stick together, or to the nest. Implicitly, such eggs likely would not hatch. In the present study, we found yolk on Northern Oriole eggs in two nests that remained after cowbird eggs had been ejected, by spiking in one nest and breakage in the other. At one of these nests, part of the lining adhered to two eggs but still they hatched. Ingestion of some or all of the cowbird egg's contents might minimize the chances of soiling the host's own eggs and individuals certainly gain extra energy from the eggs in the process (see Scott et al. 1992). Furthermore, there was no significant difference in the number of damaged or missing Northern Oriole eggs at nests where eggs were removed by spiking compared with breakage (Table 1). These observations indicate that egg breakage may be a relatively cost-free method of removing cowbird eggs from nests.

DETERMINATION OF PARASITISM FREQUENCY

We detected parasitism on 3.3% of 153 nests monitored from 1974–1992 (Neudorf and Sealy 1994). The rapidity with which Northern Orioles usually eject cowbird eggs (Table 1) probably caused us to underestimate the parasitism frequency (see also Scott 1977). Neudorf and Sealy (1994) witnessed parasitism on two of 13 (16%) Northern Oriole nests watched just before sunrise, which is the time parasitism normally occurs (see also Scott 1991). Female Northern Orioles at both of these nests ejected the cowbird eggs within 40 min of parasitism (Neudorf and Sealy 1994).

Friedmann et al. (1977) suggested that searches for cowbird eggs beneath nests may reveal cowbird parasitism on Northern Orioles that would otherwise not be detected. In 13 of 14 ejections we observed, Northern Orioles carried the cowbird eggs several meters from the nests. Rothstein (1977) also recorded cowbird eggs dropped by Northern Orioles several meters from their nests, but other workers have found them directly underneath nests (Friedmann 1963, Smith 1972). Observations indicate that other rejecter species also drop ejected cowbird eggs several meters from their nests (Table 2). Direct observations or video-taping of nests of ejecter species such as Northern Orioles during the minutes before sunrise when cowbirds normally parasitize nests (Scott 1991, Neudorf and Sealy 1994) provide the only reliable way of determining the frequency of cowbird parasitism on ejecter species.

In summary, our observations indicate that male Northern Orioles eject cowbird eggs. Whether males of other species also remove cowbird eggs is crucial to our understanding of the evolution of rejection behavior. Direct observations of banded individuals at parasitized nests are required before this important question can be addressed thoroughly.

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