

## MECHANISMS OF EGG ACCEPTANCE BY MARSH-DWELLING BLACKBIRDS

CATHERINE P. ORTEGA AND ALEXANDER CRUZ

Department of Environmental, Population and Organismic Biology, B-334,  
University of Colorado, Boulder, CO 80309-0334

**Abstract.** The parameters of egg acceptance in Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) were investigated by introducing into their nests various eggs and objects. With the exception of miniature eggs, both species accepted all eggs, real and artificial, and rejected all nonegg-shaped objects. Egg shape and size were necessary components of egg acceptance whereas color and markings were not. The rejection of nonegg-shaped objects as large as Brown-headed Cowbird (*Molothrus ater*) eggs demonstrated that inability to remove cowbird eggs was not responsible for blackbird acceptance responses. Nests parasitized before the onset of egg laying did not increase the probability of either the egg being rejected or the nest being inactive.

**Key words:** Brown-headed Cowbird; Red-winged Blackbird; Yellow-headed Blackbird; accepters; rejecters; icterids; *Molothrus ater*; *Agelaius phoeniceus*; *Xanthocephalus xanthocephalus*; brood parasitism; Colorado.

### INTRODUCTION

Brood parasites usually have a detrimental impact on the reproductive success of their hosts. Selection should, therefore, favor defenses against brood parasitism, particularly in species regularly subjected to parasitism, whether interspecific or intraspecific (Rothstein 1975a, 1975b; Lanier 1982). The most common defense is rejection of the parasitic egg (Friedmann 1929, 1963; Robertson and Norman 1976, 1977; Finch 1982; Cruz et al. 1985), which may occur through (1) ejection of the egg, (2) puncturing the egg, (3) nest desertion, or (4) constructing a new nest floor over the parasitized clutch.

North American species, thus far experimentally parasitized, divide into two discrete groups: accepters and rejecters. As defined by Rothstein (1975b, 1977, 1978, 1982a, 1982b), accepter species are those in which all, or nearly all, individuals accept nonmimetic eggs, and rejecter species are those in which all, or nearly all, individuals reject nonmimetic eggs. Although relatively few hosts and potential hosts have been tested for acceptor/rejecter status, no species intermediate between accepters and rejecters have been reported (Rothstein 1975b, 1976, 1977, 1978, 1982a, 1982b; Rich and Rothstein 1985).

Since rejecters tend to eject parasitic eggs from

their nests before investigators can detect them, the rate of egg ejection can only be detected through experimental parasitism (Rothstein 1975b, 1977; Finch 1982). Extensive experiments, using a variety of eggs and objects, may elucidate the parameters of acceptance and provide insight as to why birds accept alien eggs.

Because of their relative abundance in North America, Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) provide an opportunity to experiment on a large number of nests in a relatively short period of time. The comparison between two related accepter species, nesting in the same marshes, is of particular interest since only one, the redwing, is parasitized by the Brown-headed Cowbird (*Molothrus ater*) (Bailey 1965, Friedmann et al. 1977). The incidence of parasitism on the redwing has been reported as low as 1.6% (Brown and Goertz 1978) and as high as 54% (Hergenrader 1962). The rate varies geographically, locally, annually, and with habitat (Hanka 1979, Facemire 1980, Linz and Bolin 1982).

The purpose of this study was to identify the parameters of egg acceptance in blackbirds and to suggest why they may tolerate the presence of parasitic eggs in their nests. In addition, it is important to determine whether the apparent lack of parasitism on the yellowheads is due to rejection of the parasitic eggs or to actual absence of parasitism.

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## STUDY AREAS AND METHODS

### STUDY AREAS AND EXPERIMENTAL PROCEDURES

We conducted investigations from 1984 through 1986 within nine cattail (*Typha latifolia* and *T. angustifolia*) marshes and two flooded willow (*Salix* sp.) stands in Boulder County, Colorado. Red-winged Blackbirds nested in all of the study sites, and Yellow-headed Blackbirds nested in four.

Blackbird nests were located and identified with coded tags. Visits to each nest were made every 1 to 3 days. At each visit, nest contents were recorded, and, to aid in assessing reproductive success, nestlings were weighed and measured. In 1985 and 1986 we introduced 112 experimental models to yellowhead nests and 329 to redwing nests during the egg-laying stage and early in incubation. Additionally, we added 36 experimental models to redwing nests during the pre-egg-laying stage—the period between completion of nest construction and the beginning of egg laying—which was typically 1 to 3 days. Limited sample size of yellowhead nests in the pre-egg-laying phase prevented us from adding experimental models during this phase. Twenty-three yellowhead nests and 63 redwing nests failed before the completion of experiments and were not included in our analyses of acceptance/rejection experiments. No nest was used for more than one experiment, and only one model was added per nest, except for tests using two and three cowbird eggs.

### MODELS

Artificial plastic eggs were filled with water, sealed, and painted with acrylic polymer paints to simulate the density and coloration of real eggs. The dimensions, colors, and markings are listed in Table 1. We also used a series of nonegg-shaped models described in Table 2.

### CRITERIA USED TO CLASSIFY RESPONSES

Responses were scored as "accepted" if the model remained undamaged in the active nest for 5 days and "rejected" if the model disappeared from the nest and the host eggs remained. For both the yellowhead and redwing, there was no significant difference in the rate of abandonment between control nests and experimental nests; therefore, we considered abandoned nests as nest failures rather than a form of rejection and did

not include them in the statistical analyses of acceptance/rejection experiments. Twenty yellowhead nests were abandoned at the rates of 5.0% in control nests and 7.1% in experimental nests ( $\chi^2_c = 0.306$ , Yate's correction,  $P < 0.75$ ). Twenty-seven redwing nests were abandoned at the rates of 4.2% in control nests and 4.3% in experimental nests ( $\chi^2_c = 0.037$ , Yate's correction,  $P < 0.90$ ).

### CRITERIA USED TO CLASSIFY PARASITISM

For the purpose of assessing reproductive success, a nest was considered parasitized if it contained a real cowbird egg(s) regardless of whether we or a cowbird introduced it. All real cowbird eggs introduced by us were taken directly from redwing nests in the same study area and introduced while still warm from incubation. Eggs which were transferred between nests were the same age within 2 days. Although nests from which we removed a cowbird egg(s) were initially parasitized, we considered them to be nonparasitized for the purpose of determining how the presence of a cowbird egg affects host success.

### STATISTICAL ANALYSES

For experimental tests of acceptance or rejection of introduced eggs and objects, binomial probabilities were computed (Zar 1984). To check for differences in mean nest success of hosts, the two-tailed Mann-Whitney *U*-test was employed (Zar 1984). For all tests,  $P < 0.05$  was considered significant.

## RESULTS

### PRE-EGG-LAYING STAGE

Reactions to eggs added to redwing nests before egg laying are listed in Table 3. They accepted 92% of the cowbird and 79% of the redwing models.

### EGG-LAYING STAGE

Reactions to eggs and objects added to blackbird nests during the egg-laying stage and early incubation are shown in Tables 4 and 5. All real eggs, both cowbird and conspecific, were accepted by both species. Chicks hatching from the cross-fostered eggs were cared for, and most, which were not preyed upon, fledged. All cowbird models were accepted by redwings (Table 4), and nearly all were accepted by yellowheads (Table 5). There was no difference when one, two,

TABLE 1. Egg models added to blackbird nests in Boulder County, Colorado, 1985 and 1986.

Model	Dimensions (mm)	Background color	Markings
<b>Artificial eggs</b>			
<b>Varied colors</b>			
Miniature	12.9 × 9.6	Flesh Color #5*	None
	12.9 × 9.6	Spectrum Orange #17*	None
	12.9 × 9.6	Orange Yellow	None
	12.9 × 9.6	Cobalt #68*	None
	12.9 × 9.6	Spinel Pink #108C*	None
Oversized	33.4 × 25.3	White	None
	33.4 × 25.3	Pastel Pink	None
	33.4 × 25.3	Pastel Blue	None
	33.4 × 25.3	Pastel Yellow	None
Small	20.1 × 16.1	Rose Pink #108D*	Maculated with Burnt Sienna #132* and Poppy Red #108A*
	20.1 × 16.1	Pastel Peach	Maculated with Burnt Sienna #132* and Poppy Red #108A*
	20.1 × 16.1	Light Sky Blue #168D*	Maculated with Burnt Sienna #132* and Poppy Red #108A*
	20.1 × 16.1	Light Sky Blue #168D*	None
	20.1 × 16.1	Pale Yellow	None
	20.1 × 16.1	Pale Yellow	Maculated with Burnt Sienna #132* and Poppy Red #108A*
	20.1 × 16.1	White	None
	20.1 × 16.1	White	None
<b>Cowbird models</b>			
Small	20.1 × 16.1	Off white with blue hue	Maculated with Mars Brown
Large	26.1 × 17.2	Off white with blue hue	Maculated with Mars Brown
<b>Redwing models</b>			
Miniature	12.9 × 9.6	Pale greenish blue	Spotted and scrawled with Sepia #219*
Large	26.1 × 17.2	Pale greenish blue	Spotted and scrawled with Sepia #219*
<b>Real eggs</b>			
Redwing	25.0 × 18.0† (n = 1,614)	Pale greenish blue	Spotted and scrawled with browns or black
Yellowhead	26.3 × 18.1† (n = 842)	Pale greenish gray	Heavily speckled with browns
Cowbird	21.1 × 16.3† (n = 56)	White or off white	Heavily speckled with browns

\* Colors compared to the *Naturalist's Color Guide* (Smithe 1975).

† Average dimensions.

TABLE 2. Nonegg-shaped models added to blackbird nests in Boulder County, Colorado, 1985 and 1986.

Model	Dimensions (mm)	Color
Pom-pom	16.4 × 16.4	Sky Blue #168C*
Pom-pom	16.4 × 16.4	White
Large, round, smooth bead	20.1 × 20.1	Sky Blue #168C*
Large, round, smooth bead	20.1 × 20.1	White
Round bumpy bead	15.3 × 15.3	Turquoise Blue #65*
Round bumpy bead	15.3 × 15.3	White
Small, round, smooth bead	10.2 × 10.2	White
Oblong	19.2 × 6.0	Cyan #164*
Oblong	19.2 × 6.0	White
Star-shaped	18.2 × 18.2	Cerulean Blue #67*

\* Colors compared to the *Naturalist's Color Guide* (Smithe 1975).

TABLE 3. Percent (and number) of reactions of Red-winged Blackbirds to eggs added to their nests before egg laying in Boulder County, Colorado, 1985 and 1986.

Model introduced	Accept	Reject	<i>P</i> *
<b>Artificial eggs</b>			
Large cowbird models	92% (12)	8% (1)	0.00159
Large redwing models	79% (11)	21% (3)	0.02222

\* Binomial probability.

or three models were added at once (Table 4). For both species, there was no significant difference between the acceptance and rejection responses to miniature eggs. Acceptance rates for oversized eggs were 82% and 100%, respectively, for redwings and yellowheads. The redwings accepted artificial redwing eggs which were similar in size to their own but rejected 67% of the miniature redwing models. Rejection responses to non-egg-shaped objects were 100% for the yellowhead and 98% for the redwing (Tables 4 and 5).

#### REPRODUCTIVE SUCCESS

Table 6 shows that a mean of 1.1 yellowheads fledged per nonparasitized nest and 0.9 fledged per parasitized nest ( $P = 0.753$ , Mann-Whitney  $U$ -test). A mean of 0.8, 1.0, and 1.1 redwings fledged per nonparasitized nest and a mean of 0.6, 1.5, and 0.7 fledged per parasitized nest in

1984, 1985, and 1986, respectively (Table 7). When only successful nests—nests that fledged at least one host—were considered (Table 8), a mean of 2.4, 2.9, and 2.9 redwings fledged per nonparasitized nest and a mean of 1.3, 2.4, and 1.4 redwings fledged per parasitized nest in 1984, 1985, and 1986, respectively.

#### DISCUSSION

Ejection behavior may have originated from the need for nest sanitation and predation avoidance (Swynnerton 1918, Tinbergen et al. 1962). Typically, birds carry fecal sacs, egg shells, and dead nestlings away from the nest site in the beak so as not to reveal the nest location to predators (Tinbergen et al. 1962, Rothstein 1975a). Rothstein (1975a) suggested that the motor patterns involved in nest sanitation are virtually identical to those used in egg ejection and may have been a preadaptation to the egg ejection response.

TABLE 4. Percent (and number) of reactions of Red-winged Blackbirds to eggs and objects added to their nests during the egg-laying phase or early incubation in Boulder County, Colorado, 1985 and 1986.

Model introduced	Accept	Reject	<i>P</i> *
<b>Artificial eggs</b>			
Varied colors			
Miniature	56% (30)	44% (23)	0.06921 ns
Oversized	82% (9)	18% (2)	0.02686
Small	71% (15)	29% (6)	0.02590
Cowbird models			
Small	100% (12)		0.00024
Large	100% (20)		0.00000
2 Large†	100% (14)		0.00006
3 Large†	100% (15)		0.00003
Redwing models			
Miniature	33% (3)	67% (6)	0.16406 ns
Large	83% (19)	17% (4)	0.00106
Real eggs			
Redwing	100% (10)		0.00098
Cowbird	100% (7)		0.00781
Nonegg shapes			
Varied shapes	2% (1)	98% (43)	0.00000

\* Binomial probability.

† Refers to two and three eggs added to one nest.

TABLE 5. Percent (and number) of reactions of Yellow-headed Blackbirds to eggs and objects added to their nests during the egg-laying phase or early incubation in Boulder County, Colorado, 1985 and 1986.

Model introduced	Accept	Reject	P*
<b>Artificial eggs</b>			
<b>Varied colors</b>			
Miniature	70% (7)	30% (3)	0.11719 ns
Oversized	100% (4)		0.06250 ns
<b>Cowbird models</b>			
Small	88% (28)	12% (4)	0.00001
Large	100% (11)		0.00049
<b>Real eggs</b>			
Yellowhead	100% (3)		0.12500
Cowbird	100% (23)		0.00000
<b>Nonegg shapes</b>			
Varied shapes		100% (6)	0.01563

\* Binomial probability.

Ejection behavior may also have been enhanced in some species, such as the Blue Jay (*Cyanocitta cristata*), due to their egg-robbing habits.

For a bird to become a rejecter species, all that may be needed is for the motor pattern of nest sanitation to be released early during incubation and in response to alien eggs rather than refuse. Yet, even though brood parasites typically have a detrimental impact on the reproductive success of their hosts, most host species continue to accept cowbird eggs. However, several factors must be considered in the determination of why birds should tolerate the presence of a parasitic egg in their nest. These factors include (1) egg ejection capability, (2) the ability to discriminate their own eggs from others, (3) the degree to which they are parasitized, (4) the effects of parasitism, and (5) the cost associated with rejection.

#### EJECTION CAPABILITY

Typically, ejected eggs are carried away whole from the nest between the mandibles. Ejections may also be accomplished by spiking the egg

TABLE 6. Mean number ( $\pm$ SD) of Yellow-headed Blackbirds fledged per nest, Boulder County, Colorado, 1986.

	Mean number fledged $\pm$ SD	n	Significance*
Nonparasitized nests	1.1 $\pm$ 0.51	247	P = 0.753
Parasitized nests	0.9 $\pm$ 1.02	22	Z = 0.314

\* Mann-Whitney U-test, 2-tailed.

before it is carried from the nest, but this behavior has been observed in only a few species that have small beaks or construct pendulous nests from which it may be more difficult to remove eggs intact (Rich and Rothstein 1985). Since ejection capability is limited by the host's ability to grasp the egg and by the egg width, some birds may accept foreign eggs involuntarily because they are physically incapable of removing them (Rothstein 1975a). By comparing the beak length to egg width ratios of acceptor and rejecter species, Rothstein (1975a) was able to estimate ejection ability of acceptor species. His analyses indicated that nearly all acceptors may be capable of ejecting cowbird eggs.

The rejection response for objects other than eggs and live nestlings should be present in all birds which practice nest sanitation. Therefore, the addition of such objects, in which the smallest dimensions are as large as the width of a cowbird egg, should clearly demonstrate the ability of a bird to remove a cowbird egg, providing that the object is as difficult to handle as an egg. The addition of all nonegg-shaped objects listed in Table 2 resulted in ejection by both blackbird species (Tables 4 and 5). Some of these objects, such as pom-poms, were easy for the birds to handle; however, the round beads, both bumpy and smooth, were as difficult, or more so, to handle than a cowbird egg. Holes in the beads were less than 1.5 mm in diameter, and beads could not be removed by spiking or by placing the beak in the hole; therefore, the birds must have ejected these objects by picking them up between their mandibles. We were thus able to

TABLE 7. Mean number ( $\pm$ SD) of Red-winged Blackbirds fledged per nest, Boulder County, Colorado, 1984, 1985, and 1986.

	Year	Mean number fledged $\pm$ SD	<i>n</i>	Significance*
Nonparasitized nests	1984	0.8 $\pm$ 1.26	121	<i>P</i> = 0.865
Parasitized nests	1984	0.6 $\pm$ 0.73	9	<i>Z</i> = -0.170
Nonparasitized nests	1985	1.0 $\pm$ 1.48	176	<i>P</i> = 0.024
Parasitized nests	1985	1.5 $\pm$ 1.36	30	<i>Z</i> = -2.260
Nonparasitized nests	1986	1.1 $\pm$ 1.51	299	<i>P</i> = 0.801
Parasitized nests	1986	0.7 $\pm$ 0.82	15	<i>Z</i> = 0.253

\* Mann-Whitney *U*-test, 2-tailed.

determine that inability to remove cowbird eggs was not responsible for egg acceptance response in both birds.

#### THE PARAMETERS OF ACCEPTANCE

Our results showed that egg shape was a necessary component of acceptance, whereas non-egg-shaped objects consistently elicited ejection responses. Egg size was also an important parameter of acceptance. Tables 4 and 5 show that nearly all eggs the size of, or close to the size of, their own eggs were accepted.

Oversized eggs were also accepted by redwings (Table 4). The acceptance of oversized eggs was probably not due to ejection inability since the ejection of two such eggs demonstrated the ability of the redwings to remove them. Tinbergen (1951) and Beer (1961) found that some birds preferentially incubated eggs larger than their own. On the other hand, Holcomb (1970) found that only two out of seven (28.6%) redwings incubated eggs larger than their own, but he did not view his experiments in the context of brood parasitism, and his methods differed from ours in that he gradually removed all host eggs. Although yellowheads accepted all oversized eggs added, the sample size was too low to generate any definitive conclusions.

Miniature eggs were not accepted at a signifi-

cant rate by either blackbird (Tables 4 and 5), and the redwings rejected more, albeit not significant, miniature eggs mimicking their own. This may suggest that the occurrence of runt eggs in the redwing population is more frequent than Koenig (1980) and Rothstein (1973) reported. The miniature egg models (12.9  $\times$  9.6 mm) were only slightly smaller than one runt egg (15.3  $\times$  12.7 mm) we found and three (17.39  $\times$  13.74, 17.20  $\times$  13.60, and 14.19  $\times$  12.5 mm) which Rothstein (1973) measured.

The consistent egg ejection rate within size classes (Tables 4 and 5), regardless of color, markings, or whether the introduced egg was real or artificial, suggests that color and markings of eggs were not responsible for eliciting acceptance responses whereas size and shape were. In contrast, for Northern Orioles (*Icterus galbula*), American Robins (*Turdus migratorius*), and Gray Catbirds (*Dumetella carolinensis*), all rejecter species, maculation was more important than size in eliciting rejection (Rothstein 1982a).

#### EXPERIMENTS PRIOR TO THE ONSET OF EGG LAYING

A significant proportion of artificial redwing and cowbird eggs were accepted by redwings prior to the onset of their own egg laying (Table 3). Friedmann (1963) and McGeen (1971) suggested that

TABLE 8. Mean number ( $\pm$ SD) of Red-winged Blackbirds fledged per successful nest, Boulder County, Colorado, 1984, 1985, and 1986.

	Year	Mean number fledged $\pm$ SD	<i>n</i>	Significance*
Nonparasitized nests	1984	2.4 $\pm$ 0.97	39	<i>P</i> = 0.249
Parasitized nests	1984	1.3 $\pm$ 0.50	4	<i>Z</i> = 1.243
Nonparasitized nests	1985	2.9 $\pm$ 0.93	60	<i>P</i> = 0.034
Parasitized nests	1985	2.4 $\pm$ 0.90	19	<i>Z</i> = -2.125
Nonparasitized nests	1986	2.9 $\pm$ 0.99	111	<i>P</i> = 0.000
Parasitized nests	1986	1.4 $\pm$ 0.54	7	<i>Z</i> = 3.509

\* Mann-Whitney *U*-test, 2-tailed.

nest desertion is more likely to occur if the parasitic egg is laid before the host eggs. A typical interpretation (Norris 1947, Friedmann 1963, McGeen 1971) of host eggs not appearing is that the nest has been abandoned due to presence of the cowbird egg or that birds have a weaker bond to their nests at this stage. Several problems exist with such interpretation. The nest might never have been active, the nest might have been active but emptied by predators, or the nest may have been abandoned for reasons unrelated to cowbird activity. The number of inactive nests containing only cowbird egg(s), which remain inactive, will not reflect the frequency of this occurrence unless it is compared to the number of nests which become active subsequent to parasitism. To make this comparison, the sequence of all eggs laid in the parasitized nests of a given population must be known. Since this is not usually known, experimental parasitism allows a more cautious interpretation. By adding artificial eggs to redwing nests before egg laying, we were able to calculate the ratio of nests which subsequently became active to those which did not. The ratio of active to inactive parasitized nests was 13:2 ( $P = 0.003$ ) with the cowbird model, 14:1 ( $P = 0.000$ ) with the redwing model, and 17:21 ( $P = 0.104$ ) for the nests which were not experimentally parasitized (binomial probability). This suggests that the presence of an egg in the nest before the onset of redwing egg laying did not increase the likelihood of nest abandonment.

Nest substrate and location did not bias the experiments because we used two nest substrates (willows and cattails) and various study sites with equal frequencies. All experiments were conducted prior to the second week of June, whereas we continued to observe control nests beyond this time. However, the ratio of nests which became active to those which did not was 13:16 ( $P = 0.13$ ) before June 7 and 4:5 ( $P = 0.25$ ) after June 7 (binomial probability). Therefore, the time at which an experiment was conducted did not affect the probability that a nest would eventually become active.

In species such as the redwing that accept alien eggs and care for them as they do for their own, the presence of an egg in their nest, before they have laid any of their own, may deceive them into believing that they have some amount of investment in addition to that of nest construction. Wiley (1982) showed that Yellow Warbler (*Dendroica petechia*) nests were less likely to be

abandoned as parental investment, or number of eggs increased.

#### SELECTION PRESSURE

The selective advantage of egg rejection is determined by the degree of parasitism and the reproductive loss due to parasitism. When parasitism is rare or the reproductive loss is low, individuals possessing the rejection response to foreign eggs will not have a selective advantage; therefore, the response will not become common. However, even when the selective advantage is high, all species may not respond adaptively because the necessary genetic material for the rejection response may not have appeared in the population (Rothstein 1975a).

The Yellow-headed Blackbird is rarely parasitized (Friedmann et al. 1977), and we have never observed it to be parasitized ( $n = 351$  nests). Reasons for the lack of parasitism are presently under investigation by Ortega and Cruz. Additionally, the Yellow-headed Blackbirds which were experimentally parasitized did not suffer a significantly greater reproductive loss than did the control group. There was no significant difference between the mean number of yellowheads fledged per parasitized and nonparasitized nest (Table 6). It is unlikely, therefore, that even if the yellowheads were parasitized they would become a rejecter species.

The Red-winged Blackbird, on the other hand, is a frequent cowbird host (Friedmann et al. 1977, Hanka 1979, Facemire 1980, Linz and Bolin 1982). But, like the yellowhead, with respect to the number of hosts fledged per nest, in our study areas it did not suffer a significant loss due to the cowbird. There were differences between years, however, so each year must be treated separately. In 1984 and 1986 there were no significant differences between the number of redwing hosts fledged per nonparasitized nest and per parasitized nest (Table 7). In 1985, significantly more hosts fledged per parasitized nest than per nonparasitized nest. This difference may have been due to cowbirds selecting relatively "safe" nests, constructed in willows, in which to lay their eggs (Kittleman and Cruz 1986). In all 3 years, cowbirds preferentially selected willow nests to parasitize, but in 1984 the parasitism rate was only 6% as compared with 13% in 1985 and 9% in 1986. In 1984 and 1986 most of the willow nests (and, therefore, many parasitized nests) were flooded out due to the fluctuating water level of

Boulder Reservoir. When the predation factor was removed, as shown in Table 8, significantly more hosts fledged per nonparasitized nest.

The analysis of successful nests serves to demonstrate that individual redwings suffer reproductive loss due to cowbird parasitism and that there is a selective advantage for these individuals to become rejecters. But for the population as a whole, since the rate of parasitism is moderately low and because the few parasitized individuals produce young of their own, the selective advantage is probably not high enough to select for rejection behavior.

Redwings are extremely aggressive towards intruding cowbirds at their nest sites. Robertson and Norman (1977) argue that aggression is a more effective defense than egg rejection because it denies cowbirds access to the nest. It could be that this is, indeed, an effective defense strategy for the redwing, and perhaps this is why the rate of parasitism is kept so low. If this is so, there might not be reason to employ a second defense of egg ejection, particularly if there are costs associated with the act of ejection.

#### THE COST OF EJECTION

We observed no breakage of host eggs when either species ejected artificial eggs or objects. But since no real eggs were ejected, we could not determine whether this would cause damage to other eggs in the nest. If a real egg were to be broken and the contents spilled during the process, the other eggs would probably adhere to the nest, increasing the possibilities of predator detection of the nest. In cases where we have observed egg damage, more serious than a hair-line crack, due to partial predation or unknown reasons, the nests have always failed.

Some species may accept cowbird eggs because they cannot clearly discriminate them from their own. If a bird questions the identity of the eggs, it may be more prudent to accept all eggs in the nest.

The smaller an egg is relative to the bill of the bird ejecting it, the less chance there is of breakage. It is interesting to note that miniature eggs were ejected regularly by both species, whereas the larger eggs were accepted (Tables 4 and 5). Mason and Rothstein (1986) also found that smaller eggs were rejected more by the Rufous Hornero (*Furnarius rufus*), and Rothstein (1982a) found that, for the American Robin, small egg size was the most important parameter in elic-

iting rapid rejections within one day. However, there is no direct evidence that indicates a cost associated with egg ejection.

It is also interesting to note that species known to be rejecters—Western Kingbird (*Tyrannus verticalis*), Eastern Kingbird (*T. tyrannus*), Blue Jay, American Robin, Gray Catbird, Brown Thrasher (*Toxostoma rufum*), Crissal Thrasher (*T. crissale*), Sage Thrasher (*Oreoscoptes montanus*), Cedar Waxwing (*Bombycilla cedrorum*), and Northern Oriole (Rothstein 1975a, 1975c, 1976, 1978, 1982a; Finch 1982; Rich and Rothstein 1985)—with the exception of the waxwing, are aggressive and large relative to the cowbird; they all have large enough bills to remove cowbird eggs without breakage. Waxwings have small bills and remove cowbird eggs by spiking them, as do orioles, presumably because the pendulous nests of the latter make it difficult to remove eggs intact. Both species may damage their own eggs while removing the parasite eggs (Rich and Rothstein 1985).

It may be that smaller acceptor species, such as vireos and warblers, even if they can gape their bills wide enough to accommodate a cowbird egg, do not have the muscular control to avoid breaking the egg. The cost of egg ejection may thus be what forces such species to remain accepters. An alternative defense for these smaller species is to construct a new nest floor over the parasitized clutch, as the Yellow Warbler often does (Friedmann 1963).

#### SUMMARY

Prior to our study, the ability of acceptor species to remove cowbird eggs had not been experimentally tested, and the acceptor/rejecter status of the yellowhead had not been known. We determined that even though both Red-winged and Yellow-headed blackbirds accept cowbird eggs, they are capable of removing them. For both blackbirds, egg shape was a necessary component for eliciting the acceptance response, whereas color and maculation were not. All nonegg-shaped objects were ejected, and the addition of objects as large as cowbird eggs can serve as an important method of determining whether birds are capable of removing cowbird eggs from their nests. Miniature experimental eggs were rejected frequently, suggesting that the cost of removing smaller eggs is relatively lower and that potential breakage of larger eggs during removal may be a factor driving the acceptance response. There is little



selective pressure on either species to become egg rejecters because for the yellowhead, they are not parasitized and for the redwing, they are parasitized only modestly and are successful in producing young whether or not they are parasitized.

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