Defences Against Brood Parasitism
in the Eastern Kingbird

by

Ronald C. Bazin

A thesis
presented to the University of Manitoba
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RONALD C. BAZIN

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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Ronald C. Bazin

John R. Williams, in 1935, tells of a kingbird which repeatedly attacked a low-flying airplane. He says: "The courage and audacity of this bird in attacking a noisy and relatively huge airplane was certainly extraordinary."

<div align="right">Bent (1942)</div>

ABSTRACT

Two potential anti-brood parasite strategies, egg rejection and nest defence, were examined experimentally in eastern kingbirds, *Tyrannus tyrannus*, from 1987-1990 at Delta Marsh, Manitoba. Kingbirds rejected 87 of 88 brown-headed cowbird, *Molothrus ater*, eggs placed experimentally into their nests from laying through incubation, thus demonstrating the species' status as a rejector. Grasp ejection was the mechanism kingbirds used to remove cowbird eggs at all 23 nests where ejection was observed. Cowbird eggs were ejected, whether they were the only egg in the nest or they outnumbered host eggs, and regardless of nest stage. However, ejection time, i.e. length of time an egg remained in the nest before being ejected, varied with nest stage, being longest early in the laying stage, and shorter before and after. Gray catbird, *Dumetella carolinensis*, eggs, which differed considerably from cowbird and kingbird eggs, were ejected from all 10 kingbird nests. Results demonstrated that kingbirds recognized their own egg-type and ejected other egg-types that differed from it. The lag in ejection time observed at the early laying stage suggested that this egg recognition probably is learned from the time a naive individual sees its first-laid egg(s) in

its first nest. Experimental conspecific brood parasitism revealed that kingbirds did not discriminate between their own and other kingbird eggs, which could make them susceptible to conspecific brood parasitism. Conspecific parasitism has been detected so far in one population of eastern kingbirds. This suggests that egg ejection in kingbirds originally evolved as an adaptation to counter interspecific brood parasitism. Kingbirds at Delta Marsh presently maintain their interspecific egg ejection behaviour despite an observed rate of cowbird parasitism of 0% from 279 nests.

Freeze-dried models of a nondescript sparrow (control), a female cowbird, and an avian predator were presented near kingbird nests during the laying and nestling stages to test for nest defence against the threat of cowbird parasitism. Kingbirds responded aggressively toward the cowbird model, but only slightly more so than to the control, and less than to the predator model. The level of aggression increased slightly between the laying and nestling stages. Results suggested that kingbirds at Delta Marsh did not recognize the cowbird as a unique or dangerous threat, possibly because of low selection pressure on rejector species for aggressive nest defence against cowbirds.

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CHAPTER I

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GENERAL INTRODUCTION

Avian brood parasitism is the phenomenon in which certain birds, the parasites, lay their eggs in the nests of other birds, the hosts (Rothstein 1975a). Among the 9000 living species of birds, only 80 species or about 1% are brood parasites (Hamilton & Orians 1965; Payne 1977), although the number becomes larger when conspecific brood parasitism is considered. One interspecific brood parasite, the brown-headed cowbird, *Molothrus ater*, is a host generalist known to have parasitized the nests of over 216 species (Friedmann et al. 1977). Brood parasitism generally lowers the reproductive success of hosts, through removal of host eggs, reduced hatching success of remaining eggs, and host-parasite nestling competition (Friedmann 1963; Payne 1977; but see Smith 1968). Thus, strong selection pressure favours the evolution of anti-parasite defences by potential hosts (see Davies & Brooke 1988, Rothstein 1975a, 1990).

Rothstein (1975a, 1976, 1977, 1982a) experimentally parasitized the nests of about 50 species of passerine birds with real and imitation eggs of the cowbird. He found that potential host species could be classified as either acceptors or rejectors of cowbird eggs (see also Finch 1982; Briskie & Sealy 1987). Nearly all individuals of acceptor

species show total acceptance (Rothstein 1982a); they incubate the cowbird egg, and if it hatches, raise the cowbird nestling along with any surviving young of their own. However, in rejector species, the introduced cowbird eggs are rejected at nearly 100% of the nests (Rothstein 1982a). Few species have been found that contain acceptor and rejector individuals in the same population (Rothstein 1975b; but see Rothstein 1976, Clark & Robertson 1981).

Hosts may reject cowbird eggs in several ways. Ejection is the most common defence against parasitism (Rothstein 1975a). Some ejectors grasp the parasitic egg between their mandibles, carry it some distance from the nest, and drop it. Other rejector species impale the egg on the tip of their opened mandibles, and eject it over the side of the nest (Rothstein 1977; Rohwer & Spaw 1988). Still other species reject parasitism by deserting the nest or burying the clutch (e.g. Rothstein 1975a; Nolan 1978; Clark & Robertson 1981; Graham 1988; Burgham & Picman 1989).

The most adaptive defence against parasitism should be one that reduces the chances that cowbirds will parasitize hosts' nests in the first place. This may be achieved through nest defence. Aggressive defence by potential hosts toward cowbirds near the nest may effectively deter cowbirds, thereby avoiding parasitism (Robertson & Norman 1976; Slack 1976; Scott 1977). This defence would also prevent the loss of an egg to the cowbird, since cowbirds

often remove a host egg from nests they parasitize (Friedmann 1963).

Some host species respond aggressively to female brood parasites, recognizing them as unique threats, whereas others show little or no response (Robertson & Norman 1976, 1977; Folkers & Lowther 1985; Hobson & Sealy 1989). However, the question remains whether nest defence is actually an anti-parasite strategy. A host's behaviour can be considered an anti-parasite strategy only if it both reduces the impact of parasitism and has evolved in response to, or is currently maintained by, selection pressures arising from parasitism (Rothstein 1990). Since neither of these conditions is yet known for nest defence, it still cannot adequately be called an anti-parasite strategy. More host species must be tested to help answer this question, comparing the levels of aggressive response of hosts to their reproductive success.

I examined aspects of two potential anti-parasite defences in a population of eastern kingbirds, *Tyrannus tyrannus*, at Delta Marsh, Manitoba. In Chapter I, I tested for the consistency of egg rejection and examined the mechanisms involved in egg recognition. As well, I examined the ability of eastern kingbirds to detect conspecific brood parasitism. Previous studies have indicated that eastern kingbirds are grasp ejectors of cowbird eggs (Rothstein 1975a). However, work done on the underlying mechanisms of

egg recognition and rejection has focused mainly on only two host species, with small sample sizes. As well, different populations of these species were tested and the results lumped. Also, conspecific brood parasitism and its potential role in the evolution of egg recognition and removal in rejector species was not considered in any of these studies (e.g. Rothstein 1975a). In Chapter II, I quantified responses to models of female cowbirds over two nesting stages, and tested the prediction that eastern kingbirds, because of their propensity to eject cowbird eggs, should not respond aggressively toward the cowbird model, and as such not recognize it as a unique threat. This hypothesis has not yet been tested. The few previous studies of nest defence behaviour in rejector species have suffered from small sample sizes, and inappropriate methodology such as the use of subjective behavioural indices.

CHAPTER I

EGG RECOGNITION IN THE EASTERN KINGBIRD

INTRODUCTION

Egg rejection for most host species is incontestably an
adaptive strategy against brood parasitism. This is due to
the costs associated with accepting parasitic eggs, such as
those of the brown-headed cowbird. These costs are often
high because hosts usually fledge fewer young than
unparasitized parents (e.g. Rothstein 1975a; Payne 1977).
Indeed, some species of flycatchers and vireos often do not
fledge any young when a cowbird hatches in their nests (e.g.
Walkinshaw 1961; Klaas 1975; Rothstein 1986; Briskie & Sealy
1987; Marvil & Cruz 1989). Even when parasitism does not
lower a host's reproductive output, additional parental
effort expended may depress a host's future reproductive
output (May & Robinson 1985; Rothstein 1990). Rothstein
(1990) suggested that because of the costs of parasitism,
rejection of cowbird eggs is more favourable than acceptance
for most host species. Despite such a strong selection
pressure, and various avenues open for rejection, only a
handful of species are known to reject brown-headed cowbird
parasitism consistently.

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What mechanisms do rejector species possess that allow them to adopt such an adaptive strategy? Rothstein's (1974, 1975a, 1978) experimental parasitizations on three rejector species, the gray catbird, *Dumetella carolinensis*, northern oriole, *Icterus galbula,* and American robin, *Turdus migratorius,* demonstrated that these species learned to recognize their own egg-types, probably after seeing their first-laid egg(s) in their nests. Rothstein's (1978) work on orioles also suggested that age may influence learning (see also Victoria 1972). However, since information is still lacking for most rejector species, more studies are needed before we can generalize about egg rejection. Knowledge of the mechanism by which species reject parasitic eggs might contribute to an understanding of the reasons most hosts accept cowbird eggs.

Rothstein (1975a) classified the eastern kingbird, (hereafter kingbird), as a rejector species, and noted that it grasps foreign eggs when it removes them from its nest. However, no other experiments have dealt sufficiently with the egg ejection behaviour of kingbirds, in comparison with other known rejector species. Thus the first objectives of my study were to determine 1) the frequency of natural parasitism on kingbirds at Delta Marsh, Manitoba, 2) the kingbirds' rate of egg rejection, and 3) the underlying mechanisms involved in their rejection behaviour.

Cruz et al. (1985) suggested that conspecific brood

parasitism may have been the selective force for egg recognition and removal in rejector species, rather than interspecific brood parasitism, as commonly believed. Conspecific brood parasitism, in which a female lays one or more eggs in the nest of another conspecific without helping to rear the young, has been assumed to be rare among altricial birds (Yom-Tov 1980; Brown 1984). However, techniques such as starch gel electrophoresis have increased the number of altricial species found to exhibit this reproductive strategy, and recently, conspecific brood parasitism was discovered in one population of kingbirds, in northern Michigan (McKitrick 1990).

Rothstein (1982a) found that rejector species tolerate foreign eggs to different degrees, in proportion to how widely their own eggs differ from foreign eggs. Since kingbird and cowbird eggs are similar in size and pattern, and kingbirds reject cowbird eggs (Rothstein 1970), one would expect kingbirds to be relatively intolerant of other foreign eggs that differed even slightly from their own. In fact, Rothstein (1982a) found kingbirds rejected eggs that differed from their own largely on the basis of maculation, but he did not test kingbirds with conspecific eggs. My final objective, therefore, was to determine if kingbirds reject conspecific eggs found in their nest, which will reveal whether their recognition and ejection behaviour is consistent with the hypothesis that it evolved in response

to conspecific brood parasitism.

MATERIALS AND METHODS

Study site

The study was conducted during four breeding seasons (1987-1990) in the forested dune ridge that separates Lake Manitoba and the Delta Marsh, Manitoba. The study area was located on the contiguous properties of the Portage Country Club, University of Manitoba Field Station (UMFS), rural municipality of Delta, and the Delta Waterfowl and Wetlands Research Station (DWWRS), and covered a distance of about 20 km. Overstory vegetation for the UMFS and DWWRS properties has been described by MacKenzie (1982), Harcus (1973), and Pohajdak (1988). A map and aerial photograph of the area are shown in Goossen (1978) and Sealy (1980). Some nests were also found in woodlots in and along the southern edge of Delta Marsh.

Nesting season

Kingbirds began building nests each year from 25 May to 3 June and this activity extended to late July, as failed nests were replaced. Clutches varied from three to five eggs. The study area was searched repeatedly throughout the breeding season for nests, which were numbered with orange flagging tape, classified and used according to their stage. Since I could not always determine when kingbird nests were fully lined, the lined-but-empty stage (hereafter empty

stage) included nests with fully formed cups up to, but not including, the first-laid eggs. Nests that contained one or two kingbird eggs were classified as the early laying stage. The late laying stage included nests containing three to five eggs, and ended on the day the last egg was laid. The incubation stage began the day after the last egg was laid and terminated when the first young hatched. For nests found with completed clutches, I determined the nesting stage by back-dating from the day the first young hatched, based on an incubation period of 13 days (Bent 1942). In some experiments, the early and late laying stages were combined and called the laying stage.

Experimental inter- and conspecific brood parasitism

Two interspecific brood parasitism experiments, one involving cowbird eggs and the other catbird eggs, and one conspecific brood parasitism experiment, were conducted to test for egg recognition and removal in kingbirds. The real cowbird, catbird, and kingbird eggs (Figure 1) were placed experimentally into kingbird nests between 0700 and 1200 h. I placed cowbird eggs into kingbird nests at the empty, early and late laying, and incubation stages. Empty, laying and incubation stages were used for the conspecific parasitism experiment whereas only the laying and incubation stages were used in the experiment that involved catbird eggs. All eggs were placed carefully in the nests and checked to ensure that none was damaged or broken. No host

Figure 1: Photogragh of an eastern kingbird, brown-headed
cowbird and gray catbird egg.
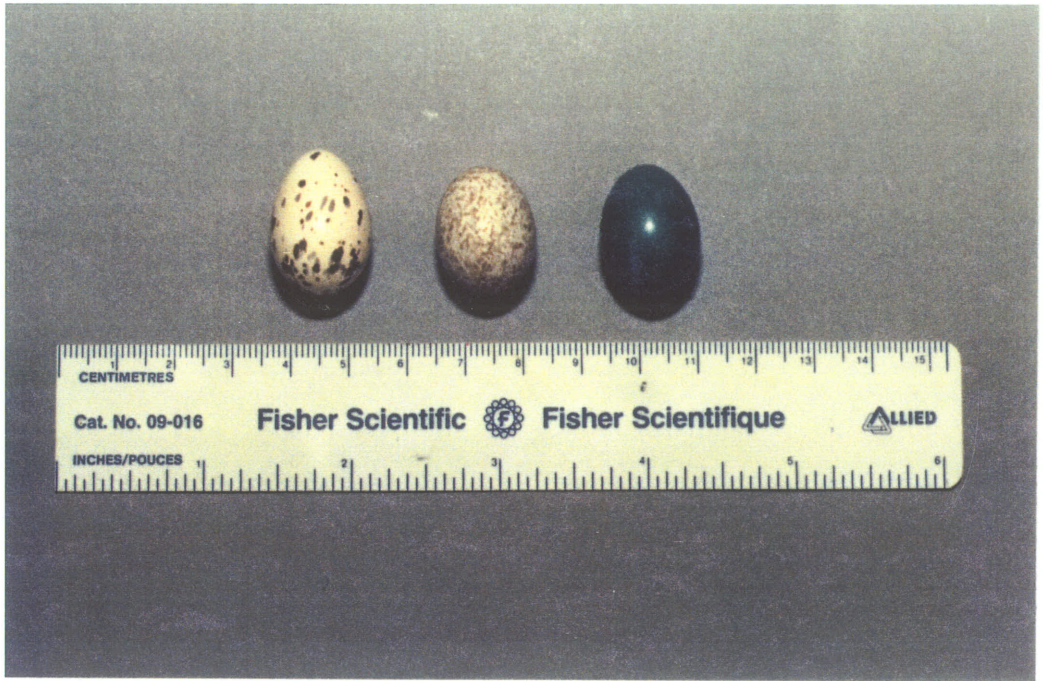
egg was removed from nests when they were parasitized experimentally. Conspecific eggs were marked with a small dot on their blunt end to identify them. At the time of parasitization, I observed each nest for one hour from a concealed blind placed at least 5 m from the nest and recorded the initial responses of the kingbird to the foreign egg. I also recorded the amount of time kingbirds were in contact with their nests during the one-hour period. If the egg was removed within the hour, observations ceased and the time and method of rejection was recorded. Nests that still contained the experimental egg after one hour were checked five hours after the time of initial parasitization. If they still contained the foreign egg, I checked them the following morning, and every morning thereafter, noting the time at which the nest was checked. For example, if an egg was rejected within 48 hours, this meant that the egg had been removed between 24 and 48 hours.

For the interspecific parasitism experiments, nests were checked until the foreign egg was ejected, or the host eggs hatched, whichever came first. Since cowbird eggs take an average of 11.9 days to hatch (Briskie & Sealy 1990), those eggs that remained in kingbird nests for this length of time or longer were considered accepted because had they been viable, they presumably would have hatched. For the conspecific parasitism experiment, nests were checked until either the conspecific egg was removed, or five days (=120

hours) had elapsed and the foreign egg was considered accepted. Less than 5% of all cowbird and catbird eggs experimentally placed in kingbird nests were rejected after five days. Each nest was tested only once with any one egg-type.

Egg-switching experiment

Another experiment involved replacing all but one kingbird egg in clutches with enough cowbird eggs to return the clutches back to their original sizes. This created a reverse discordancy on the kingbird egg. For example, a clutch that contained four kingbird eggs was manipulated to produce a clutch containing one kingbird and three cowbird eggs. Each nest was tested only once, at the incubation stage. Clutch sizes of three to five eggs were used. The methods used for this experiment were otherwise the same as for the inter- and conspecific parasitism experiments. In some cases, host eggs were placed back into the nest after the experiment was completed.

Statistical analyses

For the cowbird parasitism experiment, I used non-parametric statistical tests (Conover 1980) to analyse the data because they were not normally distributed. I used the Kruskal-Wallis one-way analysis of variance (ANOVA) to test for differences in egg rejection times over the nesting cycle. This ANOVA is applied to the ranked data, and the F test generated is often better than the usual X^2

approximation. To compare differences in egg rejection times between two stages (e.g. early laying vs. late laying), I used the Fisher's protected least significant difference procedure computed on the ranked data (Conover 1980). This procedure tests for individual comparisons only if a significant F test is first obtained, and as a result the experimentwise error rate is maintained at the chosen alpha level (Milliken & Johnson 1984). The Wilcoxon two-sample test for independent samples was used to compare differences in egg placement times between accepted and rejected conspecific eggs. Tied scores were given the mean of their corresponding ranks. I used an ANOVA to compare differences in nest contact time at the various nest stages. The Fisher exact probability test was used to compare acceptance vs. rejection of conspecific eggs from experimentally parasitized nests. Statistical tests were two-tailed with a level of significance of $p < 0.05$.

RESULTS

Interspecific brood parasitism

Eighty-eight cowbird eggs were placed into kingbird nests for the cowbird parasitism experiment. Eighty-seven (98.7%) were eventually rejected. At the 23 nests where I observed the cowbird egg being ejected, the eggs were grasped in the bill in all cases. These eggs were then dropped 5 m or more away from the nest, by the female at the

13 nests where the sex was determined during observations. One kingbird egg was missing or broken in six nests following ejection of the cowbird egg; the other kingbird eggs remained intact in each nest. The six nests above were not included in analyses.

One kingbird removed one of its own eggs. The four-egg clutch had been experimentally parasitized with a cowbird egg at the incubation stage. After 31 min a kingbird ejected the cowbird egg. A minute later, the bird returned to the nest, perched on its edge for a few minutes, then ejected one of its own eggs in a similar manner. When I checked the nest after the one-hour watch, it contained only three kingbird eggs.

In 1988, a cowbird egg was accepted at one kingbird nest. The egg was placed in the nest three days into incubation and it remained there for 12 days, at which point the nest was depredated. The inviable cowbird egg had been in the nest for 10 days when the first kingbird nestling hatched. The 17 other cowbird eggs placed experimentally into kingbird nests at the incubation stage were ejected before any host nestlings hatched; at least four of them were placed in nests after three days into incubation.

Ejection time, defined as the time the foreign egg remained in the nest before a kingbird removed it, was recorded for each experimentally parasitized nest (Table 1). There was a statistically significant relationship between

Table 1: Ejection times of brown-headed cowbird eggs placed into eastern kingbird nests at various stages of the nesting cycle, and the results of multiple comparison tests for differences between nest stages.

Status of nest when parasitized	No. of nests	Egg ejected within (h)									
		1	5	24	48	72	96	120	144	168	240
Empty[c]	23	6	10	2	2		2		1		
Early laying[a,b,c]	22	1	2	3	6	2	3	1	2	1	1
Late laying[a]	25	2	7	6	6	1	2	1			
Incubation[b]	17	3	7	3	2	1		1			
Total	87	12	26	14	16	4	7	3	3	1	1

Rows with the same superscripts are significantly different, [a]p=0.0165, [b]p=0.0007, [c]p=0.0001.

nest stage and ejection time (Kruskal-Wallis one-way ANOVA, $F=7.26$, $df=3$, $p=0.0002$). Cowbird eggs placed into nests during the early laying stage remained there significantly longer than those deposited at the empty, late laying, or incubation stages. The median ejection times for each nest stage were: five hours for the empty stage; 48 and 24 hours for the early and late laying stages, respectively; and five hours for the incubation stage.

At three of the 23 kingbird nests experimentally parasitized at the empty stage, the cowbird egg was ejected after the host had begun laying. These eggs had been placed in nests from two days before to the same day on which the first host egg was laid. Two of the 23 nests were abandoned after the cowbird egg was ejected. At the other 20 nests, the foreign egg was removed before laying began. Egg introductions for these nests varied from 10 days to one day before laying.

For the other interspecific parasitism experiment, catbird eggs were added to 10 kingbird nests during the laying or incubation stages. All of the eggs were ejected, from 5-72 hours after deposition.

Nest contact

The results of the one-hour nest watches following experimental parasitization of host nests were compiled to determine the amount of time kingbirds contacted their nests at each stage (Figure 2). Nest contact was quantified by

Figure 2: Nest contact in relation to nesting stage. Square
is mean, vertical bar is $\pm$ S.E. Values correspond
to the number of minutes within the hour of
observation. Number of one-hour observations is
given above vertical bar.
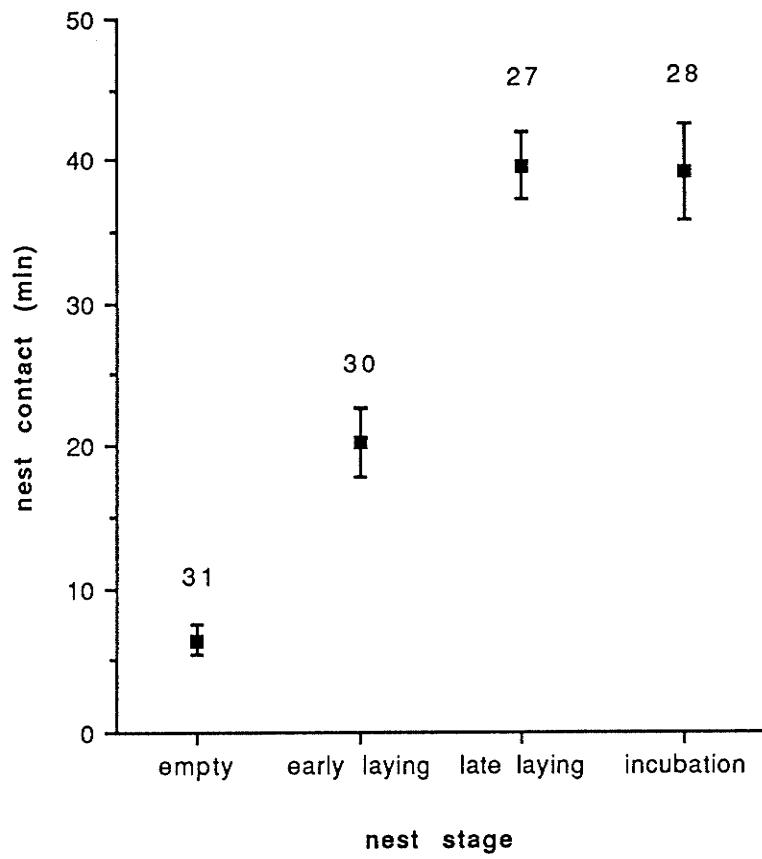
recording the amount of time over the hour that a kingbird either sat in the nest or perched on the rim. Individuals often peered into their nests, especially when perched on the rim, and hence during these times they potentially could gather information on nest contents. Nest contact increased significantly from the empty stage to the late laying stage, but levelled off during the incubation stage (one-way ANOVA, $F=45.47$, $df=3$, $p<0.0001$). Kingbirds spent most of their time at the nest sitting in the nest rather than perching on the rim for all stages (Table 2).

Egg-switching experiment

Eleven completed kingbird clutches were experimentally manipulated by replacing all but one of the eggs with enough cowbird eggs to return the clutch to its original size. In 10 of the clutches, kingbirds ejected all of the cowbird eggs leaving only the kingbird egg in the nest (Table 3). Ejection times for the cowbird eggs in these 10 nests ranged from four minutes to 48 hours. Nine of the 10 nests had their cowbird eggs removed by the kingbird within 24 hours. At the only nest with a clutch of three eggs, the cowbird eggs were not removed. Instead, the nest was abandoned within 24 hours. It is not known whether the nest originally had a larger clutch that might have been reduced, possibly due to predation. Both kingbirds responded aggressively when I manipulated the clutch, but neither returned to the nest during the one-hour observation. No

Table 2: Percent of total nest contact time spent sitting in the nest or perched on its rim for each stage of the nesting cycle.

Stage	Sitting in nest (%)	Perched on rim (%)
Empty	91.4	8.6
Early laying	96.2	3.8
Late laying	99.4	0.6
Incubation	97.0	3.0

Table 3: Summary of egg-switching experiment on eastern
kingbird nests indicating the fate of all cowbird eggs at
each nest.

Clutch size	N	time to eject all cowbird eggs			
		<1h	1-5h	5-24h	24-48h
4	8	2	3	2	1
5	2	1	0	1	0

other kingbird nest experimentally parasitized with any egg-type was abandoned prior to ejection.

Experimental conspecific brood parasitism

Conspecific eggs were added to 20 kingbird nests at the empty stage and to 11 nests during the laying and incubation stages. All 11 conspecific eggs were accepted at the laying and incubation stages, but during the empty stage, 14 of 20 eggs (70%) remained in the nest for five days (Table 4). The six other conspecific eggs were ejected from 1-72 hours after being placed into host nests. One of the six nests was abandoned after the conspecific egg was removed. The difference in ejection of conspecific eggs between the pre-egg and egg stages was significant (Fisher exact probability test, p=0.05).

The ejected conspecific eggs had been experimentally placed in nests from five to three days prior to laying of the first host egg (Table 5), and all were removed before the first egg appeared. For the remaining 14 nests "parasitized" at the empty stage, the time difference between egg placement and laying of the first egg ranged from four days to the same day. This difference in egg placement between accepted and rejected conspecific eggs was not significant.

An interesting series of events occurred at one kingbird nest that had been experimentally parasitized on three separate occasions. The first time was three days

Table 4: Outcome of experiment in which single, conspecific eggs were placed into eastern kingbird (EK) nests at two different stages of the nesting cycle.

Status of nest when parasitized	No. of EK eggs	Egg in nest for (h)						
		1	5	24	48	72	96	120[a]
Empty	20	1	2	1	1	1		14
Laying/ incubation	11							11

[a] Eastern kingbird eggs were removed from the nest after 120 h (=5 days)

Table 5: Number of days prior to clutch initiation when empty eastern kingbird nests were experimentally parasitized with conspecific eggs.

Fate of introduced egg[a]	No. of EK eggs	No. days prior to clutch initiation when parasitized					
		0	1	2	3	4	5
Accepted	14	2	1	3	6	2	0
Rejected	6[b]	0	0	0	3	1	1

[a] Nests were separated according to the fate of the introduced egg.

[b] One nest was abandoned after rejection of the conspecific egg.

prior to laying; the conspecific egg was ejected five hours later. The second time was two days prior to laying, and again the conspecific egg was ejected within five hours. However, two days later, roughly four hours prior to the laying of the kingbird's first egg, the nest was experimentally parasitized again and this time the conspecific egg was accepted. Only the first observation at this nest was used in the analysis.

At another kingbird nest, a conspecific egg, which had been in the nest for three days prior to laying, was still present after five days (17 June). The nest then contained three host eggs and one conspecific egg. The next day, the conspecific egg was gone while the number of host eggs remained the same. On 19 June, a new conspecific egg was added to the clutch. It remained in the nest for 48 hours before disappearing on 21 June. By 0630 h the following day, the nest had been destroyed. The first observation was considered an acceptance and used in the analysis, but the second observation was excluded.

DISCUSSION

Egg rejection as an adaptation

Rothstein (1975a) classified the kingbird as a rejector species based on experiments in which he placed real or artificial cowbird eggs in their nests (N=33). Its status as a rejector species was demonstrated in the present study,

where kingbirds rejected 87 of 88 real cowbird eggs I experimentally deposited in their nests. Rothstein (1976, 1977) found that species that rejected foreign eggs by puncture ejection had higher incidences of missing or broken eggs than those using grasp ejection. Two host species that puncture eject cowbird eggs have been estimated to incur costs of 0.42 to 0.45 host eggs per ejection (Rothstein 1977; Rohwer et al. 1989). Only six experimentally parasitized kingbird nests in this study had missing or broken eggs. This is only 0.06 host eggs per ejection, supporting the conclusion that grasp ejection is the primary means of egg rejection for this species (see Rothstein 1975a, Hamas 1980).

Although most kingbirds reject cowbird eggs, a few isolated cases exist in the literature in which kingbirds accepted cowbird eggs and even fledging nestling cowbirds (Berger 1960; Friedmann 1963; Graber et al. 1974). Friedmann et al. (1977) compiled 24 reported instances of cowbird eggs being accepted by kingbirds. In the present study, only one case of acceptance was recorded, a nest that was experimentally parasitized three days into incubation. Despite being placed in the nest during incubation, the cowbird egg would have hatched along with the first kingbird eggs, had it been viable. Rothstein (1976) stated that the incubation periods of some rejector species, such as the kingbird, are so long relative to the cowbird's that

parasitic eggs laid in the nest after a host has begun incubating might still hatch before the host eggs. Several cowbird eggs experimentally placed in kingbird nests later in incubation were ejected quickly.

Thus, although egg rejection is apparently strongly developed in kingbirds, some individuals seem to lack the necessary behavioural mechanisms needed to remove foreign eggs from their nests. Why this is so is uncertain, but it may have to do with events occurring earlier on in an individual's breeding career, as will be discussed below.

Occurrence of natural cowbird parasitism

None of the 166 kingbird nests examined in the present study or 113 nests checked on the study area between 1974 and 1987 (S. G. Sealy, pers. comm.) was found to be naturally parasitized. Robertson and Norman (1977) also did not record any parasitism on 81 kingbird nests at Delta Marsh, however, one nest containing a cowbird egg was reported from Delta on 12 June 1979 (Friedmann & Kiff 1985). The probability of detecting natural parasitism was not the same for all nests since they were found at different stages of the nesting cycle, and hence ejection might have occurred before observations began at some nests, or between nest checks (see Scott 1977). Murphy (1986) stated that parasitism rates of rejectors are best determined when host nests are observed during laying (see also Scott 1977). This agreed with the results from the present study, since

cowbird eggs placed in kingbird nests during their laying stage remained in the nests longer than at other times in the nesting cycle. Also, cowbirds normally parasitize nests just before or during the hosts' laying (Rothstein 1975a). Considering that at least 50% of the nests I found during the present study, and all of the nests monitored by Sealy and co-workers, were at the laying stage, I believe we should have detected at least some instances of natural parasitism, had they occurred. Thus, I am confident that kingbirds at Delta Marsh are parasitized by cowbirds rarely.

Elsewhere, Southern & Southern (1980) compiled a parasitism rate for the kingbird of only 0.7% over 38 years in Michigan, and other workers similarly have found low rates, from 0% to 0.8% (Friedmann 1963; Goertz 1977; Lowther 1977). Murphy (1986), on the other hand, reported a rate of parasitism of 9% for kingbirds in Kansas and New York State. The different rates of parasitism probably reflect geographic variation in factors such as host nesting phenology (e.g. Klaas 1975), habitat (e.g. Zimmerman 1983), or nest placement (e.g. Newman 1970; Buech 1982; Briskie et al. 1990) that may affect the frequency of parasitism in local host communities (Fleischer 1986).

Rothstein (1975a) hypothesized that rejector species should be subjected to occasional to heavy parasitism in order for them to evolve and maintain their rejection behaviour. He provided evidence that some rejectors are

parasitized more frequently than some acceptors, but, in general, he found no strong support for his hypothesis. Interestingly, kingbirds at Delta Marsh maintain their rejection behaviour, despite being parasitized rarely. Cruz et al. (1985) and Post et al. (1990) found that gray kingbirds, *T. dominicensis*, which have only recently become sympatric with the shiny cowbird, *M. bonariensis*, in the Caribbean region exhibit rejection behaviour despite initially experiencing no interspecific parasitism at all. Briskie et al. (in press) observed a 67% ejection rate of experimentally introduced brown-headed cowbird eggs in an allopatric population of robins, and Davies & Brooke (1989) found that some birds in allopatric populations of meadow pipits, *Anthrus pratensis*, and white wagtails, *Motacilla alba*, in Iceland rejected experimentally introduced common cuckoo, *Cuculus canorus*, eggs. The expression of rejection behaviour may persist when parasitism is absent or rare because of its low cost (Davies & Brooke 1989). However, Cruz & Wiley (1989) found that village weaverbirds, *Ploceus cucullatus*, which reject dissimilar cuckoo eggs in Africa, have lost most of their rejection behaviour after being introduced to Hispaniola sometime before 1797, where there were no parasites. This implies some cost in maintaining rejector genes. Another possibility for the maintenance of rejection behaviour in a population is the introgression of rejector genes from other more moderately parasitized

kingbird populations (i.e. gene flow). Possibly, kingbirds at Delta Marsh simply are parasitized more frequently than observed. However, as discussed above, this last possibility seems unlikely.

Egg recognition

Ejection of cowbird eggs provides evidence that kingbirds acted specifically against the foreign eggs in their nests (Rothstein 1970). However, it reveals little about how kingbirds and other ejectors choose the correct egg to be removed. The birds may differentiate between their own and foreign eggs in one of two ways. First, they might reject either by recognizing their own eggs or those of the parasite, called true egg recognition, or they might reject any egg-type that is in the minority, called rejection via discordancy (Rothstein 1975c).

Rensch (1925) was one of the first investigators to test this experimentally, and he concluded that birds acted against the egg-type that was in the minority, thus rejecting via discordancy. Despite previous evidence for true egg recognition (see Swynnerton 1916) rejection via discordancy was considered the mechanism of egg ejection until Victoria (1972) demonstrated that captive village weaverbirds rejected eggs on the basis of true egg recognition. Since then, true egg recognition has been shown to occur in several potential hosts of the brown-headed cowbird: catbirds, robins, orioles, loggerhead

shrikes, *Lanius ludovicianus*, and scrub jays, *Aphelocoma coerulescens* (Rothstein 1975c, 1977, 1982a).

Rothstein (1975c) experimentally parasitized one kingbird nest to determine the mechanism this species used to eject eggs. However, all of the eggs, including the kingbird's, disappeared. Results of the egg-switching experiment in the present study, however, demonstrated that kingbirds also use true egg recognition, removing cowbird eggs even when they were in the majority, and never removing their own egg. Thus, all rejector species tested to date use true egg recognition when they remove foreign eggs from their nests (Rothstein 1975c, 1990).

In the present study, kingbirds ejected both cowbird and catbird eggs, and Rothstein (1982a) determined that they ejected immaculate, blue eggs. It seems unlikely that kingbirds recognized specifically both cowbird and catbird egg-types, as parasitic eggs to be removed, since under natural conditions neither catbird nor blue eggs should ever appear in their nests. A more plausible explanation is that kingbirds, like other rejector species, recognize their own egg-type and reject other eggs found in their nests that differ from it (Rothstein 1982a, b), regardless of whether they are cowbird or catbird eggs as in the present case.

Kingbirds at one nest in the egg-switching experiment responded to cowbird eggs by abandoning their nest altogether, without removing any eggs. Rothstein (1975c)

observed desertions at one of 13 robin nests and two of three brown thrasher, *Toxostoma rufum*, nests. He concluded that the desertions were due to the large-scale egg-manipulations at these nests and not to human disturbance since such desertions prior to egg removal rarely occurred at other nests subjected to similar amounts of human disturbance but with less severe egg-manipulations. I reached the same conclusion for the kingbird nest because no other nests subjected to similar amounts of human disturbance but less severe egg-manipulations were abandoned before the foreign egg had been ejected. I do not know why the individuals at the kingbird nest did not first remove the foreign eggs as the others did.

Effect of nest stage on ejection time

Several workers have stated that nest stage does not influence the likelihood that a species will accept or reject cowbird eggs (e.g. Rothstein 1977, 1982a; Rich & Rothstein 1985). The cedar waxwing, *Bombycilla cedrorum*, and yellow warbler, *Dendroica petechia*, are exceptions (Rothstein 1976; Clark & Robertson 1981). Response was also independent of nest stage in this study because kingbirds ejected experimentally placed cowbird eggs from all but one nest regardless of its stage at the time of experimental parasitization. However, little information exists on the relationship between nest stage and ejection time (e.g. Rothstein 1974).

Kingbirds in this study tolerated foreign eggs significantly longer at the beginning of laying and ejected them more quickly later (Table 1). For example, 27% of kingbirds at the early laying stage ejected the cowbird egg within 24 hours whereas 60% did so at the late laying stage. Interestingly, Rothstein (1974) observed a similar early tolerance of foreign eggs by catbirds, as did Davies & Brooke (1989) for five cuckoo host species.

Perhaps the larger number of host eggs at the late laying stage provided kingbirds with a stronger reference against which to identify the "correct" egg-type, and this resulted in more rapid ejection of the cowbird egg. Rothstein (1975c) observed this in robins, and to some degree in catbirds. However, the median ejection time of cowbird eggs in the egg-switching experiment, in which cowbird eggs outnumbered host eggs, was only five hours, whereas for the cowbird parasitism experiment it was between five and 24 hours. Thus kingbirds were able to eject cowbird eggs from their nests just as quickly whether or not their own eggs were the prominent egg-type in the nest.

Another factor that might promote differential ejection time is host presence at the nest (i.e. being able to see the eggs). At early laying, kingbirds visited their nests less frequently than at all of the later stages. Indeed, nest contact time was significantly higher during the late laying and incubation stages than early laying stage (Figure

2). However, empty nests received even less nest contact time, yet the median ejection time (five hours) at this stage was the same as for the incubation stage, and much lower than that for the early laying stage (48 hours). Rothstein (1974) suggested also that while incubating birds are in greater contact with their nests, they may look at their eggs less frequently than birds do early in the laying stage because later they tend to keep the eggs covered. I found no difference in time spent in the nest or on its rim for any of the nest stages. Kingbirds spent most of their time at the nest covering the eggs. Thus, none of these explanations adequately accounts for the greater tolerance of cowbird eggs early in the nesting cycle.

Learned egg recognition

The delay in ejecting foreign eggs at the beginning of the nesting cycle could involve the amount of time a host has been exposed to its own eggs. At the late laying and incubation stages, individuals have been exposed to their own egg-type for a few more days. They may therefore be more familiar with it, making it easier to detect differences. As mentioned earlier, Rothstein (1974) found that catbirds tolerated cowbird eggs longer during early laying, and he used this as evidence that egg recognition is learned. Others have similarly suggested that egg recognition in passerines is learned (e.g. Victoria 1972), as well as in nonpasserines (Tschanz 1959).

Rothstein (1974) believed that a delayed ejection period at the onset of laying allowed for prolonged exposure of a host to its egg-type so that it can sharpen its recognition capabilities by reinforcing what it has already learned, namely the appearance of its own eggs. Thus, learning is reinforced during this period. The sooner that a host's learning is strengthened and refined, the sooner it can eject foreign eggs (Rothstein 1974). This would explain why in the egg-switching experiment, at the incubation stage, despite the reversed discordancy, kingbirds ejected the cowbird eggs relatively quickly.

Rothstein (1974) suggested that birds learn to recognize their eggs through an imprinting-like process on the first egg or eggs that they see. From work done on orioles, Rothstein (1978) suggested that learning occurs only once in an individual's lifetime, during a hypothesized sensitive period around the onset of laying. Recognition may then be progressively sharpened during each successive nesting attempt through prolonged contact with the eggs (Rothstein 1974).

The age-specific plumages of orioles allowed Rothstein (1978) to differentiate between naive, first-time breeders, and experienced adults. Though I could not determine whether the kingbirds in this study were naive or experienced, I believe my results provide support for Rothstein's (1978) findings. Six of 20 conspecific eggs

experimentally placed into empty kingbird nests were ejected. The birds at these six nests might have been yearlings, i.e. naive individuals breeding for the first time. Given the high mortality of passerines it is reasonable to assume that within a sample of nests, some will be tended by naive and others by experienced individuals (Rothstein 1974). Naive individuals would not as yet have had a chance to learn their own egg-type, and therefore might have ejected the "foreign" conspecific egg.

Naive birds should be expected to remove foreign eggs from their nests before learning has occurred so that they do not accidentally learn the wrong egg-type. However, this behaviour should change just prior to laying, otherwise they may remove their own eggs. This scenario was observed at one kingbird nest in 1989, where a conspecific egg placed in the nest just four hours prior to laying was accepted despite two previous ejections. This was possibly the beginning of the hypothesized sensitive period when learning begins, as Rothstein (1978) suggested.

If a sensitive period exists, then individuals might accept naturally or experimentally deposited cowbird eggs if they were added at the proper time. Interestingly, Rothstein successfully carried out such an experiment. Catbirds accepted a clutch of artificial cowbird eggs when the eggs were deposited such that each cowbird egg replaced a catbird egg soon after it was laid (Rothstein 1974). In his

experiments on yearling and adult orioles, Rothstein (1978) observed acceptance of cowbird eggs at two nests tended by yearlings, and rejection at all but one other nest when the eggs were added within four days of laying.

Finally, the variability observed in ejection times of cowbird eggs at the early laying stage might have been due to differences in learned recognition. More experienced birds might eject the eggs relatively quickly since their learning has been more strongly reinforced over previous breeding seasons. The six kingbirds that removed cowbird eggs within 24 hours at early laying apparently knew their own egg-type right from the beginning of clutch initiation. The longer ejection times might have involved less experienced or naive birds. Variability in ejection time was much less during the late laying stage.

Conspecific brood parasitism

Most kingbirds did not discriminate between their own and the eggs of conspecifics before they began laying, despite sometimes noticeable differences in ground colour and pattern of spotting between eggs of different clutches (pers. obs.). This is perhaps not surprising since no species of birds have been shown to be able to discriminate between their own and conspecific eggs before laying has begun.

Several species reject conspecific eggs before they have initiated their own clutches, but accept them after

their own laying has begun (Vehrencamp 1977; Lanier 1982; Brown 1984; Emlen & Wrege 1986; Møller 1987; Stouffer et al. 1987; Lombardo et al. 1989). These species probably respond to any egg or object in the nest prior to laying since they cannot differentiate between their own and conspecific eggs once laying has begun. Only a few species are able to differentiate between their own and conspecific eggs after the onset of laying (e.g. Tschanz 1959; Victoria 1972; Buckley & Buckley 1972; Shugart 1987). Kingbirds appear to recognize the kingbird egg-type because they accepted conspecific eggs deposited prior to laying. However, they do not seem to be able to distinguish between their own and another's eggs.

Kingbirds obviously can remove conspecific eggs since six eggs were ejected from empty nests, and I observed one individual remove one of its own eggs. Did the six kingbirds recognize the foreign eggs as differing from their own? Probably not, although the differences in size and spotting pattern between the conspecific and host eggs were not compared to determine the extent of variability. Also, kingbirds never ejected conspecific eggs at the laying and incubation stages. Finally, the ejections were not a generalized response toward objects placed in the nest prior to laying since 14 other conspecific eggs introduced at that stage were accepted.

Conspecific brood parasitism was not detected in the

Delta Marsh population of kingbirds. McKitrick (1990), however, using electrophoretic techniques, demonstrated that conspecific brood parasitism occurred in a population of this species in Michigan. This seems surprising considering kingbirds generally defend their territories aggressively against intruding conspecifics of both sexes as well as other species (Davis 1941; Bent 1942; Blancher & Robertson 1982). However, if parasitic kingbirds lay their eggs in just a few seconds, as other conspecific brood parasites do (e.g. Brown 1984), then successful parasitism might be possible, despite aggressive hosts, especially if the egg was deposited after the host's laying had begun.

Since kingbirds do not discriminate between their own and alien conspecific eggs, rejection of cowbird eggs cannot be an epiphenomenon of conspecific brood parasitism (see Briskie et al. in press), as others have suggested (e.g. Cruz et al. 1985). The results in the present study suggest that recognition and removal of parasitic eggs by kingbirds evolved directly as an adaptation to counter cowbird parasitism (see also Brown et al. 1990).

CHAPTER II

GENERALIZED RESPONSES OF A REJECTOR SPECIES TO THREATS OF PREDATION AND COWBIRD PARASITISM

INTRODUCTION

One of the best defences that a bird could have against brood parasitism is to avoid being parasitized in the first place (Rothstein 1970). One means to achieve this might be through nest defence. Acceptor species, especially, should be expected to defend their nests vigorously because when parasitized their reproductive success is usually decreased due to egg stealing by laying parasites and competition between host and parasite nestlings (Rothstein 1975a; Payne 1977). Rejector species such as the eastern kingbird, on the other hand, arguably may not need to defend their nests against would-be parasites because they can simply remove the foreign egg from their nests. Nevertheless, egg ejection occurs after parasitism and consequently the possibility of losing an egg(s) to a laying parasite, such as the brown-headed cowbird, still exists. Cowbirds frequently remove a host egg from nests they parasitize (Friedmann 1963), which usually reduces the host's reproductive success (Smith 1981). Also, the rejector may

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damage its own egg(s) accidentally when removing a cowbird egg, or it may eject the wrong egg (Rothstein 1982a). Murphy (1986) reported that at least one host egg was ejected or damaged, probably by cowbirds, at 69% of naturally parasitized eastern kingbird nests in Kansas and New York State.

Most studies that have addressed the responses of hosts towards cowbirds have focused on acceptor species. Investigators have identified several acceptor species that respond uniquely to female brood parasites, both cowbirds and cuckoos (e.g. Robertson & Norman 1976, 1977; Folkers & Lowther 1985; McLean 1987; Burgham & Picman 1989; Hobson & Sealy 1989; Duckworth 1991). This suggests that the hosts recognize parasites for the unique threats they pose. Recognition is generally characterized by antics or vocalizations and/or high-level aggression in response to the parasite in comparison to a control model presented during laying or early incubation, when the consequences of parasitism are potentially the greatest. Also, the response is reduced later in the nesting cycle as the threat diminishes (e.g. Hobson & Sealy 1989). Briskie & Sealy (1989) observed a sustained level of aggression later in the nesting cycle, but this was for reasons unrelated to parasitism.

Few studies have quantified the behavioural defences that rejector species exhibit when confronted by cowbirds

(but see Robertson & Norman 1976, 1977; Folkers 1982).
These studies suffered from small sample sizes and the use
of a subjective index to score the responses (see Hobson &
Sealy 1989). As well, the authors did not test the rejector
species later in the nesting cycle and thus did not quantify
changes in the nature of responses as they relate to the
real threat of parasitism. Finally, none of the studies
used a third model, a non-parasitic nest predator, in the
tests to compare with responses given to the cowbird model.

In this chapter, I quantified the responses of eastern
kingbirds (hereafter kingbirds) at Delta Marsh, Manitoba, to
models of a female cowbird, an avian predator, and a control
placed near the nest during the laying and nestling stages.
My goal was to determine whether kingbirds responded to
models, and if so whether the nature of the responses
suggested a unique recognition of the cowbird. I
hypothesized that kingbirds at Delta Marsh should respond
relatively unaggressively to the cowbird model because of
the low selection pressure for such a response by a rejector
species.

MATERIALS AND METHODS

Choice of models

Freeze-dried models of a fox sparrow, *Passerella
iliaca*, female brown-headed cowbird, and male common
grackle, *Quiscalus quiscala,* were used to study the nest

defence behaviour of kingbirds over the nesting cycle. The
fox sparrow served as a control because it is similar in
size and shape to a female cowbird but neither parasitizes
nor preys upon kingbird nests, and occurs on the study area
only during migratory stopovers. Thus, I expected it to
elicit low-level aggression from kingbirds, because the two
species should seldom interact. The grackle, which breeds
on the study area, represented a nest predator that preys on
eggs and nestlings of many passerine birds (Godfrey 1986),
including those on the study area (S. G. Sealy, unpub.
obs.). Presentation of the grackle allowed me to determine
whether any responses to the cowbird model were unique or
simply part of a generalized response to nest intruders.
Grackles are slightly larger than female cowbirds and fox
sparrows (Table 1), although Robertson & Norman (1976) found
that the sizes of different model species had little
influence on host response.

Freeze-dried models were used because they are durable
and convenient, yet maintain life-like appearances. Each
was mounted in a perched position with its head pointing
straight forward and with wings folded over the tail.

Model testing

Testing was conducted in 1989 and 1990 at kingbird
nests situated throughout the study area (see Chapter I).
Nests were tested at the laying (N=32) and nestling (N=29)
stages. Nests at the laying stage contained from one to

Table 1: Means and ranges of body mass of eastern kingbirds and the three species used for model testing (from Dunning 1984).

Species	N	Mean weight(g)	Range
eastern kingbird[a]	14	30.5	35.8 − 40.8
fox sparrow[a]	711	32.3	21.7 − 42.1
brown-headed cowbird[b]	692	38.8	30.5 − 51.2
common grackle[c]	197	127	

[a] Males and females not distinguishable.
[b] Females only.
[c] Males only.

three kingbird eggs when tested. The nestling stage involved nests containing one to four nestlings, about four days of age. To prevent the development of positive reinforcement and loss of fear that can occur when an observer repeatedly exposes the occupants of a nest to a specific model (Knight & Temple 1986a, b), all nests were tested only once, with all three models. The order presented was random, but in such a way to ensure that one was not presented first, second, or third disproportionately often (Knight & Temple 1986a). Payne et al. (1985) found that the responses to a model were not affected by models presented previously.

I set up a portable blind, usually 5-15 m from the nest, about 20 min prior to testing, along with a ladder when needed to reach the nest. The models were attached either to the nearest available vegetation or to the top of an aluminum pole, but always approximately 0.5 m from the nest and facing the nest bowl. Generally, I required 1-3 min to place the model and retreat to the blind. Each model was tested for 5 min, beginning only after I had returned to the blind and when one of the parents appeared within 5 m of the nest. After 5 min, I removed the model and waited 10 min before presenting the next one. This rest period eliminated habituation effects or carry-over aggression between models (Smith et al. 1984). Observations were spoken directly into a portable tape recorder and later

transcribed.

I employed methods similar to those detailed by Smith et al. (1984) and Hobson & Sealy (1989) to score proximity and behavioural activities of kingbirds during each model presentation, according to the following categories: 1) distance of closer parent from the model in one of three distance classes: <2 m, 2-5 m, >5 m; 2) vocalizations, specifically the incipient locomotory hesitance vocalization and harsh repeated vocalization given by agitated and/or attacking kingbirds of both sexes (Smith 1966); 3) hovers, defined as flights from a perch, over the model momentarily, then back to a perch; 4) close-fly-bys, defined as breaks in horizontal flight directed toward the model, but without striking it; and 5) strikes, defined as above except that the individual contacts the model. For each trial, I recorded whether one or two birds responded. Observations suggested that the birds responding to a model were the residents, i.e. parents, since kingbirds are highly territorial and do not tolerate other conspecifics near their nests (Davis 1941; Bent 1942). Indeed, in the trials in which an additional kingbird responded (N=5), each was immediately chased away by one of the parents. Behavioural activities were recorded for both unsexed parents because I was interested in the overall level of defence against a model rather than the response of individuals.

The categories of distance, vocalizations, and hovers

were analysed as the number of 10-s periods within a trial
that a kingbird engaged in these activities. Strikes and
close-fly-bys were analysed as absolute counts within the 5-
min trial period.

I considered the distance variable >5 m as a lack of
response to the model, since from that distance a perched
kingbird is unlikely to deter a laying brood parasite; all
other variables indicated a positive response. Following
previous workers (Curio 1975; Barash 1975; Weatherhead 1979;
Andersson et al.1980; Greig-Smith 1980; Regelmann & Curio
1983; Buitron 1983; Reid & Montgomerie 1985), I assumed that
actions that brought the parent closer, or made it more
visible, to the model indicated a higher level of defence.
Thus, the order of activities from least to most defensive
was vocalizations -> hovers -> close-fly-bys -> strikes.
Vocalizations indicated a positive response to the model,
but they are neither highly energetically costly nor as
defensive as the other activities (Knight & Temple 1988).
Close approaches of <2 m were also considered as a risky
response and approaches of 2-5 m somewhat weaker.

Statistical analyses

The data were analysed using non-parametric statistical
tests (Conover 1980) because activity and distance scores
were not normally distributed and all variances were
unequal. Friedman tests were used to determine if there
were significant differences in the response variables

between the three model types. Friedman's two-way analysis
for block designs is obtained by ranking the data within
blocks (nests) and then performing a main-effects analysis
of variance on the ranks (Conover 1980). It has a test
statistic "F". If a significant difference was observed,
the Fisher's protected least significant difference
procedure applied to the ranks was used to compare
differences between pairs of models (e.g. strikes against
the sparrow model vs. strikes against the cowbird model).
Changes in the response variables between the two nesting
stages were analysed using Wilcoxon two-sample tests, which
compare differences between two independent samples. Tied
scores were given the mean of their corresponding ranks.
Chi-square tests were used to compare the number of birds
responding to a model between the two different stages of
the nesting cycle. All statistical tests were two-tailed
with a level of significance of $p < 0.05$.

RESULTS

Responses to the models

Overall, both kingbird parents responded during 81% of
the 183 trials. The number of trials in which either one or
two birds was observed responding to a model did not vary
significantly with nesting stage or model type ($X^2 < 1.73$,
df=1, p>0.10 for all comparisons; Table 2). At the laying
stage, kingbirds spent significantly more time <2 m, and

Table 2: Number of trials in which one or two eastern kingbirds responded when fox sparrow, female brown-headed cowbird, and common grackle models were presented at the nest.

| | Number of eastern kingbirds responding to model | | | | | |
| | Sparrow | | Cowbird | | Grackle | |
Stage	one	two	one	two	one	two
Laying	10	22	7	25	5	27
Nestling	4	25	4	25	4	25
Total	14	47	11	50	9	52

consequently significantly less time >5 m from the cowbird model compared to the sparrow model (Table 3). They also hovered significantly more. Responses that differed significantly between the cowbird and grackle models at the laying stage included close-fly-bys, and vocalizations; responses were both higher for the grackle model. Contrary to the last two comparisons, most of the responses between the grackle and sparrow models differed significantly at the laying stage. Close-fly-bys, hovers, vocalizations, and amount of time spent <2 m from the model were all significantly higher for the grackle model whereas time spent >5 m from the model was significantly lower.

At the nestling stage, again responses to the sparrow and cowbird models differed little (Table 4), although the number of strikes and hovers on the cowbird increased significantly. On the other hand, kingbirds struck the grackle model significantly more often than the cowbird model, and exhibited more close-fly-bys and hovers. They also spent significantly more time <2 m and significantly less time 2-5m from the grackle than from the cowbird model. There were also many significant differences in the responses between the grackle and sparrow models. I observed significant increases in the number of strikes, close-fly-bys, hovers, and in time spent <2 m from the grackle than from the sparrow model. There was also a significant decrease in amount of time spent 2-5 m from the

Table 3: Mean (±SE) responses over five minutes of eastern kingbirds to fox sparrow, female brown-headed cowbird, and common grackle models presented at the nest during the laying stage, and results of Friedman tests for differences between models (N=29).

Response variable[a]	Model			
	Sparrow	Cowbird	Grackle	p
Strikes	3.9 ± 2.5	6.4 ± 2.2	5.8 ± 2.2	0.096
Close-fly-bys	5.0 ± 2.0^1	5.2 ± 1.5^1	18.5 ± 5.3^2	0.001
Hovers	2.8 ± 0.7^1	4.0 ± 0.8^2	5.5 ± 1.0^2	0.023
<2 m	16.5 ± 2.3^1	23.1 ± 1.8^2	22.5 ± 1.8^2	0.001
2-5 m	9.5 ± 1.9	5.4 ± 1.4	7.1 ± 1.7	0.096
>5 m	4.1 ± 1.5^1	1.5 ± 1.0^2	0.4 ± 0.2^2	0.008
Vocalizations	19.4 ± 1.7^1	22.8 ± 1.4^1	26.7 ± 1.2^2	0.0001

[a] Categories of hovers, distance, and vocalizations are given as the mean number of 10-s intervals within trials that the bird was engaged in these behaviours. Strikes and close-fly-bys are given as the mean number recorded in the 5-min trial.

[1,2] Means within rows with different superscripts are significantly different, p<0.05.

Table 4: Mean ($\pm$SE) responses over five minutes of eastern
kingbirds to fox sparrow, female brown-headed cowbird, and
common grackle models presented at the nest during the
nestling stage, and results of Friedman tests for
differences between models (N=32). Conventions as in Table
3.

Response variable	Model			p
	Sparrow	Cowbird	Grackle	
Strikes	2.3 ± 1.7^1	12.4 ± 4.8^2	36.0 ± 9.6^3	0.0001
Close-fly-bys	5.8 ± 2.8^1	7.1 ± 2.2^1	31.2 ± 6.9^2	0.0001
Hovers	2.8 ± 0.9^1	4.1 ± 1.0^2	7.1 ± 1.3^3	0.0001
<2 m	20.2 ± 2.2^1	22.5 ± 1.9^1	25.3 ± 1.8^2	0.002
2-5 m	7.2 ± 1.7^1	6.0 ± 1.6^1	3.0 ± 1.3^2	0.008
>5 m	2.6 ± 1.2	1.6 ± 0.7	1.7 ± 0.9	0.214
Vocalizations	26.2 ± 1.3	26.8 ± 1.4	28.7 ± 0.6	0.075

model. These differences, for the most part, were greater than those found between the grackle and sparrow models at the laying stage.

Effects of nest stage

Vocalizations increased significantly over the nesting cycle in response to the sparrow model (Wilcoxon two-sample test, $z=3.52$, $p=0.0004$), while time spent <2 m from the model increased slightly. However, the more aggressive variables such as strikes, hovers, and close-fly-bys remained the same. Thus, kingbirds responded similarly, but at a low level, to the sparrow during the laying and the nestling stages.

As with the sparrow model, vocalizations increased significantly from laying to nestling stage for the cowbird model ($z=2.50$, $p=0.01$). There was nearly a two-fold increase in the number of strikes during the nestling stage, compared with laying stage, but this difference was not significant. Otherwise, kingbirds exhibited little difference in their level of aggression toward the cowbird model during the laying and nestling stages.

The number of strikes directed toward the grackle model increased significantly over the nesting cycle ($z=2.52$, $p=0.01$), and time spent 2-5 m from the model decreased significantly ($z=2.11$, $p=0.04$). Consequently, the time kingbirds spent <2 m from the model increased, although not significantly so. The number of close-fly-bys nearly

doubled over the nesting cycle, but this difference was not significant. The grackle model, therefore, received the largest increase in aggressive response over the nesting cycle.

DISCUSSION

Response to the cowbird model

Kingbirds responded slightly more aggressively to the cowbird model later in the nesting cycle (Tables 3, 4). Increased levels of response in intensity toward the cowbird model at the nestling stage, when the threat of parasitism did not exist, suggests that kingbirds at Delta Marsh did not recognize the cowbird as a unique threat, but rather simply as another potential predator. Cowbirds are known egg predators (Friedmann 1929; Burgham & Picman 1989; pers. obs.) and occasionally prey on nestlings (DuBois 1956; Tate 1967). A similar, but larger, increase between nest stages was also observed for the grackle model, a known egg and nestling predator (Tables 3, 4).

Smith et al. (1984) found that song sparrows, *Melospiza melodia*, on Mandarte Island also did not recognize the cowbird as a unique threat. Interestingly, the costs of parasitism to these sparrows were low, and due mainly to the removal of a host egg by cowbirds when parasitizing a nest. They concluded that selection did not promote the recognition of the cowbird as an enemy different from other

nest predators.   The same probably holds true for kingbirds at Delta Marsh.   Rothstein (1990) suggested that aggression in some or all hosts may reflect general responses to nest intruders, rather than specifically evolved host defences.

Robertson & Norman (1977) suggested that aggressive individuals should be favoured with selection pressures proportional to the incidence of parasitism.   Thus, selection pressure may be low for kingbirds with regards to recognizing or responding more strongly to the cowbird model since parasitism is rare on kingbirds at Delta Marsh (see Chapter I).   Models of cuckoos were attacked violently by often-parasitized host species, but not by those seldom parasitized (Edwards et al. 1949; Smith & Hosking 1955). Interestingly, cowbird egg ejection by kingbirds at Delta Marsh remains strong despite apparently relaxed selection pressure for such a response.

Whether parasite or predator, cowbirds nonetheless steal eggs from nests.   Thus, host species should be expected to respond as aggressively to a cowbird as they would to any other potential predator near their nests, such as a grackle.   Blancher & Robertson (1982) recorded that high-level aggression by kingbirds effectively reduced losses to predators.   However, constant high-level aggression and activity about the nest is costly energetically, and defending parents could be at risk of injury or death (e.g. Curio & Regelmann 1985; Brunton 1986).

It could also potentially attract other more dangerous
predators, just as it attracts cowbirds (e.g. Smith et al.
1984). Thus, selection should favour responses appropriate
to the specific threat and for the particular stage of the
breeding cycle (Patterson et al. 1980). In response to a
garter snake, *Thamnophis elegans*, which is an effective
predator on nestlings but not on eggs or fledglings,
Patterson et al. (1980) found that adult white-crowned
sparrows, *Zonotrichia leucophrys*, responded most when they
cared for nestlings and least when they had eggs and
fledglings (see also Armstrong 1954; Curio 1975; Gottfried
1979; Buitron 1983; Gottfried et al. 1985 for other examples
of predator-specific responses). If kingbirds at Delta
Marsh responded this way to intruders near their nests, then
results from this study indicate that they consider the
cowbird to be slightly more of a threat than the sparrow,
but definitely less than the grackle. This is suggested
because the response directed at the cowbird was at a level
intermediate to that of the sparrow and grackle models
during both laying and nestling stages.

Robertson & Norman (1977) found that four of six, and
six of eight known rejector species in Ontario and Manitoba,
respectively, did not react significantly more aggressively
to a cowbird compared with a sparrow model, although all but
one showed a trend in that direction. For kingbirds, there
was a significant increase in their mean level of aggression

from the sparrow to the cowbird model in Ontario, but not at Delta Marsh (Robertson & Norman 1977). Folkers (1982) observed that gray catbirds exhibited low scores against models of both a male cowbird and a vesper sparrow, *Pooecetes gramineus*. However, one must be cautious when comparing the results of these studies, because sample sizes were often small, and the index used to quantify aggression levels was subjective and has been criticized because it mixed motor patterns and distance measures (e.g. Smith et al. 1984; Hobson & Sealy 1989). Another downfall of these and other nest defence studies (e.g. Smith et al. 1984) is that they did not test for host responses to a model of a non-parasitic predator. Without the use of such models, it is not possible to categorize the aggression levels directed towards cowbirds relative to those of other nest intruders, and to determine whether any observed responses are unique to the cowbird, which implies recognition of it as a specific threat.

The relative impact of cowbirds and grackles as predators on kingbird nests at Delta Marsh is not known, nor is it known if cowbirds or grackles interact with kingbirds. Smith et al. (1984) found that recognition of the cowbird as an enemy is based mainly on experience gained through encounters near their nests (see also Rothstein & O'Loghlen, unpub. data). Kingbirds might therefore exhibit a low level of response toward the cowbird model because they encounter

female cowbirds infrequently. The low rate of observed parasitism on kingbirds at Delta Marsh supports this suggestion. Greater aggression directed toward the grackle model suggests that kingbirds perceive them to be more of a real threat than cowbirds, perhaps because they are a more common nest predator.

There is always the possibility that kingbirds reacted strongly to the grackle model because it is larger. Although this is possible, it is probably of little consequence (see Robertson & Norman 1976), and does not explain the low level of response to the cowbird model. Other species that suffer substantially from parasitism because they accept cowbird eggs have been shown to respond strongly to a cowbird model (e.g. Briskie & Sealy 1989; Hobson & Sealy 1989). High-level aggression by kingbirds against cowbirds may not be needed because they can avoid most costs of parasitism by simply ejecting the cowbird eggs. Thus, there may not have been a strong selection pressure for kingbirds to evolve specific recognition or aggression towards cowbirds.

All things considered, there remains the obvious question of whether nest defence is effective. This question is difficult, if not impossible, to answer since nobody knows the rate of parasitism that would prevail on a species if hosts did not guard their nests aggressively. It is usually assumed that high levels of aggression towards

models imply relatively effective defences. However,
Rothstein & O'Loghlen (unpub. ms.) recently questioned this
assumption. They suggested that aggression by hosts much
smaller than the parasites may not effectively deter
parasitism (but see Briskie & Sealy 1987). Rothstein &
O'Loghlen (unpub. ms.) found that cowbirds attracted to host
nests by playbacks of calls usually stood their ground for
several minutes despite repeated attacks by western wood
pewees, *Contopus sordidulus*, but always retreated quickly
when approached by larger species, such as robins, Brewer's
blackbirds, *Euphagus cyanocephalus*, and red-winged
blackbirds (see also Hann 1937; Prescott 1947; Selander &
LaRue 1961; Robertson & Norman 1976). Observations of
relatively small hosts of the common cuckoo also suggest
that host aggression is ineffective (Wyllie 1981). However,
even for larger hosts, aggression may not be a reliable
defence because parasites may persist in their efforts to
enter host nests even if chased away repeatedly (see Scott
1977; Rothstein & O'Loghlen, unpub. ms.). Once at the nest,
a female cowbird can lay its egg within about 25 s (e.g.
Hann 1941; Nolan 1978). Still others have found that
aggressive nest defence may be used by the parasite as a cue
to find a host's nest, resulting in a higher frequency of
parasitism on nests of more aggressive individuals (e.g.
Smith et al. 1984).

Whether or not nest defence is effective, if a host is

not always present at its nest, successful parasitism might occur even if it could easily drive off a parasite. Blancher & Robertson (1982) found that a substantial proportion of kingbird nests were preyed upon in their study area, despite high levels of aggression against a human predator. This may be due to the absence of both kingbirds from the nest area, which I observed occasionally for kingbirds at Delta Marsh. Smith (1966) reported a coordinated nest guarding system for kingbirds during incubation, but did not look for it during laying. A similar nest-guarding system in catbirds still left the nest unattended 13% of the observed time (Slack 1976). Perhaps kingbirds cannot constantly watch the nest effectively due to foraging constraints during egg laying.

Although kingbirds in general exhibited a low level of aggression towards cowbirds, some individuals responded with higher aggression levels. Many studies of avian nest defence behaviour have found that enormous variation exists among individuals in their responses to threats at their nests (Montgomerie & Weatherhead 1988; Hobson et al. 1988; Westmoreland 1989). Variation among individuals may be important for a species in being a factor on which natural selection can act. As well, individuals may show variability in their responses as an adaptation to being unpredictable when confronted by a predator (see Montgomerie & Weatherhead 1988).

SUMMARY

1. Eastern kingbirds eject, by grasping, brown-headed cowbird and other foreign eggs from their nests.

2. Eastern kingbirds recognize their own egg-type and eject all other egg-types that differ from it.

3. This recognition apparently is learned from the first egg or eggs that they see in their first nest, and is possibly reinforced with each subsequent nesting attempt.

4. Eastern kingbirds at Delta Marsh presently maintain their interspecific egg ejection behaviour despite an apparent lack of cowbird parasitism.

5. Eastern kingbirds did not discriminate between their own and other conspecific eggs, which suggests that their egg ejection behaviour originally evolved as an adaptation to counter cowbird parasitism.

6. Eastern kingbirds do not recognize the brown-headed cowbird as a unique or dangerous threat, but rather simply as another nest intruder.

7. This pattern of recognition may be due to low selection pressure on rejector species for specific aggressive nest defence against brown-headed cowbirds.

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Appendix: Ejection time as compared to the number of days prior to clutch initiation when eastern kingbird nests were experimentally parasitized with brown-headed cowbird eggs at the empty stage.

Nest no.[a]	Ejection time(h)	No. days prior to clutch initiation when parasitized
87-2	48	10
87-3	1	4
87-5	1	7
89-3	48	4
89-9	24	4
89-15	1	2
89-20	96	6
89-13E	5	6
89-14E	5	2
89-1BE	1	3
89-2BE	5	4
89-5BE	5	3
89-3E	5	5
90-7	5	1
90-8	5	4
90-12	96	2
90-3E	144	2
90-7E	24	0
90-1BE	1	1
90-5BE	1	4
90-6BE	5	5

[a] Two nests were abandoned following removal of the single cowbird egg.