

# Evolution of defenses against brood parasitism: quantifying the costs and benefits of egg ejection in Gray Catbirds

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## Introduction

Obligate brood parasites lay all their eggs in host nests and leave the care of their offspring entirely to the hosts. The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite that can be reared by 140 other species (Friedmann and Kiff 1985). Hosts of the cowbird often incur a reproductive cost when they raise parasitic young (Payne 1977, May and Robinson 1985); therefore, there is a strong selection pressure for hosts to evolve antiparasite defenses. Defenses range from nest concealment (Grieff 1995), nest defence (Gill and Sealy 1996), nest desertion (Hill and Sealy 1994), egg burial (Sealy 1995), to egg ejection (Rothstein 1975). Egg ejection is the most effective method to avoid the costs of raising cowbird young because it is targeted specifically at the cowbird egg, unlike nest desertion and burial, which may involve deserting or burying the host's own eggs. Thus, it is surprising that only 15 species in North America have evolved egg ejection behavior.

Selection pressure from brood parasitism is the only reasonable explanation for the evolution of egg ejection behavior. Results from my 1996 field season indicate that egg ejection by Gray Catbirds (*Dumetella carolinensis*) has not evolved in response to conspecific brood parasitism. Catbirds did not eject any conspecific eggs that were added experimentally to their nests ( $n = 10$ ) or switched with one of their own eggs ( $n = 17$ ). Furthermore, no evidence of conspecific brood parasitism was detected in 72 catbird nests that were found on or before the date on which the first catbird egg was laid (LD1) and survived to at least LD6 in 1996 and 1997. Therefore, I proposed that egg ejection in catbirds has evolved in response to parasitism by the Brown-headed Cowbird. I tested the hypothesis that egg ejection by catbirds has evolved as an antiparasite strategy by comparing the costs of ejection and the costs of rearing a cowbird. This hypothesis predicts that the cost of accepting a cowbird egg is greater than the cost of ejecting it. Ejection would be costly if the catbird damaged or ejected one or more of its own eggs along with the parasitic egg (Davies and Brooke 1988). This is only the second study to determine whether it is costly

for an ejecter species to raise a cowbird nestling. Røskaft *et al.* (1993) found that Bullock's Orioles (*Icterus bullockii*) did not experience a significant cost of rearing a cowbird chick.

## Methods

The 1997 field season occurred at Delta Marsh, Manitoba from May 15 to July 10. A total of 113 catbird nests were found on the properties of the University Field Station (Delta Marsh), the Portage Country Club, Delta Beach Cottage Area, and the Delta Waterfowl and Wetlands Research Station.

## Cost of ejection

All cowbird eggs were added before noon (i.e. earlier during the day to more closely resemble actual parasitism events that usually occur a few minutes before sunrise, Scott 1991). Catbird nests found early in the nesting stage were parasitized with one model cowbird egg on LD2 (i.e., the day that the second catbird egg is laid). Nests found at a later stage were parasitized on LD5 or during early incubation. Model eggs were made of plaster-of-Paris from casts of real Brown-headed Cowbird eggs, painted with acrylic paints and polyurethane (as in Rothstein 1975). Model eggs have been used successfully in many studies of host responses to brood parasitism (e.g. Rothstein 1975, Davies and Brooke 1989, Hill and Sealy 1994). Catbird eggs were numbered according to their laying order, which was useful in determining when partial predation had occurred during the egg-laying stage and whether conspecific brood parasitism occurred. I did not remove a catbird egg from experimental nests because cowbirds do not always remove a host egg from the nests they parasitize, and host-egg removal does not influence host acceptance (Davies and Brooke 1989, Sealy 1992, 1995).

Nests were checked five hours after parasitism and every morning thereafter until the cowbird egg was ejected. The cowbird egg was recorded as ejected if it was missing, and accepted if it remained in the nest for at least six days and the nest remained active. When one

host egg was missing along with the model cowbird egg, but the nest remained active, this was considered an ejection cost (i.e. accidental breakage or ejection of a host egg during the ejection of the cowbird egg). This inference has been used also by Rohwer *et al.* (1989), Sealy and Bazin (1995), Sealy and Neudorf (1995), and Sealy (1996).

#### *Cost of acceptance*

Nests of accepter species that are commonly parasitized (Song Sparrows *Melospiza melodia*, Yellow Warblers *Dendroica petechia*, and Red-winged Blackbirds *Agelaius phoeniceus*) were found and monitored for cowbird eggs. All cowbird eggs that were found during the time that catbird clutches are being initiated were collected and kept in an incubator until they hatched to eliminate the risk of predation. Cowbird eggs that were collected before catbird clutches were initiated were kept in a refrigerator at 10°C until they needed to be incubated. Cool temperatures arrested embryonic development and allowed the embryo to remain viable longer (Drent 1975). To maximize the number of cowbird eggs collected, female cowbirds were captured using baited tunnel traps. Females were fed and maintained in cages for a maximum of three mornings, and any eggs laid by the female during this time were collected and kept in the incubator (methods follow D.G. McMaster, pers. comm.). Eggs in the incubator were turned four times daily to prevent embryonic membranes from adhering to the shells, and candled and massed every two days to track embryo development.

Newly hatched cowbird chicks were placed into experimental nests, whereas no chicks were added to control nests. Newly hatched cowbird chicks were placed in randomly chosen catbird nests that contained catbird chicks that hatched on that same day. Catbird chicks in both groups were color-marked with non-toxic red or black marker on their right or left tarsus so that the development of each chick could be tracked. The left tarsus length and mass of all chicks were measured daily. Chicks were not measured past day 8 (where day 0 is the day that the first catbird chicks hatched) because doing so may cause chicks to fledge prematurely (pers. obs.). The number of catbird chicks that fledge was defined as the number of chicks present in the nest at 8 days post-hatch.

The fates of the catbird nests were classified as surviving to day 8, or failing due to predation, inclement weather, or desertion. The nest failed due to predation if all of the eggs or nestlings were gone. The nest failed due to inclement weather when all the nestlings were found dead or missing on July 3, the day after a cold, stormy, windy day. The nest was deserted if all of the eggs remained in the nest, but the eggs were cold and

the adults were not present on consecutive days.

A one-way ANOVA was used to test whether the presence of the cowbird nestling affected the proportion of catbird eggs that fledged from a nest. Only nests that fledged at least one catbird chick were included in this analysis. Clutch size, effective brood size (the mean number of chicks in nest per day including the cowbird nestling), and number of unhatched catbird eggs were used as covariates.

## Results and Discussion

#### *Cost of ejection*

Only  $0.02 \pm 0.15$  catbird eggs (or 2 eggs out of 90 nests) were lost per ejection; therefore, only a small cost of acceptance is needed to explain the evolution of ejection behavior in response to cowbird parasitism. In both cases, the cowbird egg was added to the catbird nest on LD2 and the cowbird egg was ejected within 24 hours. In one nest (GC-97-9), the second-laid catbird egg was found on the rim when the cowbird egg was detected missing. In the second nest (GC-97-C2), the second laid catbird egg was missing along with the cowbird egg. In both cases, the third catbird egg was laid on schedule.

#### *Cost of acceptance*

Thirty-eight percent of the 111 catbird nests found survived to day 8. The remaining nests were depredated (43%), failed due to the storm (18%), or were deserted (1%). When clutch size, effective brood size, and number of unhatched catbird eggs were used as covariates, the presence of the cowbird chick significantly decreased the fledging success of catbird chicks (Fig. 1,  $F = 49.6$ ,  $p < 0.0005$ ).

#### *Does the cost of acceptance exceed the cost of ejection?*

When clutch size, effective brood size, and number of unhatched catbird eggs were used as covariates, the adjusted proportion of catbird eggs laid in a clutch that fledged in control nests (no cowbird chick) and experimental nests (with cowbird chick) was 0.84 and 0.77, respectively. This indicates that the presence of the cowbird chick decreased the proportion of catbird eggs laid that fledged by 7%. Using the fact that the average clutch size of catbird nests in 1997 was  $4.39 \pm 0.57$  ( $n = 92$ ), the presence of a cowbird chick caused 0.31 fewer chicks per nest to survive to day 8.

Conversely, only  $0.02 \pm 0.15$  catbird eggs were lost per ejection. The cost of ejection and the cost of rearing a cowbird chick must be in the same units. Eggs are not

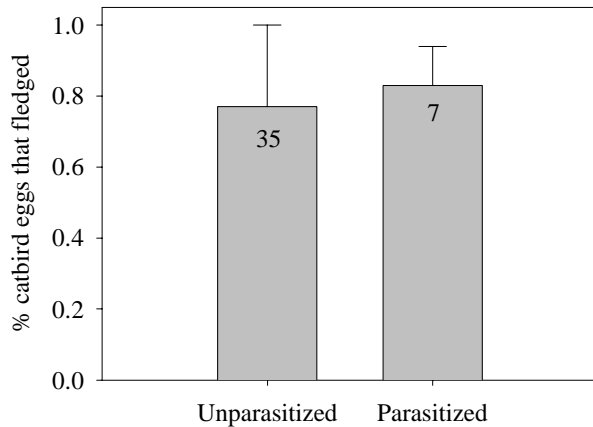


Figure 1. Observed proportion of catbird eggs that fledged in parasitized and unparasitized nests. Error bars indicate standard deviations.

as valuable as nestlings because eggs have a lower probability of fledging. The cost of ejection was, therefore, devalued by 31.1%, which is the percentage of catbird eggs that survived to day 8 in nests that did not receive a cowbird chick (calculated from 389 catbird eggs laid in 97 nests). Therefore, the cost of ejection (0.0062 catbird chicks per nest) is much less than the cost of accepting the cowbird chick (0.31 catbird chicks per nest), and the hypothesis that catbirds have evolved ejection behavior in response to cowbird parasitism is supported.

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