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VIDEO RECORDING REVEALS THE METHOD OF EJECTION OF BROWN-HEADED COWBIRD EGGS AND NO COST IN AMERICAN ROBINS AND GRAY CATBIRDS

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Abstract. Despite the importance of knowing the method and cost of ejection in understanding the persistence of brood parasitism, anecdotal records of witnessed ejections of real Brown-headed Cowbird (*Molothrus ater*) eggs exist for only eight of ~30 ejecter species. The probability of a host damaging its own egg while ejecting a parasite's egg is thought to be lower for hosts that grasp-eject, but grasp-ejection is an option only for hosts with appropriate bills. For hosts incapable of grasp-ejection, the cost of puncture-ejection may render acceptance adaptive. We video-recorded 12 ejections of real cowbird eggs by American Robins (*Turdus migratorius*) and 17 by Gray Catbirds (*Dumetella carolinensis*). With no damage to their own eggs, robins grasp-ejected all cowbird eggs, whereas catbirds grasp-ejected 14 eggs and puncture-ejected three eggs. Our study revealed that a few species use a mixture of ejection methods and even large species may puncture-eject with little cost.

Key words: cost, Brown-headed Cowbird, eggs, grasp-ejection, Molothrus ater, *parasitism, puncture-ejection, video.*

Grabaciones de Video Revelan el Método de Eyección de los Huevos de *Molothrus ater* Sin Costo en *Turdus migratorius* y *Dumetella carolinensis*

Resumen. A pesar de la importancia de conocer el método y el costo de eyección para entender la persistencia del parasitismo de nidada, sólo existen registros anecdóticos de eyecciones observadas de huevos reales de *Molothrus ater* para ocho de las 26 especies que eyectan huevos. Se piensa que la probabilidad de que un hospedero dañe su propio huevo mientras eyecta el huevo de un parásito es más baja para los hospederos que eyectan los huevos agarrándolos, pero este tipo de eyección es una opción sólo para los hospederos con los picos apropiados. Para los hospederos incapaces de eyectar un huevo agarrándolo, el costo de eyección por perforación puede hacer que la aceptación del huevo sea adaptativa. Registramos con video 12 eyecciones de huevos reales de *M. ater* por parte de *Turdus migratorius* y 17 por parte de *Dumetella carolinensis*. Sin hacerle daño a sus propios huevos, *T. migratorius* eyectó todos los huevos de *M. ater* agarrándolos, mientras que *D. carolinensis* eyectó 14 huevos agarrándolos y tres huevos perforándolos. Nuestro estudio revela que unas pocas especies usan una mezcla de métodos de eyección e incluso las especies grandes pueden eyectar por perforación con bajo costo.

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Raising young of the Brown-headed Cowbird (*Molothrus ater*) reduces the host's reproductive success (Lorenzana and Sealy 1999), selecting for host behavior that reduces the cost of brood parasitism (anti-parasite behavior; Rothstein 1990). Of the anti-parasite behaviors used by hosts, such as nest vigilance, aggressive nest defense, nest desertion (including burial), or egg ejection, the most effective appears to be ejection of parasitic eggs (Rothstein 1975, Sealy 1996, Winfree 1999, Underwood and Sealy 2006). Hosts use one of two methods to eject cowbird eggs; both involve the bill (Table 1; Rohwer and Spaw 1988, Marchetti 1992, Underwood and Sealy 2006). Hosts either puncture a hole through the shell of the cowbird egg and use it to lift and carry the punctured egg out of the nest (puncture-ejection) or they grasp the entire unbroken egg between the mandibles and carry it from the nest (grasp-ejection; Rothstein 1975, Rohwer and Spaw 1988). Bill size may limit grasp-ejection to larger hosts, but all hosts should be able to remove cowbird eggs by puncturing them. Yet fewer than 30 of the more than 140 host species known to have raised a cowbird eject cowbird eggs regularly (rejecter hosts; Friedmann and Kiff 1985, Peer and Sealy 2004a).

One hypothesis for this enigma, "evolutionary lag," states hosts accept parasitism because anti-parasite behavior takes time to appear, to be selected, and to spread within a population, providing cowbirds with a temporal and spatial window of opportunity for success with each population of hosts (Mayfield 1965, Rothstein 1982). Alternatively, the "evolutionary equilibrium" hypothesis proposes that acceptance is selected in hosts for which the mean number of host eggs damaged during ejection (i.e., cost of ejection) exceeds the equivalent mean number of host fledglings lost in raising a cowbird (Rohwer and Spaw 1988). Because the cost of ejection likely varies by species because of differences in the hosts' physical abilities to eject foreign eggs (Martín-Vivaldi et al. 2002), knowing the net balance of cost of ejection and acceptance incurred by each species is essential for understanding whether lag or equilibrium best explains acceptance (Røskaft et al. 1993, Lorenzana and Sealy 2001).

The method of ejection and its associated cost have been witnessed and measured directly for very few hosts despite their importance for understanding acceptance in cowbird hosts (Table 1). The method of ejection a host uses when faced with a real cowbird egg has been identified for eight of the ~30 ejecter

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TABLE 1. Method used by hosts of the Brown-headed Cowbird for ejecting experimentally introduced eggs or models. Experiments using models are indicated by the type of material.

Host species	Method of ejection	*n*	Video-recorded?	Egg type	Cost of ejection $\bar{x} \pm$ SE (*n*)	Reference
Eastern Kingbird	Grasp	23	No	Real		Bazin 1991
Warbling Vireo	Puncture	4	No	Real	0 (4)	Sealy 1996
	Grasp	2	Yes	Plaster	0 (2)	Underwood and Sealy 2006
	Grasp	1	Yes	Real	0 (1)	Underwood and Sealy 2006
	Grasp	1	Yes	Real	0 (1)	J. L. Rasmussen, unpublished data
American Robin	Puncture	1	No	Real		Friedmann 1929:185
	Puncture	1	Photo	Real		Friedmann 1929:192
	Grasp	2	No	Real		Nice 1944
	Puncture	2	No	Real		Briskie et al. 1992
	Grasp	12	Yes	Real	0 (10)	This study
Gray Catbird	Grasp	2	No	Brown Thrasher[a]		A. Wilson *in* Brewer 1840:242
	Not mentioned	1	No	Real		Berger 1951
	Grasp	1[b]	No	Plaster		Rothstein 1975
	Grasp[c]	1	Yes	Plastic	n/a[d]	Hauber 1998
	Grasp (14), Puncture (3)	17	Yes	Real	0 (9)	This study
Brown Thrasher[a]	Grasp	1	No	Plaster		Rothstein 1970
	Grasp	3[b]	No	Plaster		Rothstein 1975
	Grasp	1	Yes	Real	0 (1)[e]	J. L. Rasmussen, unpublished data
Crissal Thrasher[f]	Grasp	1	No	Real		Finch 1982
Great-tailed Grackle[g]	Grasp	34	No	Real, Wood[h]		Peer and Sealy 2004b
Bullock's Oriole[i]	Puncture	1	No	House Sparrow[j]		Rothstein 1977
	Puncture	5	No	Real		S. Rohwer *in* Sealy and Neudorf 1995
Baltimore Oriole	Puncture	14	No	Real	0.43 ± 0.17 (14)	Sealy and Neudorf 1995

[a] *Toxostoma rufum*.
[b] Rothstein (1975) observed eleven ejections at one catbird and three Brown Thrasher nests.
[c] After one catbird grasp-ejected one plastic model, a second catbird appeared and pecked at the other model eggs in the nest without ejecting any of them.
[d] Not applicable; the catbird was depredating an artificial nest with artificial eggs.
[e] But two eggs were damaged during a previous ejection of a real cowbird egg, which was not video-recorded.
[f] *Toxostoma crissale*.
[g] *Quiscalus mexicanus*.
[h] Nests were tested with real (*n* = 3) and artificial (*n* = 77) Bronzed Cowbird (*Molothrus aeneus*) eggs and real (*n* = 6) and artificial (*n* = 74) Brown-headed Cowbird eggs.
[i] *Icterus bullockii*.
[j] *Passer domesticus*.

hosts by observation of ejections (Table 1), and it has been determined indirectly for the remainder of these species. Of the eight species, fewer species puncture-eject than grasp-eject (Table 1). Large samples of observed ejections suggest the Eastern Kingbird (*Tyrannus tyrannus*) grasp-ejects only and the Baltimore Oriole (*Icterus galbula*) puncture-ejects only (Bazin 1991, Sealy and Neudorf 1995). Smaller samples of witnessed ejections of the other five species suggest they use both methods but that any one population uses only one method. By contrast, Warbling Vireos (*Vireo gilvus*) breeding at Delta, Manitoba, were observed to puncture-eject by Sealy (1996) but were more recently observed to grasp-eject by Underwood and Sealy (2006).

Researchers have assumed the method of ejection is homogeneous within a host's population and have used this information to generalize about the cost of ejection. Furthermore, for some species the method and cost of ejection have been assessed by tests with eggs of species other than the cowbird or with model eggs, for certain hosts eliminating or increasing the options of ejection over those with a real cowbird egg (Prather et al. 2007). Use of model eggs and eggs of nonparasitic species is inadequate because it prevents or facilitates puncture-ejection by the host, respectively. For example, all witnessed ejections of model eggs have been by grasp-ejection (Table 1). Measured indirectly, the cost incurred by hosts assumed to puncture-eject is higher than the cost incurred by hosts assumed to grasp-eject (Rohwer and Spaw 1988, Rohwer et al. 1989, Røskaft et al. 1993, Antonov et al. 2006). The difference in cost is attributable to the relatively thicker shell and rounder shape of cowbird eggs, which are believed to have evolved as an adaptation to prevent puncture-ejection by increasing the probability the host's bill will ricochet from the parasitic egg into the host's eggs during attempts at ejection (Rohwer and Spaw 1988, Picman 1989, Rohwer et al. 1989, Antonov et al. 2006) and by increasing the energy required to puncture the shell (Soler et al. 2002). Alternatively, grasp-ejection is more common (Table 1) because it is believed to be less costly (Rohwer and Spaw 1988, Underwood and Sealy 2006).

Although direct observations of hosts ejecting real cowbird eggs are few, the putative higher cost of puncture-ejection relative to grasp-ejection has become dogma, even leading some to suggest the cost associated with puncture-ejection may force hosts too small to grasp-eject to accept parasitic eggs (Rohwer and Spaw 1988) and others to use the cost of ejection as an indicator of the method of ejection (see Moksnes et al. 1991). Direct observations of the cost of puncture-ejecting real cowbird eggs are available for only two cowbird hosts, and they suggest the cost of ejection in the two species varies. Baltimore Orioles lost ($\bar{x}$ ± SE) 0.43 ± 0.17 eggs per puncture-ejected cowbird egg (n = 14; Sealy and Neudorf 1995), but no Warbling Vireos damaged their own eggs in four witnessed puncture-ejections (Sealy 1996). An appropriate assessment of the cost of ejection according to the method by which it is accomplished requires direct observations of hosts ejecting real cowbird eggs.

Here, we present results of video recordings of American Robins (*Turdus migratorius*) and Gray Catbirds (*Dumetella carolinensis*) ejecting real cowbird eggs from their nests. From these recordings we determined the method of ejection and associated cost. The method of ejection used by both of these species was known previously only through anecdotal observations (Table 1), and both were assumed to be grasp-ejecters from their ability to eject nonpuncturable models from their nests (Rothstein 1975).

METHODS

We located robin and catbird nests at Delta, Manitoba, Canada (50° 11′ N, 98° 19′ W), on the properties of the Delta Marsh Field Station (University of Manitoba), Portage Country Club, cottage owners of the Delta Beach Cottage Area, Delta Waterfowl and Wetlands Research Station, and Bell Family Estate during May and June 2006 and 2007.

We tested nests once with randomly selected cowbird eggs, collected freshly laid from nests of the Yellow Warbler (*Dendroica petechia*) and Song Sparrow (*Melospiza melodia*). The dimensions of a subset of the eggs used in robin nests were ($\bar{x}$ ± SE) 16.54 ± 0.19 mm wide, 21.59 ± 0.25 mm long, and 3.24 ± 0.23 g (n = 7). Eggs used in catbird nests were ($\bar{x}$ ± SE) 16.83 ± 0.08 mm wide, 21.24 ± 0.22 mm long, and 3.30 ± 0.13 g (n = 10). We recorded the cost of ejection as the number of host eggs damaged or removed by the host per ejection in 2007 but not in 2006.

Video cameras were set up between 1 and 8 m from nests. Nests were checked ~30 min later to ensure the camera did not disturb the adults and prevent them from returning to the nest. We used cameras similar to those described by Sabine et al. (2005): camouflaged JVC camcorders with 30-GB hard drives and Sony CCD-TRV308 NTSC Hi 8 cameras connected to Sony 160-GB DVD/HDD recorders. Motomaster Eliminator 1200W Powerboxes powered the cameras, which recorded continuously for 8 hr before the batteries had to be replaced. Cameras were set up in the morning and taken down at dusk or during inclement weather.

RESULTS

We video-recorded 12 and 17 ejections of real cowbird eggs by robins and catbirds, respectively, two and seven in 2006, and the rest in 2007. Robins grasp-ejected all 12 real cowbird eggs (Fig. 1A), whereas catbirds grasp-ejected 14 of 17 (82%, Fig. 1B) and puncture-ejected three of 17 (18%, Fig. 2). No host eggs were damaged in 10 of 10 and 9 of 9 observed grasp-ejections by robins and catbirds, respectively, in which the cost was measured. No damage was incurred by the catbird in puncture-ejecting a cowbird egg, but the cost of puncture-ejection was measured at only one nest.

DISCUSSION

Video-recordings of robins and catbirds ejecting real cowbird eggs revealed that these species use grasp-ejection most frequently. Our result for the robin differs from three of the four previously published observations of robins ejecting cowbird eggs (i.e., Friedmann 1929, Briskie et al. 1992), which suggested puncture-ejection. Previous observations have suggested catbirds are grasp-ejecters, thus ours is the first documentation of puncture-ejection in this species. Although robins at Delta Marsh only grasp-ejected, catbirds both grasp- and puncture-ejected. Our results combined with other observations of ejections of real cowbird eggs, the Warbling Vireo, robin, and catbird all use a

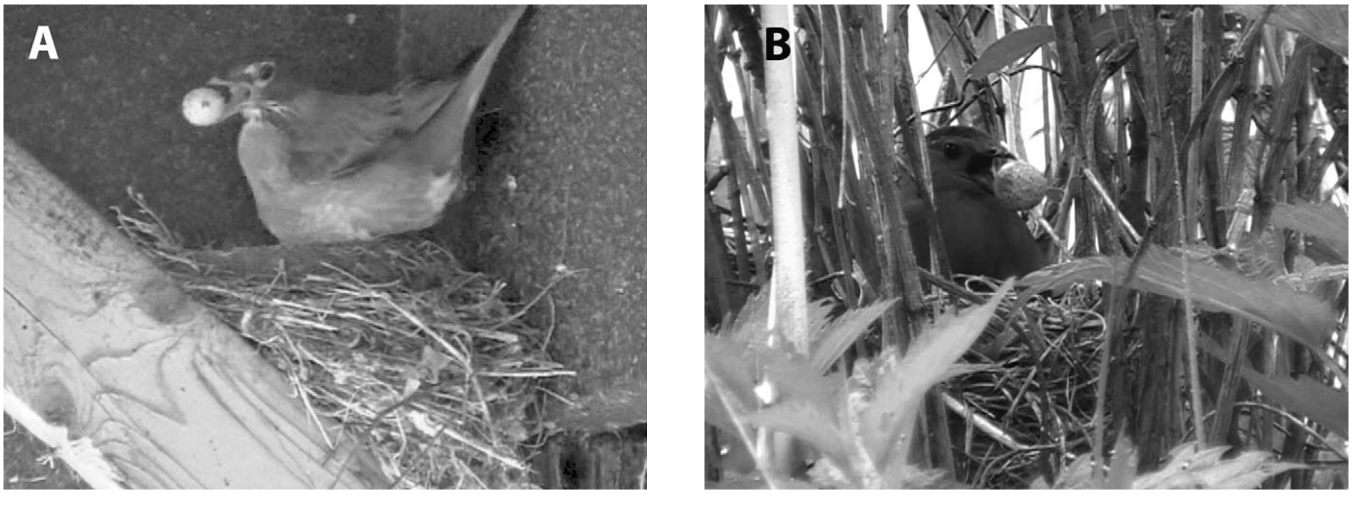

FIGURE 1. Grasp-ejection of real Brown-headed Cowbird eggs by an American Robin (A) and a Gray Catbird (B).

FIGURE 2. Puncture-ejection of a real Brown-headed Cowbird egg by a Gray Catbird.

mixture of ejection methods, whereas the six other species in which ejections have been observed either all grasp-eject or all puncture-eject (Table 1).

When ejecting real cowbird eggs robins and catbirds did not damage any of their own eggs, regardless of the method of ejection. For none of the previously witnessed ejections was the cost of ejection reported. In two previous studies where the cost was measured indirectly, catbirds incurred losses of 0.02 eggs per ejection of model cowbird eggs (Rothstein 1976, Lorenzana and Sealy 2001). For the robin, Rothstein (1976) recorded 0.03 damaged or missing eggs per ejection of model eggs. Similarly, Sealy (*in* Lorenzana and Sealy 2001) recorded 0.08 damaged or missing eggs per ejection of model cowbird eggs by robins, and Rohwer et al. (1989) recorded no damage to the host's eggs in two ejections of real cowbird eggs by robins.

The slightly higher cost of ejection recorded by others may reflect partial depredation of eggs, egg-recognition errors, or the use of model eggs, which may have rendered puncture-ejection more difficult (Martín-Vivaldi et al. 2002). In our study we controlled these factors, however, because video recordings permitted us to monitor partial depredation and we used real cowbird eggs. It is also possible that our small sample sizes did not allow any cost to be detected.

In one instance, a catbird puncture-ejected a cowbird egg at no cost, suggesting that this type of ejection is not as costly as previously thought, at least in larger hosts, but, again, a larger sample size is required. Similarly, Warbling Vireos puncture-ejected four real cowbird eggs with no cost (Sealy 1996). Yet even if puncture-ejection is adaptive in hosts the size of a Warbling Vireo or larger, it may not be in smaller hosts because they may lack the strength to puncture eggs efficiently (Spaw and Rohwer 1987, Sealy 1996). The cost of ejection for hosts smaller than the Warbling Vireo cannot be measured because currently none is known to eject cowbird eggs. By contrast, puncture-ejection is more costly in the larger Baltimore Oriole (Table 1). Puncture-ejection and its high cost in the Baltimore Oriole is perplexing but might be related to that species' straight, acute bill or deep, pendant nest (Rothstein 1977, Underwood and Sealy 2006).

A mixture of puncture- and grasp-ejection has been documented in the Warbling Vireo and catbird at Delta Marsh and in the robin for North America as a whole. The use of some puncture-ejection by large hosts is surprising. This mixture of methods suggests either plasticity in the rejection behavior of individuals or the mixture of individuals that grasp-eject and puncture-eject in the same population, indicating that grasp-ejection as a trait may not be fixed (Underwood and Sealy 2006). Testing the same individual repeatedly could determine which scenario prevails. Repeated tests of individual Blackcaps (*Sylvia atricapilla*) found puncture-ejection used in all ejections of eggs of the Common Cuckoo (*Cuculus canorus*) (Honza et al. 2007). This is not surprising because the small size of a Blackcap's bill relative to the size of cuckoo eggs may limit the options for ejection to puncture-ejection. Recording multiple ejections by the same individual will reveal whether ejection by cowbird hosts is flexible or whether each individual is limited to either puncture- or grasp-ejection. Occasional puncture-ejection by larger hosts also raises the possibility that puncture-ejection may have evolved first in these larger hosts and drove selection for stronger cowbird eggshells (Underwood and Sealy 2006). Further work is needed to determine how widespread the use of puncture-ejection is by large cowbird hosts that are assumed to be grasp-ejecters.

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