

**LIMITS OF GRASP-EJECTION IN BROWN-HEADED COWBIRD HOSTS:
IMPLICATIONS FOR EVOLUTIONARY EQUILIBRIUM AND
EVOLUTIONARY LAG**

BY

JUSTIN LEE RASMUSSEN

A Thesis Submitted to the Faculty of Graduate Studies of
The University of Manitoba
in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

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Abstract

It is not known why small hosts of the Brown-headed Cowbird (*Molothrus ater*) accept parasitic eggs. One reason that has been suggested for small hosts is that rejection is not adaptive because they cannot reject the eggs efficiently. Yet, grasp-ejection has a negligible cost, but it likely requires a bill of a certain length, a length that is not known. In Chapter 1, to estimate the minimum bill length required to grasp-eject a cowbird egg, I tested the ability of known grasp-ejectors, American Robins (*Turdus migratorius*) and Gray Catbird (*Dumetella carolinensis*) to eject widths larger than a cowbird egg by adding sequentially larger, non-puncturable objects to their nests. Not all ejections were video-recorded and, thus, it was assumed that the absence of a model at an active nest meant that it was grasp-ejected by the host. Preliminary video-recordings, taken to confirm grasp-ejection as the method of ejection revealed that American Robins and Gray Catbirds ejected real Brown-headed Cowbird eggs and models 16-mm by grasping them by their entire width (i.e., grasp-ejection) and they would eject models 29-mm wide by grasping only part of their width (i.e., pinch-ejection). The width at which American Robins and Gray Catbirds switched from grasp-ejection to pinch-ejection, I assumed, was the limit width of grasp-ejection, because grasping the entire width of the model is the less complicated option for ejecting the model.

In Chapter 2, I present the results of another experiment that involved augmenting the sample of video-recorded ejections already taken to determine the method of ejection used by American Robins and Gray Catbirds for models of different widths. By using the ratio of the maximum width of grasp-ejected objects to host tomial length as determined from 105 video-recorded ejections, I predicted that the minimum tomial length required

for grasp-ejection is between 14.91 mm and 17.08 mm. This estimate allows for the identification of hosts physically capable of efficient rejection of parasitic eggs, but further experiments are required to reduce the range of the predicted interval.

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Chapter 1: Physical constraints on egg ejection behavior: approaches for anatomical indexes to identify hosts capable of grasp-ejection in avian brood parasitic systems

Obligate brood-parasitic Brown-headed Cowbirds (*Molothrus ater*; hereafter cowbirds) lay their eggs in the nests of other passerine species and leave the incubation of their eggs and the fostering of their young to the hosts (Rothstein 1975). Raising a cowbird decreases host fitness by reducing the number of host young that reach independence (Lorenzana and Sealy 1999, Rasmussen and Sealy 2006). The cost of cowbird egg acceptance results from interference during incubation (i.e., the cowbird egg prevents a host from properly incubating its own eggs, thus reducing hatching success of host eggs; Sealy et al. 2002) and nestling competition (i.e., a cowbird chick outcompetes host nestlings for parental care; Soler et al. 1995, Dearborn et al. 1998). Additionally, the presence of a cowbird chick also decreases host hatching success (McMaster and Sealy 1999) and, because of its loud and incessant begging, increases the probability of nest predation (Massoni and Reboresda 1998, Dearborn 1999). The costs of parasitism should select for behaviors that counter parasitism and egg rejection appears to be the most effective defense (Rothstein 1975). Yet despite the cost of parasitism, only 26 of the approximately 140 suitable host species are known to reject cowbird eggs at frequencies higher than 75% and only four of the approximately 140 suitable host species reject cowbird eggs at frequencies between 30 and 75% (Rothstein 1975, Friedmann and Kiff 1985, Ortega 1998, Peer and Sealy 2004).

Acceptance by so many hosts is puzzling because of the costs involved (Winfree 1999). Adding to the enigma is that the appearance (i.e., color, pattern, and shape) of

cowbird eggs differs from the eggs of many accepters (Mermoz and Ornelas 2004), thus, providing hosts with the opportunity to evolve ejection behavior given the precedence of refined egg discrimination in some hosts such as the Brown Thrasher (*Toxostoma rufum*; Rothstein 1975, Haas and Haas 1998). Two hypotheses have been proposed to explain acceptance: evolutionary lag and evolutionary equilibrium.

The evolutionary lag hypothesis posits that there is a lag between the cost of parasitism and evolution of adaptive behaviors by the hosts. This hypothesis suggests that acceptance will be manifested in host species for which the appearance of appropriate genetic variants has not yet occurred or where host species have not been parasitized long enough or frequently enough for rejection to have been favored (Rothstein 1975, 1982, 1990; Davies and Brooke 1989). Alternatively, the equilibrium hypothesis posits that acceptance has been selected because the cost of rejection exceeds the cost of acceptance (Rohwer and Spaw 1988, Lotem and Nakamura 1998). These hypotheses are based on different assumptions of the physical abilities of hosts (Spaw and Rohwer 1987, Rohwer and Spaw 1988). Equilibrium assumes that small hosts, with their small bill sizes, are limited to rejecting cowbird eggs through more costly methods such as puncture-ejection, egg burial, and nest desertion. Alternatively, lag does not consider the possible physical limits of hosts in terms of ejecting cowbird eggs and, therefore, bill size and acceptance need not be correlated (Rothstein 1975, Rohwer and Spaw 1988). However, there is no reason to assume that either hypothesis can be applied to all cowbird hosts (Ortega 1998, Davies 1999). Rejection costs may explain acceptance in certain hosts, whereas lag may explain acceptance in hosts that are physically capable of rejecting parasitic eggs efficiently. Therefore, knowing the minimum physical requirements for efficient ejection

of cowbird eggs and host-specific costs of cowbird egg acceptance is essential for understanding whether equilibrium or lag better explains acceptance or rejection in each host species.

Anti-parasitic behaviors should evolve only in species for which they are adaptive, that is, where the cost of rejection is less than the cost of raising the parasite (Rothstein 1975). Costs of rejection include damage to host eggs inflicted during ejection attempts (Spaw and Rohwer 1987), misidentification and subsequent ejection of own eggs instead of parasitic eggs (Davies and Brooke 1988, Davies et al. 1996, Davies 1999), ejection of a host egg in an unparasitized nest (Marchetti 1992, Røskaft et al. 2002), and loss of energy and time when the cowbird egg is buried or the nest is deserted (Sealy 1995, Lotem and Nakamura 1998). Egg ejection is believed to have evolved in Gray Catbirds (*Dumetella carolinensis*) because the cost of ejecting a cowbird egg is less than the cost of accepting a cowbird egg (Lorenzana and Sealy 2001). For Gray Catbirds, the cost of ejection is 0.01 catbird eggs per ejection, whereas the cost of acceptance is 0.79 fewer chicks fledging per ejection (Lorenzana and Sealy 2001). Similarly, ejection of cowbird eggs by Bullock's Orioles (*Icterus bullockii*) is selected for because the average cost of puncture-ejection (i.e., 0.26 host eggs per ejection; Røskaft et al. 1993) is lower than the average cost of acceptance (i.e., 0.4 chicks per brood). Yet, the cost of puncture-ejection has been measured to be as high as 0.42 host eggs per ejection in this species (Rohwer et al. 1989).

Of the anti-parasite defenses used by hosts, such as nest vigilance, aggressive nest defense, nest desertion, burial, or egg ejection, apparently the most effective defense against brood parasitism is ejection of parasitic eggs (Rothstein 1975, Briskie and Sealy

1987, Underwood and Sealy 2006a). This behavior has a genetic basis and, thus, when adaptive should spread within the population (Rothstein 1975, Martín-Gálvez et al. 2006). Rothstein (1975) suggested that egg ejection evolved from nest sanitation behavior and is believed to be an exaptation to the behavior of ejecting eggs as the motor patterns involved in both of these behaviors are nearly identical. For nest-cleaning behavior to evolve into an anti-parasite defense, it must be released early in the laying stage and in response to foreign eggs (Rothstein 1975) and the host must be physically capable of ejecting the foreign egg efficiently. Therefore, because all hosts have the basic motor patterns required for egg ejection (i.e., for feeding or nest sanitation) and because egg ejection behavior is heritable, acceptance by frequently parasitized species suggests they are not physically capable of ejecting eggs or that the associated cost is too great (Ortega 1998).

Differing in costs to the host, both puncture- and grasp-ejection have been observed within and among ejecter species (Table 1.1). A major assumption of the evolutionary equilibrium hypothesis is that bill size limits small birds to puncture-ejection (Spaw and Rohwer 1987), that is, puncturing the shell of the parasitic egg with the bill and removing it from the nest on the tip of the bill or breaking the egg and removing it piecemeal. As a counter-defense to puncture-ejection, cowbirds as well as cuckoos produce eggs that are rounder with shells that are 30% thicker than expected for their size in relation to other passerines, which according to the “puncture-resistance” hypothesis evolved to render puncture-ejection more costly (Spaw and Rohwer 1987, Picman 1989, Antonov et al. 2006). Hosts may incur fitness costs when puncture-ejecting parasitic eggs by inadvertently damaging their own eggs if their bills ricochet off the

Table 1.1. Mean number of host eggs lost or damaged per cowbird egg grasp- and puncture-ejection according to host species^a. (Adapted from Lorenzana and Sealy 2001, Peer and Sealy 2004.)

Host species ^a	Cost of ejection	<i>n</i>	Reference
<i>Grasp-ejectors</i>			
Eastern Kingbird	0.07	88	Sealy and Bazin 1995
Western Kingbird	0.00	7	Rohwer et al. 1989
American Robin	0.00	2	Rohwer et al. 1989
American Robin	0.08	32	Sealy, unpubl. data
Gray Catbird	0.02	92	Lorenzana and Sealy 2001
Sage Thrasher	0.18	11	Rich and Rothstein 1985
<i>Puncture-ejectors</i>			
Bullock's Oriole	0.26	34	Rohwer et al. 1989
Baltimore Oriole	0.38	16	Sealy and Neudorf 1995
<i>Puncture/grasp-ejector</i>			
Warbling Vireo	0.13	16 ^b	Sealy 1996
Warbling Vireo	0.00 ^c	20 ^d	Underwood and Sealy 2006a

^a Eastern Kingbird (*Tyrannus tyrannus*), Western Kingbird (*T. verticalis*), American Robin (*Turdus migratorius*), Sage Thrasher (*Oreoscoptes montanus*), and Warbling Vireo (*Vireo gilvus gilvus*).

^b All ejections are assumed to be puncture-ejections based on the observation of puncture-ejection for four of them.

^c If two unsuccessful ejection attempts are included in the sample, the cost of grasp-ejection was 0.09 ± 0.09 SE eggs damaged per ejection attempt ($n = 22$).

^d All ejections are assumed to be grasp-ejections based on one video-recording of the grasp-ejection of a real cowbird egg and one video-recording of the grasp-ejection of a model cowbird egg.

parasitic egg to their own eggs.

Puncture-ejection may also impose indirect costs on the host even if they can puncture-eject the parasitic egg without damaging any of their own, such as the time and energy invested in puncturing the parasitic egg (Spaw and Rohwer 1987, Martín-Vivaldi et al. 2002, Underwood and Sealy 2006a). Alternatively, grasp-ejection (i.e., removing the unbroken egg by clasping it between the mandibles) is nearly cost-free in hosts for which the cost has been measured (Rohwer et al. 1989, Lorenzana and Sealy 2001; Table 1.1). However, the cost of grasp-ejection may be underestimated because it has been measured only in larger hosts or hosts with longer bills. The cost of grasp-ejection has not been measured in hosts smaller than the 15-g *gilvus* subspecies of Warbling Vireo (hereafter Warbling Vireo) as none is known to grasp-eject parasitic eggs. Hosts incur costs if they damage some of their own eggs when grasp-ejecting the parasitic egg, such as dropping the parasitic egg on its own eggs. Dropping the ejected egg near the nest could attract predators and disclose the location of the nest, potentially increasing the likelihood of depredation (Rothstein 1975) and, thus, grasp-ejection may be selected against in small hosts that cannot carry foreign eggs away from the nest.

Studies investigating physical constraints in hosts of the cowbird

The dimensions of the parasitic egg probably preclude small hosts from grasp-ejecting them (Rothstein 1975). Acceptors are typically small and their short bills may prevent efficient rejection of cowbird eggs (Rohwer and Spaw 1988). On the other hand, many ejectors are larger and generally have larger bills. Rothstein (1975) compared the ratio of host tomial length (i.e., bill length measured in mm as the distance from the

commissural point to the tip of the upper mandible) with cowbird egg width of seven accepters with those of 10 records of birds ejecting large eggs from nests. Rothstein reported that species with tomial-length-to-egg-width ratios of 0.7 should theoretically be able to eject cowbird eggs.

By applying this ratio to the width of a cowbird egg, Rothstein suggested that hosts with tomial lengths as short as 11.5 mm can eject cowbird eggs. His conclusion was that all hosts can eject cowbird eggs, but, he did not distinguish between grasp-ejecters and puncture-ejecters. As bill length is not related to a species' ability to puncture-eject eggs (Spaw and Rohwer 1987, Rohwer and Spaw 1988), the inclusion of puncture-ejecters in this estimate rendered it useless because bill size is important only in grasp-ejection (Rohwer and Spaw 1988). Four of Rothstein's (1975) comparisons most certainly involved puncture-ejection: two cases involving cowbirds (Blincoe 1935, Hann 1937, Norris 1944, Morten *in* Rothstein 1975), one involving the Linnet (*Carduelis cannabina*; Rensch 1924), and one involving the Plain Prinia (*Prinia inornata*; Ali 1931). Briskie and Sealy (1987) questioned the utility of Rothstein's estimate because they could not position a cowbird egg between the mandibles of a freshly dead Least Flycatcher (*Empidonax minimus*) in a way that would allow it to be grasped, despite having a calculated tomial-length-to-egg-width ratio of 0.95 (given a mean tomial length of 15.4 mm, $n = 26$, both sexes, and a mean cowbird egg width of 16.1 mm, $n = 11$). The problems with Rothstein's (1975) ratio stemmed from including puncture-ejecters in the calculations and not necessarily from using tomial length as an index of a species' ability to grasp-eject. Despite this problem, the inability of Rothstein's (1975) ratio to identify

hosts capable of grasp-ejection led other researchers to suggest that other bill measurements would more accurately discriminate grasp-ejectors from puncture-ejectors.

Rowher and Spaw (1988) developed a grasp-index that discriminated between hosts capable and hosts incapable of grasp-ejection. The index is the host's tomial length multiplied by the commissural breadth of the bill (i.e., gape width, measured in mm as the distance between the commissural points). Almost without exception, the grasp-index revealed that species that grasp-eject cowbird eggs have larger bills than accepters. As well, no species with a grasp-index less than 200 mm^2 was known to eject cowbird eggs; this led Rohwer and Spaw (1988) to postulate that hosts with smaller grasp-indexes may not be able to remove the parasitic egg by grasp-ejection and instead accept them because the cost of rejection outweighs the cost of acceptance (Rohwer and Spaw 1988). The latter authors provided strong evidence that the dimensions of cowbird eggs are a barrier to the evolution of grasp-ejection behavior in small hosts, because they limit small hosts to more costly methods of rejection.

If the width of the cowbird egg forces acceptance upon small hosts, presenting them with smaller cowbird eggs (i.e., eggs they should be able to grasp-eject based on the grasp-index or tomial-length-to-egg-width ratio) should result in grasp-ejection.

Rothstein (1975) tested acceptor hosts with undersized eggs. Assuming that small hosts are more likely to eject eggs smaller than cowbird eggs because they are more easily manipulated, Rothstein (1975) tested four acceptor species: Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle (*Quiscalus quiscula*), Eastern Phoebe (*Sayornis phoebe*), and Chipping Sparrow (*Spizella passerina*) with undersized model cowbird eggs (i.e., length x width; undersized model cowbird eggs: 17.3 x 13.6 mm, Rothstein 1975;

real cowbird eggs: 21.45 x 16.42 mm, $n = 127$, Bent 1958). Acceptance was still recorded at most nests, but ejections were recorded in three instances for the two largest species tested, Red-wing Blackbird (2 ejections at 25 nests) and Common Grackle (1 ejection at 18 nests), which Rothstein believed had tomia long enough to grasp-eject cowbird eggs. The Eastern Phoebe (tomial length 20.2 ± 0.2 SE mm, $n = 5$) and Chipping Sparrow (11.3 ± 0.2 SE mm) did not eject the undersized models despite the fact that they possessed the capacity to eject them according to Rothstein's calculation (Rothstein 1975, Rohwer and Spaw 1988). By contrast, Dickcissels (*Spiza americana*), Grasshopper Sparrows (*Ammodramus savaanarum*), Vesper Sparrows (*Pooecetes gramineus*), and Lark Sparrows (*Chondestes grammacus*) ejected undersized cowbird eggs at higher frequencies than real cowbird eggs, but Field Sparrows (*S. pusilla*) did not eject real or undersized cowbird eggs (Peer et al. 2000). It cannot be concluded from these experiments whether hosts ejected undersized eggs because they were easier to manipulate or whether they ejected them for other reasons. The size difference between the undersized models and the host eggs, as opposed to the size difference between real cowbird eggs and host eggs, may have provided the stimulus necessary for rejection in some individuals.

Width may not be the only physical property of a cowbird egg that forces small hosts to accept cowbird eggs. Mass may be a barrier for the evolution of ejection behavior in hosts that are not strong enough to lift certain masses. However, observations of small hosts lifting and ejecting objects from their nest suggest that mass is not a barrier. Rothstein (1975) compared relative body-size-to-egg-size ratios of hosts with other species that eject certain egg types. Based on the assumption that body size is correlated with strength, Rothstein (1975) found that hosts as small as the 9.5-g Yellow

Warbler (*Dendroica petechia*) should theoretically be able to lift a cowbird egg out of their nests. This prediction was confirmed by observations of Yellow Warblers removing cowbird eggs modified to simulate the appearance of a broken egg (Sealy and Lorenzana 1998). Evidence suggests that the mass of a cowbird egg does not constrain small hosts from ejecting cowbird eggs but further research is warranted.

Insights from studies investigating physical constraints on ejection behavior in hosts of the Common Cuckoo (Cuculus canorus)

The notions that puncture-ejection costs more than grasp-ejection and small cowbird hosts that cannot grasp-eject must accept because it is less costly than rejection, are supported by investigations of the influence of bill length on the cost and method of rejection in hosts of the Common Cuckoo; hereafter cuckoo). Cuckoo hosts lose all of their young when they accept a cuckoo egg, whereas most hosts that accept cowbirds fledge some young and, thus, it is adaptive for cuckoo hosts to incur higher ejection costs than cowbird hosts (Lorenzana and Sealy 1999, Davies 2000). As a result, rejection in cuckoo hosts is adaptive at almost any cost because the alternative (i.e., acceptance), results in no host young fledging, because the newly hatched cuckoo ejects all host eggs present in the nest (Davies and Brooke 1989, Davies 2000). Because of the lower costs, however, few cowbird hosts reject through puncture-ejection or desertion (Rohwer and Spaw 1988). Consequently, only hosts large enough to grasp-eject cowbird eggs reject (Rohwer and Spaw 1988). Rejection in cowbird hosts is only adaptive up to a cost equal or below that of acceptance because they still can fledge a few of their own young along with the cowbird (Lorenzana and Sealy 1999, Rasmussen and Sealy 2006). Because of

the difference in the costs of acceptance, selection for rejection in small cuckoo hosts is expected, and observations of the methods used by small hosts and the costs involved provide insight on the potential costs as well as the physical constraint faced by small cowbird hosts.

The relationships between bill length and ejection frequency and bill length and cost of rejection in cuckoo hosts support the notions that bill size limits rejection options for small hosts and that the cost of ejection is higher for hosts with small bills (Davies and Brooke 1989). Davies and Brooke (1989) tested the abilities of various cuckoo hosts to eject cuckoo egg models and found a significant positive relationship between tomial length and frequency of ejection. Tomial length was also negatively correlated with the cost of ejection. The three largest species tested, European Blackbird (*Turdus merula*; $n = 22$), Song Thrush (*Turdus philomelos*; $n = 22$), and Common Starling (*Sturnus vulgaris*; $n = 5$) suffered no egg loss during ejections, whereas the three smallest species, Reed Warbler (*Acrocephalus scirpaceus*; $n = 16$), Chaffinch (*Fringilla coelebs*; $n = 11$), and Reed Bunting (*Emberiza schoeniclus*; $n = 1$) did (Davies and Brooke 1989). This was strong evidence that it is more difficult and costly for hosts with shorter bills to eject foreign eggs than those with longer bills.

Davies and Brooke (1989) used models made of resin, which likely could not be punctured by the species they tested. Yet two species for which ejection was recorded, Reed Bunting and Meadow Pipit (*Anthus pratensis*), had tomial lengths too small to grasp-eject a model cuckoo egg according to previous studies. By calculating Rothstein's (1975) tomial-length-to-egg-width ratio for the smallest hosts where ejection was recorded by Davies and Brooke (1989), ejections by the Reed Bunting and Meadow

Pipits represented approximate ratios of 0.65 and 0.74, respectively. These low ratios probably do not represent grasp-ejection given the fact that Briskie and Sealy (1987) could not fit a cowbird egg between the mandibles of a Least Flycatcher beyond the point where it could be grasped, a feat representing a ratio of 0.95. For this reason, models may have been ejected from nests by means other than puncture- or grasp-ejection in Davies and Brooke's (1989) study.

Although Davies and Brooke (1989) showed the cost of ejection is inversely proportional to host bill length, their data do not permit determination of the minimum tomial length required to grasp-eject a parasitic egg because they did not differentiate between grasp-ejection and other means of ejection. However, the correlation between cost of ejection and tomial length provide the basis for further investigation of the physical constraints of small hosts of the cuckoo.

Based on the observed relationship between puncture- or grasp-ejection and cost of ejection in cowbird hosts (Table 1.1), Moksnes et al. (1991) differentiated grasp- and puncture-ejecter cuckoo hosts on the basis of the cost of ejecting cuckoo egg models. They tested 19 species with tomial lengths from 25.4 ± 0.3 SE mm in Fieldfare (*Turdus pilaris*) to 11.6 ± 0.1 SE mm in Lapland Longspur (*Calcarius lapponicus*). The experiment was based on Rothstein's (1975) inference that ejections of plaster models at nests could be attributed to the host grasp-ejecting the egg, such as in the American Robin and Western Kingbird, whereas, ejections of plaster models from nests in which host eggs were damaged were attributed to puncture-ejection of the egg, such as in the Baltimore Oriole (Rohwer et al. 1989). Based on these assumptions, Moksnes et al. (1991) classified these species as grasp- or puncture-ejecters according to the cost of

ejection, and classified species that deserted clutches during experiments as deserters. As predicted, a significant negative relationship between bill size and cost of ejection was found. Hosts with the largest bills were considered to be grasp-ejecters, whereas hosts with medium-sized bills and the smallest bills were considered to be puncture-ejecters and deserters, respectively.

Based on the cost of ejection, Moksnes et al. (1991) categorized two species as grasp-ejecters that have grasp-indexes far below 200 mm^2 . This is even more impressive because the two species, Bluethroat (*Luscinia svecica*; grasp-index = 131.1 mm^2) and Spotted Flycatcher (*Musciapa striata*; grasp-index = 179.3 mm^2), ejected cuckoo egg models that are larger than cowbird eggs (i.e., mean egg width: Brown-headed Cowbird = $16.4 \pm 0.07 \text{ SE mm}$, $n = 113$, S. G. Sealy, unpublished data; Common Cuckoo = 17.23 mm , $n = 100$, Witherby et al. 1943). Yet, of the species with grasp-indexes less than 200 mm^2 , the bills of the Bluethroat and Spotted Flycatcher had bills that were among the longest, which lead Moksnes et al. (1991) to suggest that bill length may be a more important predictor of grasp-ejection than the value of the grasp-index value. Consistent with the suggestion that bill length relative to egg width is the more important factor in grasp-ejection, Martín-Vivaldi (2002) found that cuckoo hosts with bills shorter than 19 mm and grasp-indexes less than 200 mm^2 suffer high ejection costs when ejecting artificial cuckoo eggs. These results suggest that some hosts are physically constrained to accept parasitic eggs because their bills are too short to eject them efficiently. However, the method of ejection used by hosts had not been identified.

The cost of ejection according to the method (i.e., grasp- or puncture- ejection) is available for few hosts (Soler et al. 2002). Nevertheless, the following observations

suggest that small hosts are physically constrained from grasp-ejecting cowbird eggs. Moksnes et al. (1994) confirmed their prediction that puncture-ejection is costly by video-recording two puncture-ejecters, Chaffinch and Blackcap (*Sylvia atricapilla*), which damaged their own eggs when ejecting model cuckoo eggs. Likewise, Soler et al. (2002), testing the hypothesis that small hosts are limited to puncture-ejection, video-recorded three cuckoo hosts ejecting cuckoo eggs and determined that only European Blackbirds grasp-ejected cuckoo eggs, whereas the two smaller hosts, Subalpine Warbler (*S. cantillans*) and Blackcap, puncture-ejected them. Knowing the method of ejection in one large species and two small species is not sufficient to generalize that all large hosts are more likely to be grasp-ejecters, whereas smaller hosts are more likely to be puncture-ejecters. Furthermore, it does not provide an index to distinguish accepters from rejecters.

In summary, previous studies suggest that small bills in relation to the dimensions of the parasitic egg prevent efficient egg ejection by small cowbird and cuckoo hosts. The relative size of host bill to the dimensions of the egg prevent hosts from grasp-ejecting eggs, and as a result their options for rejection are limited to more costly puncture-ejection, burial, or desertion. Previous studies have failed to provide the minimum physical attributes hosts require to be able to grasp-eject parasitic eggs. Recent observations of small hosts grasping eggs suggests that Rothstein (1975) and Rohwer and Spaw (1988) may have underestimated the ability of small hosts to grasp-eject.

Recent observations

Observations of the Warbling Vireo and Song Sparrow (*Melospiza melodia*)

grasp-ejecting eggs suggest that the ability of small hosts to grasp-eject have been underestimated. Although previous observations suggested that the Warbling Vireo (grasp-index of 153.50 ± 1.44 SE mm²) only puncture-ejects (Sealy 1996), video-recordings revealed that they can grasp-eject real and model cowbird eggs at a negligible cost to their own eggs (Underwood and Sealy 2006a). An even greater feat was a Song Sparrow that grasp-ejected the egg of a conspecific (Latif et al. 2006). This is impressive because Song Sparrow eggs are 22 x 17 mm (Latif et al. 2006), whereas its grasp-index is 89.1 mm² and tomial length is 13.5 ± 0.5 SE mm (Rohwer and Spaw 1988). The sparrow did not damage any of its own eggs, however, it dropped the egg near the nest, which has been suggested to be costly because it may attract predators (Rothstein 1975). Costs incurred from dropping eggs near the nest may be reason for the low rate of cowbird-egg ejection in Song Sparrows (rejection rate = 11%, $n = 9$, Rothstein 1975). These grasp-ejections suggest the limit for grasp-ejection of cowbird eggs is lower than previously thought and hosts with bills as short as the Song Sparrow's should be able to grasp-eject cowbird eggs. Costs involved in this ejection, however, may select against it.

Problems with approaches used to discern the minimum physical requirements for grasp-ejection

Identifying grasp-ejecters based on measurements of species known to grasp-eject may be useless because factors other than physical ability have been correlated with the appearance of ejection behavior. Other factors affecting the appearance of ejection behavior in hosts may not be entirely based on size, rendering the precise distinction

between grasp- and puncture-ejecters based on bill sizes impossible. Correlations exist between the presence of rejection behavior in a species and its historic contact with cowbirds, frequency of parasitism by cowbirds, population size of the host, hence, a more variable gene pool, and taxonomic affiliations of that species (Rothstein 1975, Peer and Sealy 2004). Furthermore, other factors may explain the current observed pattern of larger rejecters and smaller accepters. Larger hosts may have been parasitized more frequently in the past because they were able to feed and defend the nestlings better and their larger nests may have been easier for parasites to locate (Rothstein 1975, Peer and Bollinger 1997, 2000). The current pattern of larger hosts being ejecters and smaller hosts accepters, therefore, may not be attributable to the physical ability of the hosts, but instead to differential parasitism pressures in the past (Peer and Sealy 2004).

A new approach

Workers who have investigated the physical constraints on egg ejection by hosts have based their findings on the current pattern of accepters and ejecters among host species. This may not be a valid approach, however, because parasitism pressures on each species likely differed in the past. A new approach is required to discriminate hosts capable and incapable of grasp-ejection. To control for different past-parasitism pressures, tests assessing the largest egg width that host species can grasp-eject are required: observations of birds grasping successively larger eggs up to a width they can no longer grasp. For reasons unknown, however, most hosts do not respond to parasitic eggs (Peer and Sealy 2004) and, thus, correlations between the upper egg width limit a

host can grasp-eject and tomial length are required to construct an index to discriminate between hosts capable and incapable of grasp-ejection.

The objective of this study was to determine which cowbird hosts are constrained by small bills to more costly methods of ejection or acceptance. Because no cowbird hosts smaller than the Warbling Vireo are known to eject cowbird eggs (Underwood and Sealy 2006a), testing the ability of small hosts to eject cowbird eggs would not be productive. Instead, I tested the ability of known grasp-ejecters, the American Robin and Gray Catbird, to eject models of widths larger than cowbird eggs. Testing within a species excludes factors such as differential past parasitism pressures that confounded previous studies. The maximum-ejectable egg width was sought for each species and was then standardized according to tomial length, which made comparisons across species possible. The possibility that the cost of grasp-ejecting a cowbird egg is greater for hosts with smaller bills was investigated by recording the costs of grasp-ejection and the distance models were transported for each model width. The cost of grasp-ejection is not known for hosts smaller than the Warbling Vireo (Underwood and Sealy 2006a), but it is likely higher in smaller hosts. Hosts with bills smaller than required to efficiently grasp-eject a parasitic egg may damage their own eggs during grasp-ejection attempts or they may drop the egg near the nest and disclose the nest to a predator, thus increasing the cost of ejection for small hosts (Rothstein 1975, Rothstein 1976). Knowing the minimum bill length required to grasp-eject a cowbird egg and the costs of grasp-ejection for bills of various lengths are necessary to understand the processes of coevolution occurring between cowbirds and their hosts. In this study, I tested the following hypotheses.

Hypotheses

- i) A minimum tomial length is required to grasp-eject a cowbird egg; all hosts with tomia shorter than the minimum length are constrained to accept cowbird eggs or reject by more costly methods.
- ii) Cost of grasp-ejection increases and distance cowbird eggs are carried from host nests decreases as egg-width-to-bill-length ratio increases.

Methods

Study Species

American Robin (hereafter robin) and Gray Catbird (catbird) were used as model grasp-ejecter species for this experiment because they recognize and grasp-eject cowbird eggs. They were assumed to be grasp-ejecters based on their ability to remove experimentally introduced non-puncturable plaster models at frequencies greater than 90% within 5 days (Rothstein 1975, Briskie et al. 1992, Lorenzana and Sealy 2001). However, anecdotal observations of robins removing cowbird eggs suggest they puncture-eject as well as grasp-eject them (Friedmann 1929: 185, Nice 1944, Briskie et al. 1992, J. V. Briskie *in* Sealy and Neudorf 1995). The catbird has also been determined to be a grasp-ejecter because it has been video-recorded removing artificial plaster cowbird eggs from its nest (Lorenzana and Sealy 2001) and grasp-ejecting a plastic egg during a predation attempt (Hauber 1998). Catbirds have also been recorded ejecting plaster eggs approximately 22-mm wide, thus approximately 8 mm wider than a cowbird egg (Lorenzana and Sealy 2001).

Tests on more than one species were required to investigate the nature of the relationship between the predictor (i.e., tomial length) and response variables (i.e.,

grasp-ejection or acceptance) and to predict more accurately the minimum tomial length required to eject a cowbird egg (Table 1.2). The utility of tomial length as a predictor of a host's ability to grasp-eject an object of a certain width can be assessed by comparing the maximum egg-width-to-tomial-length ratios of more than one species having different tomial lengths. The bills of these two species are also similar in shape, which facilitates tests of the influence of tomial length. However, the mean body mass of robins is 122.4% greater than that of catbirds despite mean tomial length being only 13.2% greater in the robin (Table 1.2). These species are highly amenable to experimental parasitism as their response does not differ significantly between the laying and incubating stages (Rothstein 1982) and they both show true egg recognition, i.e., recognize their own eggs (Rothstein 1982), allowing model introductions to occur over more of the nest cycle.

Scientific permits (CWS05-M003, CWS06-M003) covered the research on American Robins and Gray Catbirds and all procedures were conducted in accordance with the Canadian Council on Animal Care, University of Manitoba Animal Care Protocols (F05-009, F06-007).

Study Site

The study was conducted at Delta, Manitoba (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. The site is a narrow forested dune ridge along the south shore of Lake Manitoba that separates the lake and the extensive marsh to the south (see MacKenzie 1982, Neudorf 1991).

Table 1.2. Tomial lengths of American Robins and Gray Catbirds from museum specimens taken in British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario (Adapted from Underwood 2003).

Species	<i>n</i>	Tomial length (mm)		Cowbird-egg ¹ -width-to-tomial-length ratio
		mean ± SE	95% C.I.	
American Robin ²				
Male	43	27.52 ± 0.13	27.35-27.69	0.60
Female	54	27.57 ± 0.15	27.38-27.77	0.59
Both	97	27.55 ± 0.10	27.42-27.68	0.60
Gray Catbird ³				
Male	52	24.52 ± 0.10	24.38-24.65	0.67
Female	38	24.09 ± 0.14	23.90-24.26	0.68
Both	90	24.34 ± 0.09	24.22-24.45	0.67

¹ Mean (± SE) Brown-headed Cowbird egg width: 16.4 mm ± 0.07 mm, *n* = 113 (S. G. Sealy, unpublished data).

² Mean (± SE) body mass: 78.5 g ± 0.5 g, *n* = 255, males and females combined (Dunning 2008).

³ Mean (± SE) body mass: 35.3 g ± 0.1 g, *n* = 438, sex unknown (Dunning 2008).

Models

Cylindrical models varying in width and controlled for mass were used to test the limits of grasp-ejection in robins and catbirds (Figure 1.1). Models were 16-, 19-, 22-, 25-, 28-, 29-, and 32-mm wide (Table 1.3). Models were made of wood and plastic and were sanded, painted, and polished to give them the texture and appearance of cowbird eggs. Wood and plastic were used to make the models because of the inability of the study species to puncture these materials with their bills and the necessity to keep mass constant across all model sizes. Models 16-, 19-, 22-, 25-, and 28-mm wide were made of wood and models 29- and 32-mm wide were made of soda-bottle plastic (i.e., polyethylene terephthalate) and wood.

In addition to different materials, model mass was kept constant for all widths by hollowing out the larger models and inserting steel and copper pellets into smaller models. The holes were covered with hard-drying wood putty. Use of different materials was valid because the sole function of the models was to act as a non-puncturable object of a given width that the robin or catbird would have to grasp to remove from the nest. The texture of the plastic models was the same as the wood models because they were sanded, painted, and polished to have the same texture and appearance as cowbird eggs. All models were painted with Folkart™ non-toxic acrylic paint. Color #940 (Coffee Bean) was used for maculations and color #901 (Wicker White) for ground color.

The models were cylindrical rather than egg-shaped because the width of the model can be maintained constant across a cylinder in all directions, whereas it cannot with an egg-shaped model. As well, objects differing in shape from host eggs are more

Figure 1.1. Models used to test the limits of grasp-ejection of American Robins and Gray Catbirds. Models from left to right are 16-mm, 19-mm, 22-mm, 25-mm, 28-mm, and 32-mm wide. (All model sizes had similar maculation density ranges. The differences in maculation densities among model sizes depicted in this photo resulted from models of each width being randomly selected for inclusion in the photo.)

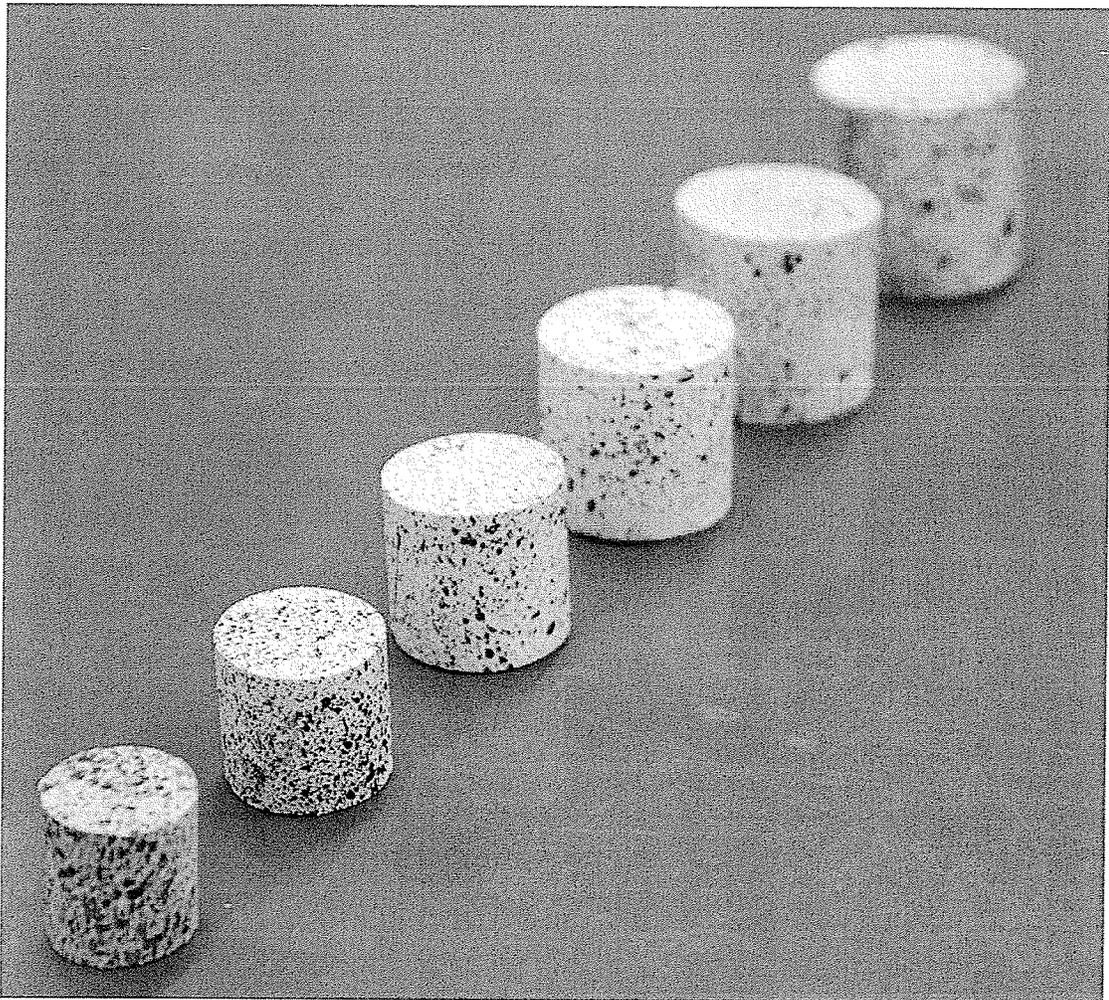


Table 1.3. Width, length, and mass (mean \pm SE) of models used in American Robin and Gray Catbird nests.

Year	Species	Model size	<i>n</i>	Width (mm)	Length (mm)	Mass (g)
2005						
	Gray Catbird					
		16 mm	22	16.46 \pm 0.04	16.49 \pm 0.04	5.57 \pm 0.02
		19 mm	24	19.28 \pm 0.01	19.25 \pm 0.02	5.78 \pm 0.03
		22 mm	22	22.25 \pm 0.03	22.25 \pm 0.04	5.65 \pm 0.03
		25 mm	20	25.46 \pm 0.03	25.41 \pm 0.04	5.72 \pm 0.05
		28 mm	24	28.38 \pm 0.02	28.40 \pm 0.03	5.78 \pm 0.05
2006						
	American Robin					
		16 mm	24	16.78 \pm 0.07	17.14 \pm 0.09	5.94 \pm 0.06
		29 mm	27	28.94 \pm 0.04	30.72 \pm 0.11	6.44 \pm 0.06
		32 mm	35	32.09 \pm 0.09	33.46 \pm 0.13	6.39 \pm 0.05
	Gray Catbird					
		22 mm	11	22.37 \pm 0.04	22.45 \pm 0.06	5.53 \pm 0.05
		25 mm	10	25.65 \pm 0.02	25.70 \pm 0.05	5.75 \pm 0.06
		28 mm	8	28.56 \pm 0.06	29.16 \pm 0.23	6.30 \pm 0.17
		29 mm	29	29.49 \pm 0.04	30.88 \pm 0.10	6.43 \pm 0.04
		32 mm	27	32.63 \pm 0.03	34.66 \pm 0.19	6.35 \pm 0.09

likely to be recognized and ejected (Underwood and Sealy 2006b). The models were painted to appear like cowbird eggs to elicit rejection behavior and because recognition of parasitic eggs by robins requires differences in at least color and shape from their own eggs (Rothstein 1982). Designing the models to stimulate ejection effectively by hosts is appropriate because I am not testing the ability of the host to recognize foreign eggs, but rather, I am testing the host's ability to grasp-eject foreign eggs.

Models were measured using calipers (accurate to ± 0.1 mm) and an electronic scale (accurate to ± 0.1 g). Model width and length were determined by taking two measurements of width perpendicular to each other and averaging the measurements. Models did not have identification numbers on the model surface. Thus, it was difficult in a few instances where nests were in close proximity to determine with certainty from which nest the model had been ejected.

To estimate the minimum tomial length required to grasp-eject a cowbird egg, the ability of robins and catbirds to grasp-eject widths larger than a cowbird egg was tested by adding sequentially larger models to nests and recording whether hosts ejected or accepted the objects. I assumed that these models limited robins and catbirds to grasp-ejection, because I believed the only way to eject them was to grasp them by their entire width. As such, I assumed their absence indicated grasp-ejection of a model of a particular width by the host. The width of the largest model that was ejected represented the maximum grasp-ejectable width.

Randomly selected models were inserted into nests of the study species during laying and incubation. As the mean laying time of catbirds is 128.7 ± 11.4 SE minutes after sunrise (McMaster et al. 2004), models were inserted in nests three hours after

sunrise so as not to interfere with normal laying. Robins were parasitized as close to sunrise as possible because their mean laying time is 290.0 ± 11.4 SE minutes after sunrise (McMaster et al. 2004).

In 2005, only catbirds were tested using models 16-, 19-, 22-, 25-, and 28-mm wide (Table 1.3). Experimentally parasitized nests were inspected every 24 hours for up to 2 days. If an undamaged model remained in a nest after 2 days, we recorded an acceptance. A 2-day acceptance criterion was followed because Lorenzana (1999) found that 96% of all real cowbird eggs in catbird nests were ejected within 2 days. Models were considered ejected if they went missing from active nests within the 2-day period. Models were considered deserted if they were present in a nest where the adults were not present at the nest for at least 24 hours and the host eggs were cold, but none was missing. A nest was considered depredated when some or all of the host eggs were missing or damaged during the 2-day period and that the host adults were not present at the nest for at least 24 hours.

In 2006, robins were also tested. The addition of the robin required a 5-day acceptance criterion instead of the 2-day acceptance criterion because time-to-ejection of cowbird eggs by robins is highly variable and because they eject less than 1% of cowbird eggs that have survived in the nest for 5 days (Rothstein 1982). In addition, to compare results obtained on robins and catbirds, a 5-day acceptance criterion was followed for catbirds in 2006. However, to be able to use the data collected on catbirds in 2005, comparisons between the results obtained on the same widths on catbirds using the 2-day and 5-day acceptance criteria were necessary.

For robins, treatments were determined by extrapolating the data obtained on catbirds in 2005 to the tomial length of robins. Based on the findings that the catbird, with a mean tomial length of 24.33 ± 0.09 SE mm (Underwood 2003), can remove models with a mean width of 28.38 ± 0.02 SE mm, American Robins (mean tomial length 27.55 ± 0.10 SE mm) should be able to eject models with a mean width of 31.96 mm, if the relationship between bill length and maximum grasp-ejectable egg width is linear. Therefore, the treatments used for the robins consisted of a control (i.e., models 16-mm wide, the width of a cowbird egg) and models 29-, 32-, and 37-mm wide. One test with a model 37-mm wide resulted in immediate desertion of the nest, possibly because the model filled the cup almost entirely, thus, models 37-mm wide were no longer used.

In 2006, catbirds were tested with models (i.e., 29- and 32-mm wide) that were larger than the ones they ejected in 2005 (i.e., 16-, 19-, 22-, 25-, and 28-mm wide). Catbirds were also tested with models 22-, 25-, and 28-mm wide again in 2006 to compare results obtained in 2005 when a 2-day acceptance criterion was used, to those obtained in 2006 when a 5-day acceptance criterion was used.

To determine whether the nest was at the laying or incubation stage when models were inserted, eggs were candled following Lokemoen and Koford's (1996) procedure. Nests were at the incubation stage if embryonic development could be seen macroscopically and determined to be at the laying stage if embryonic development could not be seen. Nests were also determined to be at the laying stage if additional eggs were laid on subsequent days until clutch completion (Slack 1973, Johnson and Best 1980). After clutch completion, nests were at the incubation stage (Slack 1973, Johnson and Best 1980).

Cost of ejection was measured by recording damaged or missing host eggs at every 24-hour nest inspection. The number of host eggs present at each inspection was compared to the expected number for that particular day (i.e., the expected number reflects the daily laying of eggs by the female until the modal clutch size is reached) and missing eggs were assumed to have been damaged and removed by the host.

In 2006, the method of ejection was confirmed for real cowbird eggs, models 16-mm wide, and models 29-mm wide by video-recording a subset of ejections. Cameras similar to that described in Sabine et al. (2005) were set up 1-3 m from active nests in which models were inserted. Cameras consisted of camouflaged SonyTM CCD-TRV308 NTSC Hi 8 cameras that were linked to SonyTM 160 GB DVD/HDD recorders. Motomaster Eliminator 1200W PowerboxesTM powered the cameras. The cameras recorded continuously, without the need to change the batteries or recording media, for at least 8 hours.

Analysis

Two-tailed Fisher exact tests were used to test the significance of differences in the response of robins and catbirds to models according to nest stage (i.e., laying or incubating). Fisher exact tests were used because the asymptotic assumptions of the chi-square test were not met (i.e., 80% of the table cell counts do not have counts greater than 5). Fisher exact tests were conducted using the JMP INTRO 5.0.1a statistical software package.

One-tailed Cochran-Armitage exact trend tests were used to test the significance of trends in rejection frequency according to increasing model size. This test checks for

correlations in the relative proportions of a dichotomous response (e.g., ejected vs. accepted) relative to treatments that are ordinal in scale (e.g., model sizes; Stokes et al. 2001). Exact trend tests were used because the assumptions of the parametric trend test were not met (i.e., 80% of the table cell counts do not have counts greater than 5). Cochran-Armitage exact trend tests were conducted using the SAS 9.1.3 statistical software package.

I used the LIFETEST procedure in the SAS statistical software package to examine differences in the time-to-ejection for models between nest stages and species, as well as among model widths. This test allows for the inclusion of data from incomplete tests, called “withdrawals,” such as tests where nest contents were depredated or deserted (Stokes et al. 2001). For these tests, I assumed that withdrawal is independent of model width, nest stage, or species (Stokes et al. 2001). Log-rank and Wilcoxon-rank tests (one-tailed) were used to compare model survival curves. Two different tests were used to test the significance of differences between survival curves because they each place greater importance on different parts of survival curves. The Wilcoxon-rank test places more weight on the earlier portion of the curve, whereas the Log-rank test places more weight on the later portion of the curve (Stokes et al. 2001). Log-rank and Wilcoxon-rank tests were conducted using the SAS 9.1.3 statistical software package.

I used the Kruskal-Wallis test to test the significance of differences in the cost of ejection among model widths and between species. This test is non-parametric and is used to test the significance of differences among multiple sample means (Conover 1980). Data on the cost of ejection suffered from small sample sizes and an ordinal scale of measurement, but met the assumptions of the Kruskal-Wallis test (i.e., independent

random samples, measurement scale is at least ordinal, some populations tend to yield higher values than others; Conover 1980). Kruskal-Wallis tests were performed using the SAS 9.1.3 statistical software package.

Results

Response to different model widths by Gray Catbirds in 2005

Responses were recorded at 112 of 119 nests into which models were introduced. No desertions were recorded during experiments but seven nests were depredated (Table 1.4). Catbirds ejected 82.1% ($n = 112$) of the models with a mean time to ejection of 1.22 ± 0.04 SE days ($n = 92$). Mean time to depredation of nests was 1.00 ± 0.00 SE days ($n = 7$). Nest stage did not significantly influence ejection frequency (80.9%, $n = 89$, during laying vs. 82.4%, $n = 17$, during incubation; Fisher exact test, two-tailed, $P = 1.000$). Smaller models were ejected more frequently than larger models (Cochrane-Armitage exact trend test, $Z = 2.9396$, one-tailed, $P = 0.002$, $n = 112$; Figure 1.2). Nest stage did not influence model survival (Log-rank test, $\chi^2 = 0.0149$, $df = 1$, $P = 0.9030$; Wilcoxon-rank test, $\chi^2 = 0.0365$, $df = 1$, $P = 0.8485$). Smaller models did not survive as well as larger models (Log-rank test, $\chi^2 = 15.4781$, $df = 4$, $P = 0.0038$; Wilcoxon-rank test, $\chi^2 = 12.9779$, $df = 4$, $P = 0.0114$; Figure 1.3). Cost of ejection did not differ significantly among model sizes (Kruskal-Wallis test: $\chi^2 = 1.9376$, $df = 4$, $P = 0.7472$). The mean cost of ejection was 0.14 ± 0.11 SE eggs/ejection ($n = 22$), 0.22 ± 0.11 SE eggs/ejection ($n = 23$), 0.07 ± 0.14 SE eggs/ejection ($n = 14$), 0.06 ± 0.13 SE eggs/ejection ($n = 16$), and 0.29 ± 0.13 SE eggs/ejection ($n = 17$) for models 16-, 19-, 22-, 25- and 28-mm wide, respectively. A significant positive trend was found between model width and the

Table 1.4. Responses of Gray Catbirds to models of different widths placed in their nests in 2005.

Model width	Response	Day 1	Day 2	Total
16 mm	Accepted			0
	Ejected	17	5	22
	Nest Deserted			0
	Nest Depredated	1		1
19 mm	Accepted		1	1
	Ejected	21	2	23
	Nest Deserted			0
	Nest Depredated	2		2
22 mm	Accepted		8	8
	Ejected	10	4	14
	Nest Deserted			0
	Nest Depredated			0
25 mm	Accepted		4	4
	Ejected	10	6	16
	Nest Deserted			0
	Nest Depredated	3		3
28 mm	Accepted		7	7
	Ejected	14	3	17
	Nest Deserted			0
	Nest Depredated	1		1

Figure 1.2. Percentage of models ejected from Gray Catbird nests according to width in 2005 (sample sizes above bars).

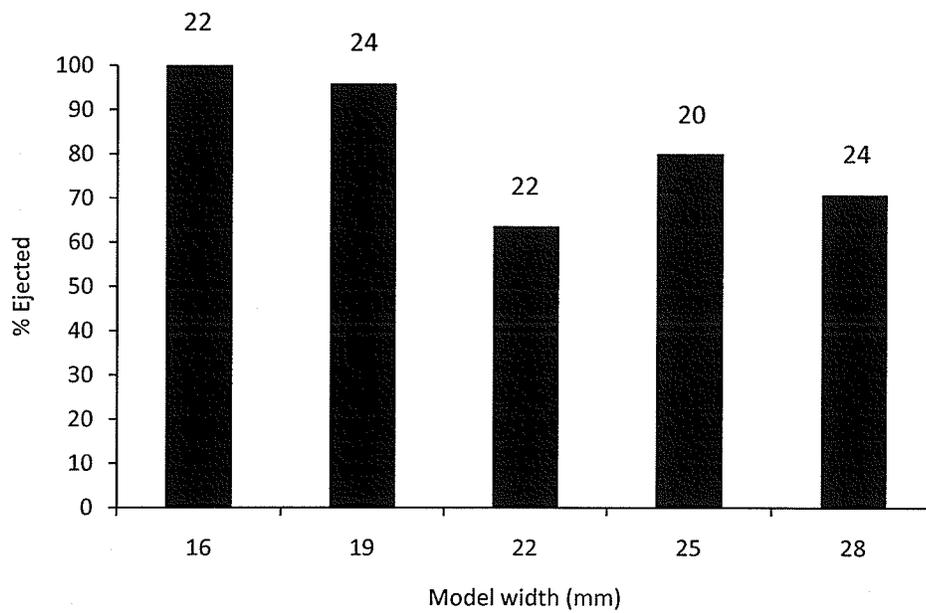
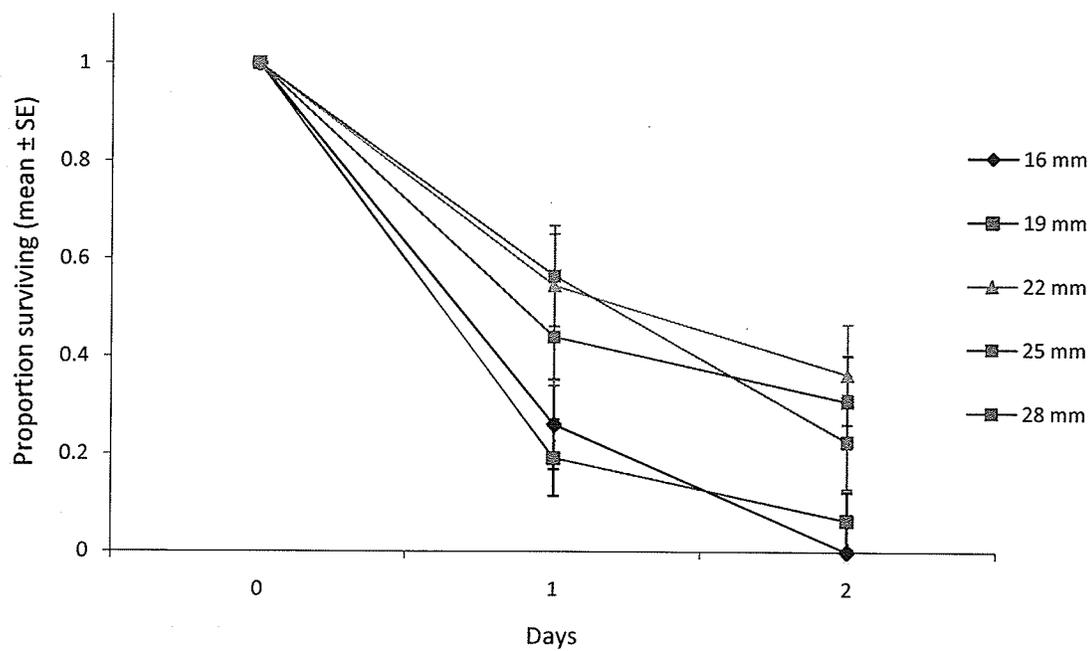


Figure 1.3. Survival curves for 112 models of different widths placed in Gray Catbird nests in 2005.



frequency at which ejected models were found within 3 m of the nest (Cochrane-Armitage exact trend test, $Z = 4.4159$, one-tailed, $P < 0.0001$, $n = 91$; Figure 1.4).

Response to different model widths by Gray Catbirds in 2006

Responses were recorded at 82 of 91 nests into which models ranging in width from 22 to 32 mm were introduced (Table 1.5). Four and five nests were deserted and depredated, respectively. Catbirds ejected 89.0% ($n = 82$) of the models with a mean time to ejection of 1.36 ± 0.09 SE days ($n = 73$). Mean times to desertion and depredation were 2.00 ± 0.32 SE days ($n = 4$) and 4.00 ± 0.41 SE days ($n = 5$), respectively. Neither model width (Cochran-Armitage exact trend test, one-tailed, $Z = 0.8726$, $P = 0.1914$, $n = 82$; Figure 1.5) nor nest stage (Fisher exact test, two-tailed, $P = 1.0000$, $n = 82$) significantly influenced ejection frequency by catbirds. Nest stage did not influence model survival in catbird nests (Log-rank test, $\chi^2 = 1.6651$, $df = 1$, $P = 0.1969$; Wilcoxon-rank test, $\chi^2 = 1.7489$, $df = 1$, $P = 0.1860$, $n = 91$), whereas size significantly influenced it (Log-rank test, $\chi^2 = 11.8483$, $df = 4$, $P = 0.0185$; Wilcoxon-rank test, $\chi^2 = 10.6392$, $df = 4$, $P = 0.0309$, $n = 91$; Figure 1.6). Cost of ejection did not differ significantly among model widths (Kruskal-Wallis test: $\chi^2 = 3.4930$, $df = 4$, $P = 0.4790$). The mean cost of ejection was 0.18 ± 0.16 SE eggs/ejection ($n = 11$), 0.00 ± 0.19 SE eggs/ejection ($n = 9$), 0.38 ± 0.19 SE eggs/ejection ($n = 8$), 0.28 ± 0.11 SE eggs/ejection ($n = 25$), and 0.00 ± 0.12 SE eggs/ejection ($n = 20$) for models 22-, 25-, 28-, 29-, and 32-mm wide, respectively. A significant positive trend was found between width and frequency at which models were recovered within 3 m of the nest (Cochrane-Armitage exact trend test, $Z = 2.3994$, one-tailed, $P = 0.0082$, $n = 73$; Figure 1.7).

Figure 1.4. Percentage of ejected models recovered within 3 m of Gray Catbird nests according to width in 2005 (sample sizes above bars).

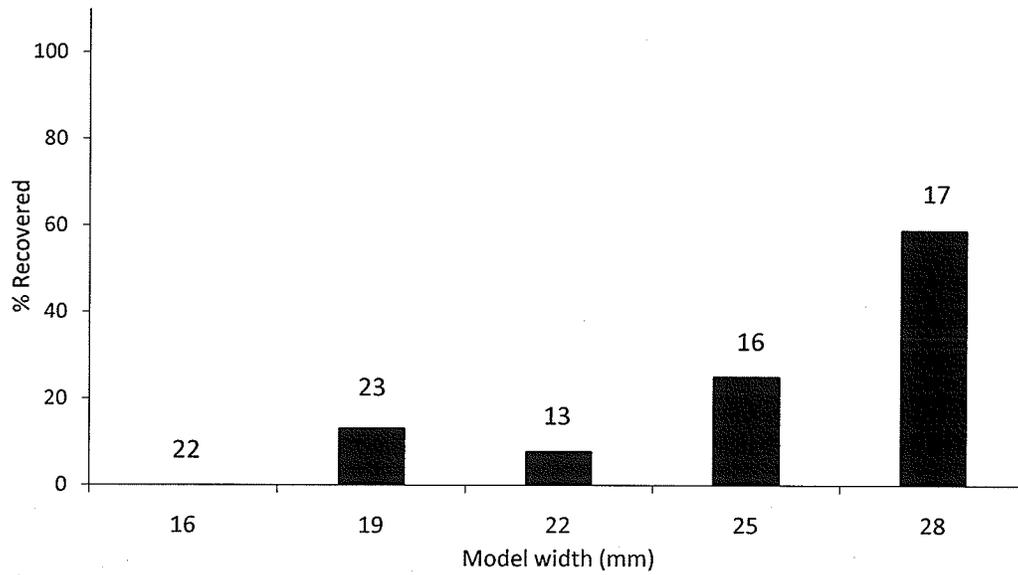


Table 1.5. Responses of Gray Catbirds to models of different widths placed in their nests in 2006.

Model width	Response	Day 1	Day 2	Day 3	Day 4	Day 5	Total
22 mm	Accepted						0
	Ejected	11					11
	Nest Deserted						0
	Nest Depredated						0
25 mm	Accepted					2	2
	Ejected	5	3	1			9
	Nest Deserted						0
	Nest Depredated						0
28 mm	Accepted						0
	Ejected	6	1		1		8
	Nest Deserted						0
	Nest Depredated						0
29 mm	Accepted					4	4
	Ejected	19	4	1	1		25
	Nest Deserted						0
	Nest Depredated			1	1		2
32 mm	Accepted					3	3
	Ejected	15	4			1	20
	Nest Deserted	1	3	1			5
	Nest Depredated				1	1	2

Figure 1.5. Percentage of models ejected from Gray Catbird nests according to width in 2006 (sample sizes above bars).

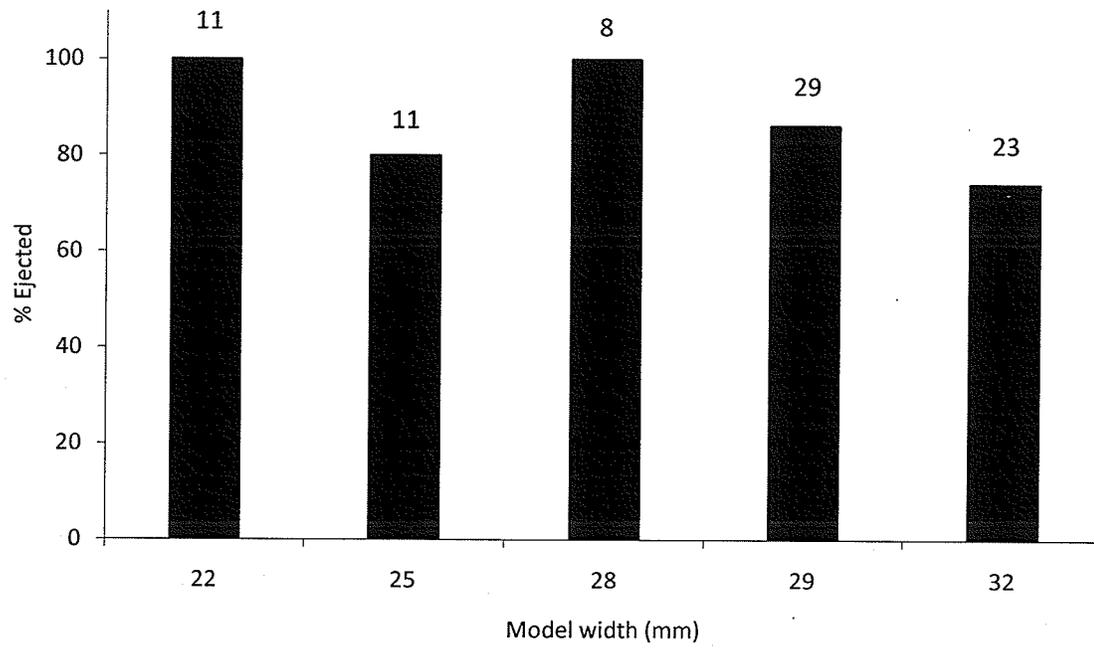


Figure 1.6. Survival curves for models placed into 85 Gray Catbird nests according to width in 2006.

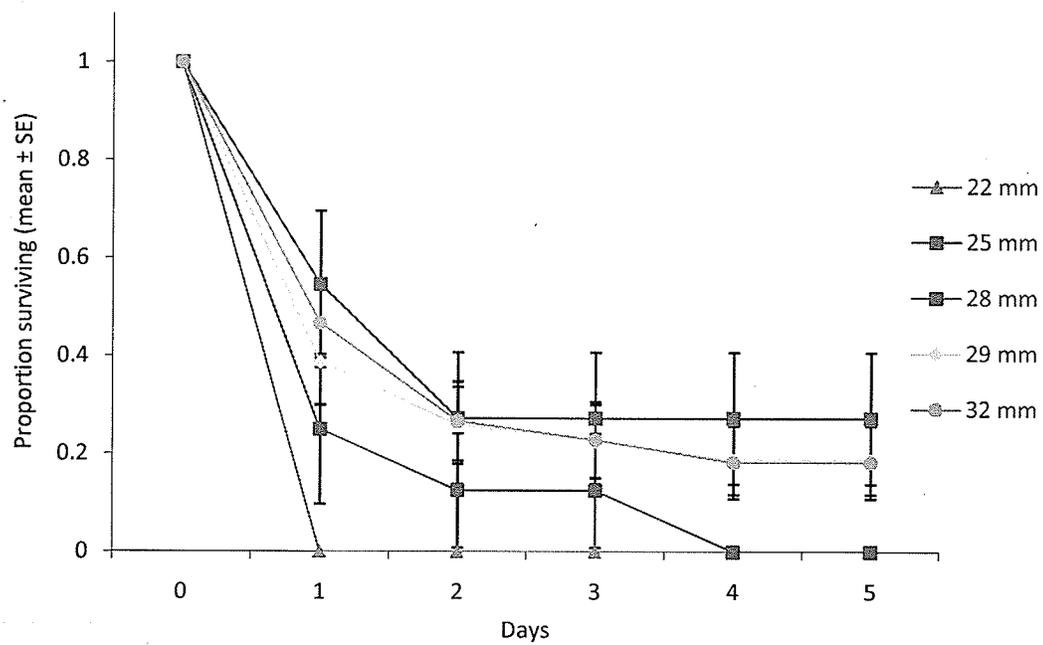
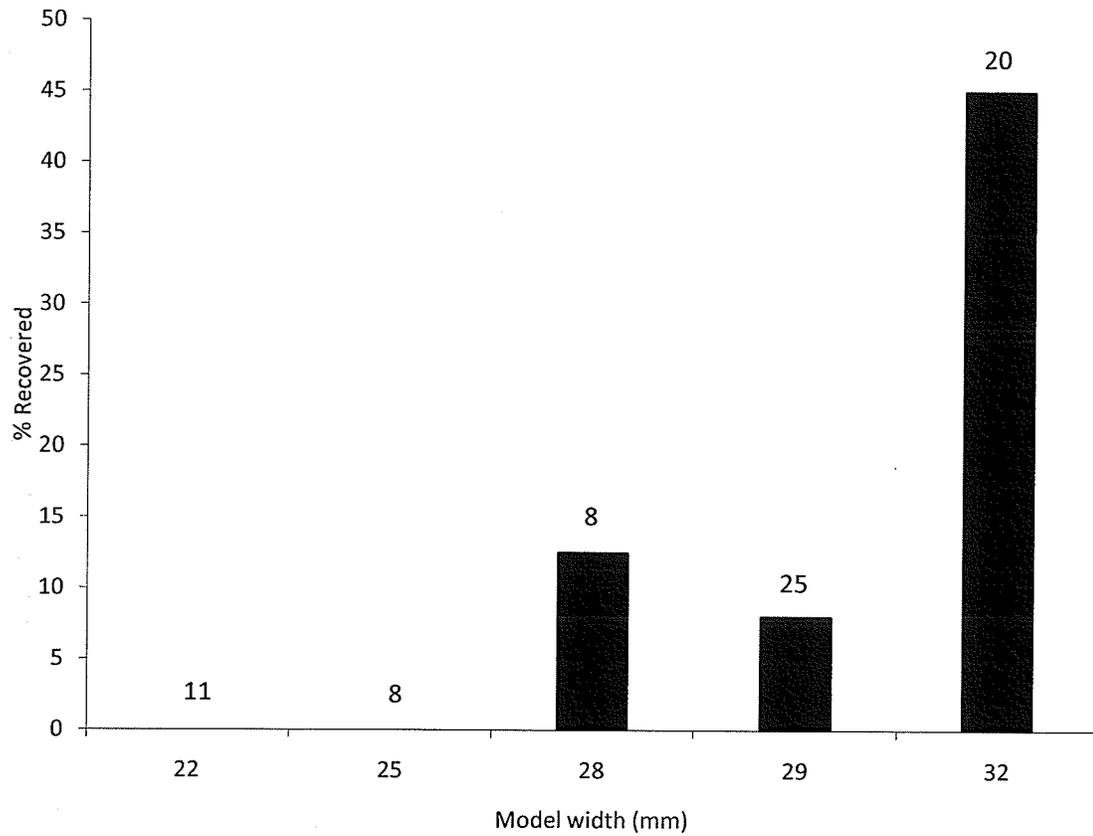


Figure 1.7. Percentage of models recovered within 3 m of Gray Catbird nests according to width in 2006 (sample sizes above bars).



Comparison of two-day (2005) vs. five-day (2006) acceptance criterion used for Gray Catbirds

In 2005, catbirds ejected 71.2% ($n = 66$) of models 22-, 25-, and 28-mm wide within 2-days with a mean time to ejection of 1.28 ± 0.07 SE days ($n = 47$). In 2006, catbirds ejected 93.3% ($n = 30$) of models 22-, 25-, and 28-mm with a mean time to ejection of 1.56 ± 0.09 SE days ($n = 28$). Time to ejection of more than 2 days was recorded in 2 of 28 ejections (0.07%), but when all widths were included in 2006 (i.e., models 22-, 25-, 28-, 29-, and 32-mm wide), 5 of 73 ejections (0.07%) took more than 2 days.

No statistically significant difference was found in the ejection frequency of models 25- and 28-mm wide by catbirds between 2005, using the 2-day acceptance criterion, and 2006, using the 5-day acceptance criterion (25 mm: Fisher exact test, two-tail, $P = 1.0000$, $n = 20$ in 2005 and $n = 11$ in 2006; 28 mm: Fisher exact test, two-tail, $P = 0.1497$, $n = 24$ in 2005 and $n = 8$ in 2006). By contrast, a significant difference was found in the ejection frequency of models 22-mm wide by catbirds between 2005 ($n = 22$), using the 2-day acceptance criterion, and 2006 ($n = 11$), using the 5-day acceptance criterion (Fisher exact test, two-tail, $P = 0.0313$).

No statistically significant difference was found in the survival of models 25- and 28-mm wide between 2005 ($n = 22$ and $n = 25$, respectively), using a 2-day acceptance criterion, and 2006 ($n = 11$ and $n = 8$, respectively), using a 5-day acceptance criterion (25 mm: Log-rank test, $\chi^2 = 0.0378$, $df = 1$, $P = 0.8458$; Wilcoxon-rank test, $\chi^2 = 0.0037$, $df = 1$, $P = 0.9517$; and 28 mm: Log-rank test, $\chi^2 = 1.1627$, $df = 1$, $P = 0.2809$; Wilcoxon signed-rank test, $\chi^2 = 1.0480$, $df = 1$, $P = 0.3060$). By contrast, a significant difference

was found in the survival of models 22-mm wide between 2005 ($n = 22$), using the 2-day acceptance criterion, and 2006 ($n = 11$), using the 5-day acceptance criterion (Log-rank test, $\chi^2 = 9.1429$, $df = 1$, $P = 0.0025$; Wilcoxon signed-rank test, $\chi^2 = 9.1429$, $df = 1$, $P = 0.0025$). Despite differences in the time to ejection of models 22-mm wide, data collected in 2005 were combined with data in 2006 because catbirds eject models within 2 days almost invariably.

Response to different model widths by Gray Catbirds (combined results from 2005 and 2006)

Combining the results from 2005 and 2006 of 210 nests, responses were recorded at 194 nests because 16 were depredated (Table 1.6). Catbirds ejected 85.1% of the models inserted into their nests. Mean time to ejection and desertion was 1.28 ± 0.05 SE days ($n = 165$) and 2.00 ± 0.31 SE days ($n = 5$), respectively. Nest stage did not significantly influence model ejection frequency (Fisher exact test, two-tailed, $P = 0.2411$, $n = 190$). Model width did not significantly influence ejection frequency (Cochran-Armitage exact trend test, one-tailed, $Z = 1.3116$, $P = 0.1995$, $n = 194$; Figure 1.8). Nest stage did not influence model survival (Log-rank test, $\chi^2 = 1.1815$, $df = 1$, $P = 0.2770$; Wilcoxon signed-rank test, $\chi^2 = 1.1430$, $df = 1$, $P = 0.2850$). Model width significantly influenced model survival in catbird nests (Log-rank test, $\chi^2 = 14.9415$, $df = 6$, $P = 0.0207$; Wilcoxon-rank test $\chi^2 = 12.6607$, $df = 6$, $P = 0.0488$; Figure 1.9). The cost of ejection did not differ significantly between model widths (Kruskal-Wallis test, $\chi^2 = 5.3007$, $df = 6$, $P = 0.5059$, $n = 164$; Table 1.7). Larger models were recovered within

Table 1.6. Responses of Gray Catbirds to models of different widths placed in their nests (results from 2005 and 2006).

Model width	Response	Days					Total
		1	2	3	4	5	
16 mm	Accepted						0
	Ejected	17	5				22
	Nest Deserted						0
	Nest Depredated	1					1
19 mm	Accepted		1				1
	Ejected	21	2				23
	Nest Deserted						0
	Nest Depredated	2					2
22 mm	Accepted		8				8
	Ejected	21	4				25
	Nest Deserted						0
	Nest Depredated						0
25 mm	Accepted		4			2	6
	Ejected	15	9	1			25
	Nest Deserted						0
	Nest Depredated	3					3
28 mm	Accepted		7				7
	Ejected	20	4		1		25
	Nest Deserted						0
	Nest Depredated	1					1
29 mm	Accepted					4	4
	Ejected	19	4	1	1		25
	Nest Deserted						0
	Nest Depredated			1	1		2
32 mm	Accepted					3	3
	Ejected	15	4			1	20
	Nest Deserted	1	3	1			5
	Nest Depredated				1	1	2

Figure 1.8. Percentage of models ejected from Gray Catbird nests according to width (results from 2005 and 2006; sample sizes above bars).

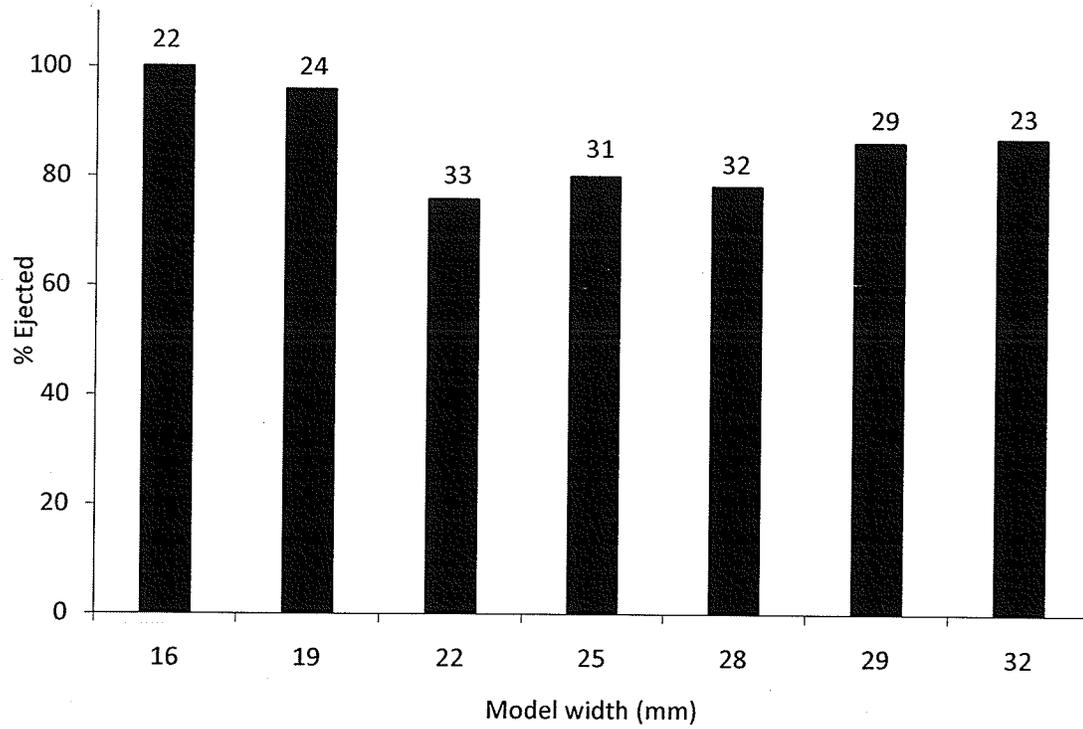


Figure 1.9. Survival curves for models placed into 197 Gray Catbird nests according to width (results from 2005 and 2006).

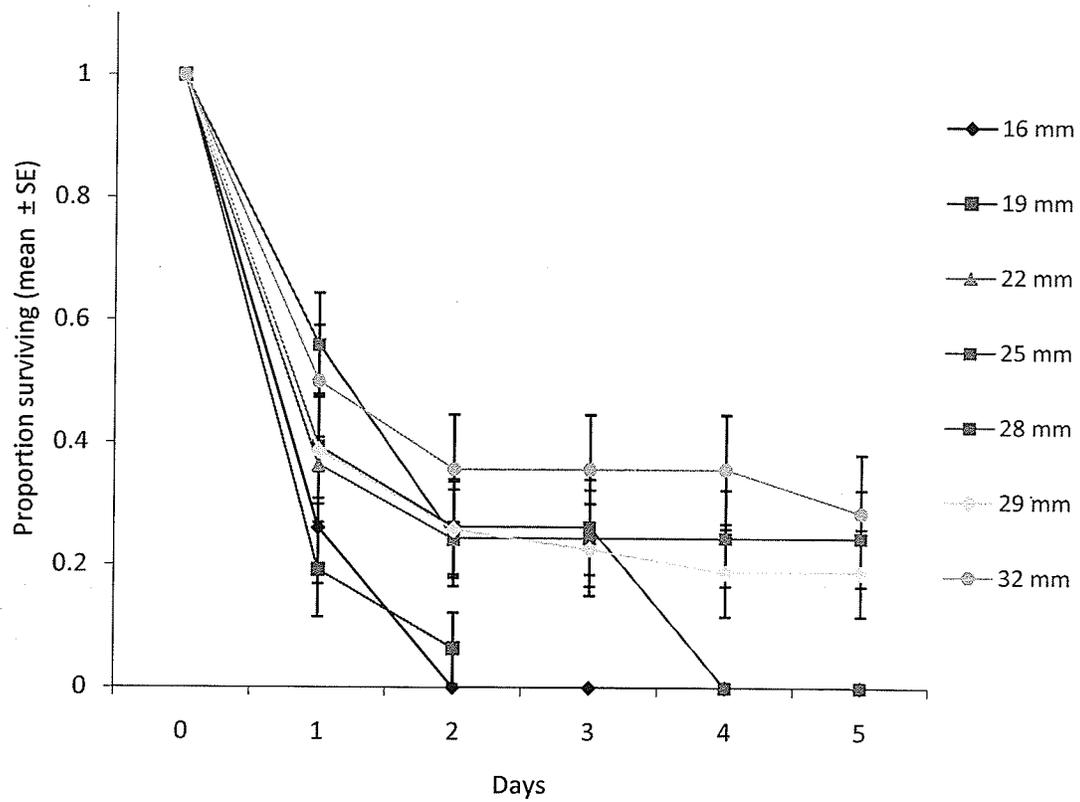


Table 1.7. Cost of ejection, in terms of the average number of host eggs missing or damaged per ejection, according to model width for Gray Catbirds.

Model width	<i>n</i>	Host eggs missing or damaged per ejection (Mean ± SE)
16 mm	22	0.14 ± 0.11
19 mm	23	0.22 ± 0.11
22 mm	25	0.12 ± 0.10
25 mm	24	0.04 ± 0.11
28 mm	25	0.32 ± 0.10
29 mm	25	0.28 ± 0.10
32 mm	20	0.00 ± 0.12

3 m of the nest significantly more frequently than smaller models (Cochrane-Armitage exact trend test, $Z = 3.6493$, one-tail, $P < 0.0001$, $n = 163$; Figure 1.10).

Response to different model widths by American Robins

Responses were recorded at 76 of 97 nests; 11 and 10 nests were depredated or deserted, respectively (Table 1.8). Robins ejected 64.5% ($n = 76$) of the models with a mean time until ejection of 1.67 ± 0.14 SE days ($n = 49$). Mean time to desertion and depredation was 2.82 ± 0.38 SE days ($n = 11$) and 2.40 ± 0.43 days SE ($n = 10$), respectively. Nest stage did not significantly influence the frequency of model ejection (Fisher exact test, two-tailed, $P = 0.5825$, $n = 76$). Smaller models were ejected more frequently than larger models (Cochran-Armitage exact trend test, one-tailed, $Z = 4.5203$, $P < 0.0001$, $n = 76$; Figure 1.11). Nests that received larger models were deserted more frequently than nests that received smaller models (Cochran-Armitage exact trend test, $Z = 3.1738$, one-tailed, $P = 0.0006$, $n = 86$). Nest stage did not influence model survival (Log-rank test, $\chi^2 = 0.0781$, $df = 1$, $P = 0.7798$, $n = 97$; Wilcoxon-rank test, $\chi^2 = 0.1193$, $df = 1$, $P = 0.7298$, $n = 97$). Larger models survived significantly longer than smaller models (Log-rank test, $\chi^2 = 28.0948$, $df = 2$, $P < 0.0001$, $n = 97$; Wilcoxon-rank test, $\chi^2 = 22.2113$, $df = 2$, $P < 0.0001$, $n = 97$; Figure 1.12). Cost of ejection did not differ significantly among model widths (Kruskal-Wallis test: $\chi^2 = 1.1138$, $df = 2$, $P = 0.5730$). The mean cost of ejection was 0.09 eggs/ejection (± 0.08 SE, $n = 23$), 0.18 eggs/ejection (± 0.09 SE, $n = 17$), 0.00 eggs/ejection (± 0.12 SE, $n = 9$) for models 16-, 29-, and 32-mm wide, respectively. Larger models were found within 3 m of the nest significantly more frequently than smaller models (Cochrane-Armitage exact trend test, $Z = 3.7960$,

Figure 1.10. Percentage of ejected models of different widths recovered within 3 m of Gray Catbird nests (results from 2005 and 2006; sample sizes above bars).

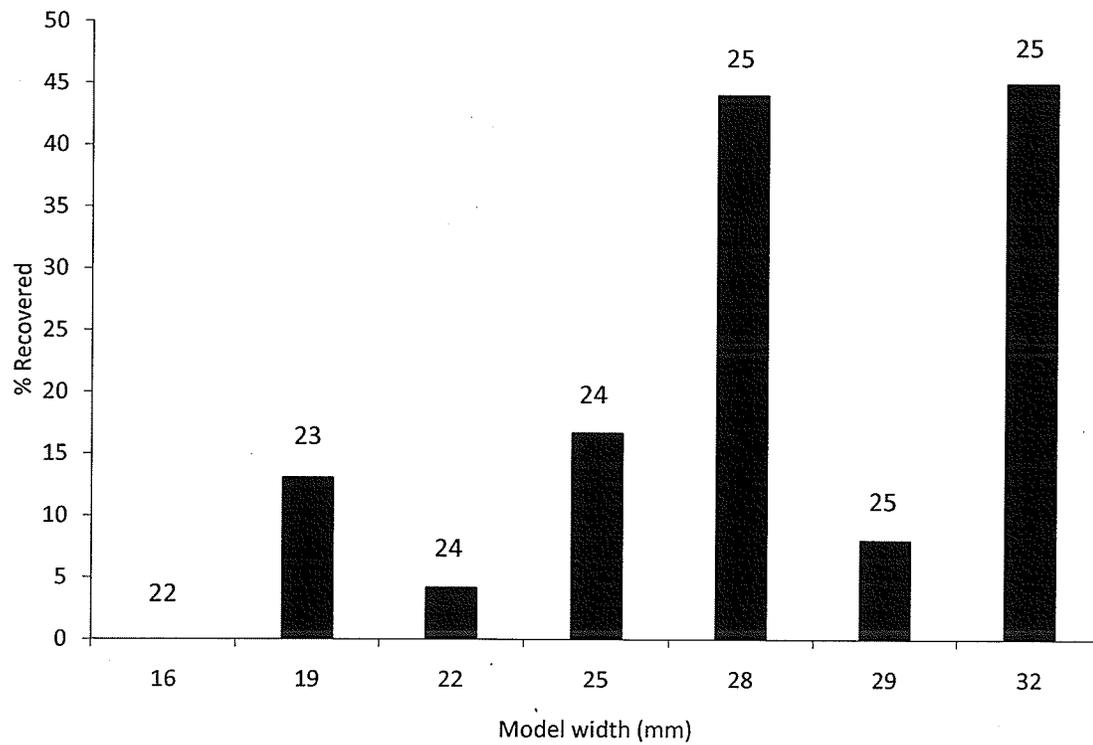


Table 1.8. Responses of American Robins to models of different widths placed in their nests in 2006.

Model width	Response	Days					Total
		1	2	3	4	5	
16 mm	Accepted					1	1
	Ejected	15	3	3	2		23
	Nest Deserted						0
	Nest Depredated	1		2			3
29 mm	Accepted					9	9
	Ejected	9	4	2	2		17
	Nest Deserted	1					1
	Nest Depredated		1			1	2
32 mm	Accepted					17	17
	Ejected	6	2	1			9
	Nest Deserted	1	2	3	2	1	9
	Nest Depredated	2	2	1	1		6

Figure 1.11. Percentage of models ejected from American Robin nests of different widths (sample sizes above bars).

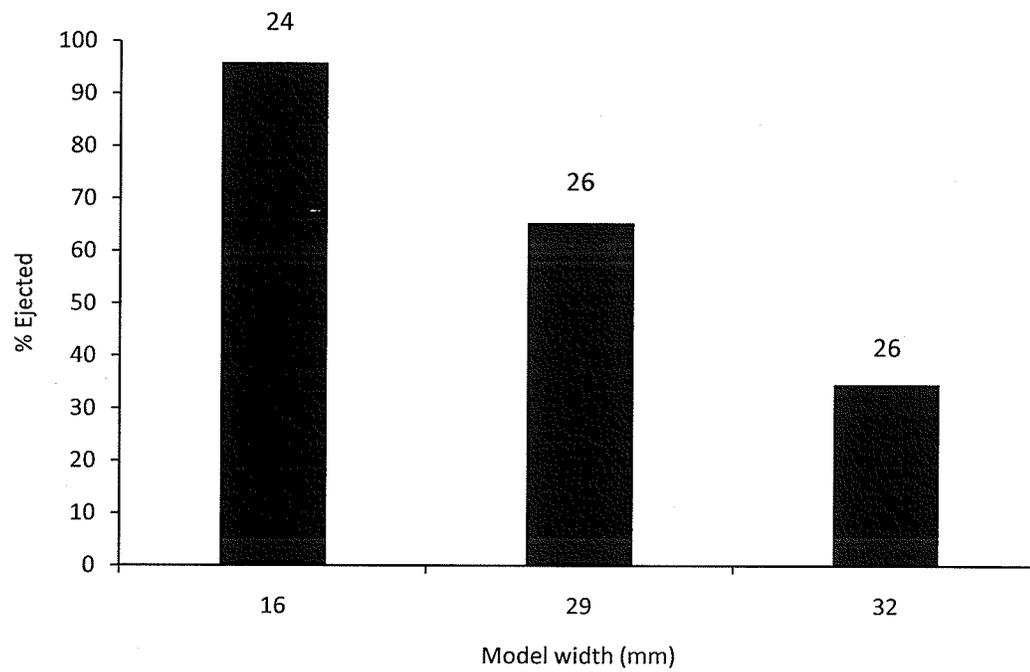
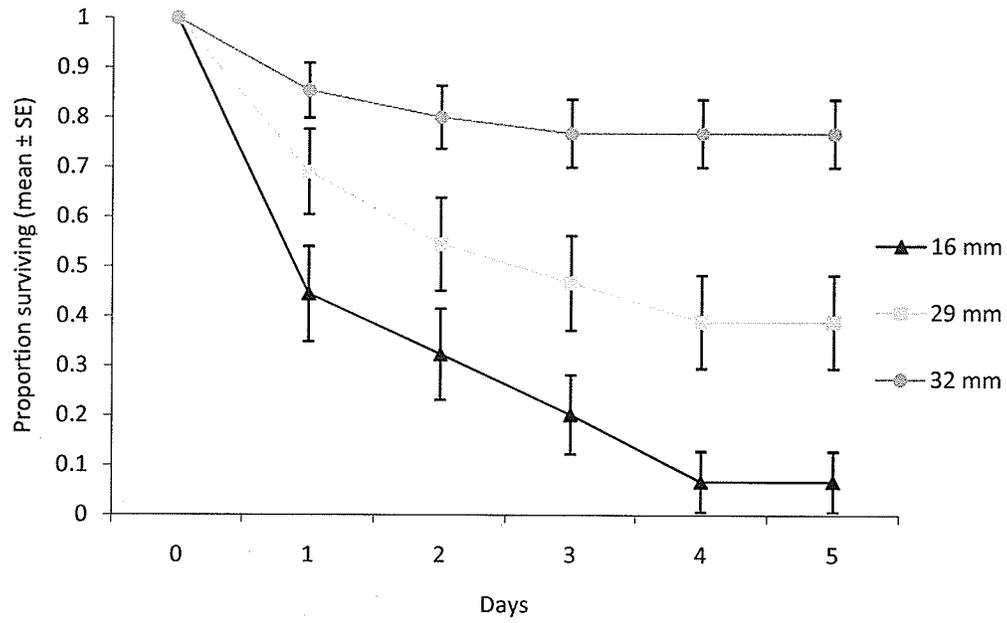


Figure 1.12. Survival curves for 97 models added to American Robin nests of different widths.



one-tailed, $P < 0.0001$, $n = 48$; Figure 1.13).

Comparison of responses of American Robins and Gray Catbirds to different model widths

No statistically significant difference was found in the ejection frequency of models 16- and 29-mm wide by catbirds and robins (16 mm: Fisher exact test, two-tailed, $P = 1.000$, $n = 46$; 29 mm: Fisher exact test, two-tailed, $P = 0.1115$, $n = 55$; Figure 1.14).

A significant difference was found between robins and catbirds in the rejection frequency of models 32-mm wide (Fisher exact test, two-tailed, $P < 0.001$, $n = 49$; Figure 1.14).

Models 16-mm wide survived significantly longer in American Robin nests compared with those in Gray Catbird nests according to the Log-rank test ($\chi^2 = 6.2985$, $df = 1$, $P = 0.0121$, $n = 50$; Figure 1.15), whereas the survival of models 16-mm wide was not significantly different between the species according to the Wilcoxon-rank test ($\chi^2 = 3.3397$, $df = 1$, $P = 0.0676$, $n = 50$; Figure 1.15). This suggests that the earlier portions of the survival curves are similar, whereas the later differ significantly (Figure 1.15).

Models 29-mm wide survived significantly longer in robin nests than catbird nests (Log-rank test, $\chi^2 = 4.4209$, $df = 1$, $P = 0.0355$, $n = 60$; Wilcoxon-rank test, $\chi^2 = 5.7125$, $df = 1$, $P = 0.0168$, $n = 60$) as did models 32-mm wide (Log-rank test, $\chi^2 = 15.3514$, $df = 1$, $P < 0.0001$; Wilcoxon-rank test, $\chi^2 = 14.1211$, $df = 1$, $P = 0.0002$).

No significant difference was found in the percentage of ejected models 16-mm and 32-mm wide recovered within 3 m from the nest (16 mm: Fisher exact test, two-tailed, $P = 1.00$, $n = 45$; 32 mm: Fisher exact test, two-tailed, $P = 0.7$, $n = 28$;

Figure 1.13. Percentage of ejected models recovered within 3 m of American Robin nests according to model width (sample sizes above bars).

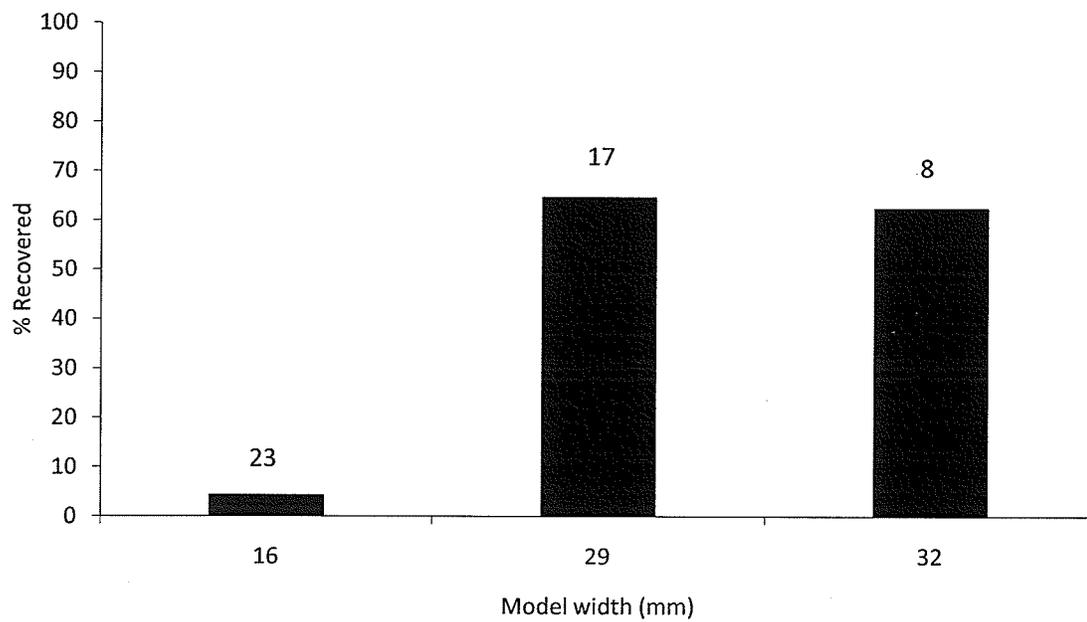


Figure 1.14. Ejection frequencies of American Robin and Gray Catbird of models 16-, 29-, and 32-mm wide (sample sizes above bars).

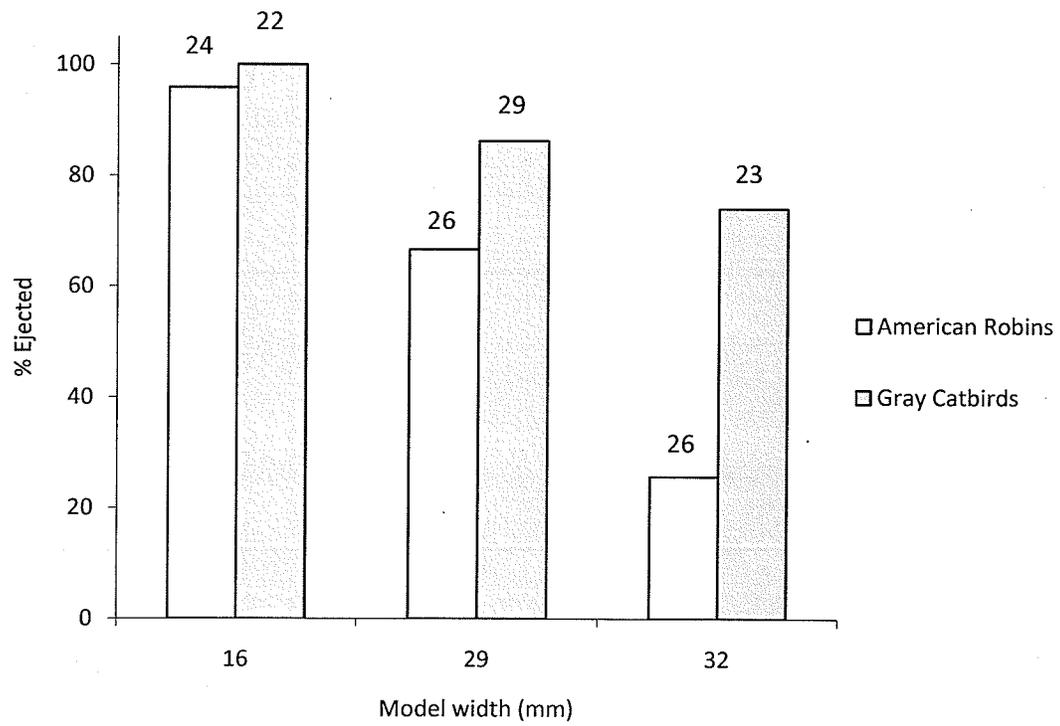


Figure 1.15. Survival curves for models 16-, 29-, and 32-mm wide placed into American Robin ($n = 97$) and Gray Catbird ($n = 84$) nests.

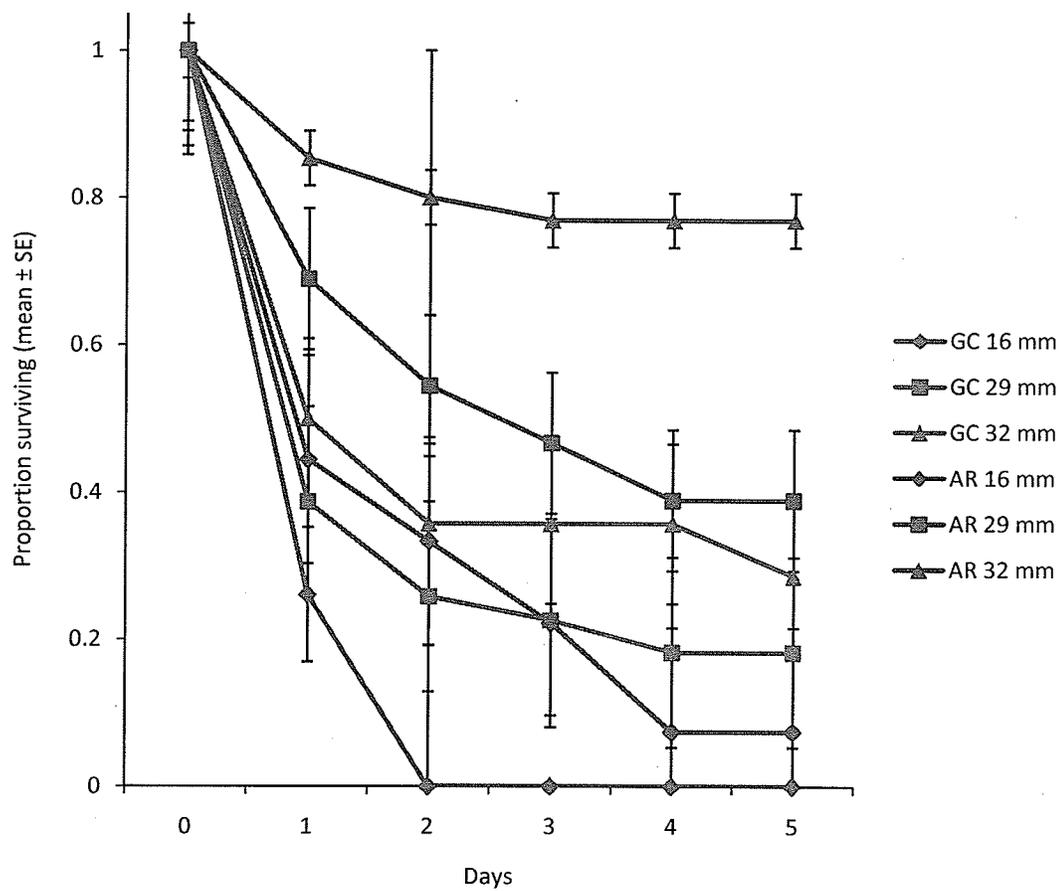


Figure 1.16). However, the distance that models 29-mm wide were carried, as measured by the percentage of models found within a 3-m radius of the nest, differed significantly between robins and catbirds (Fisher exact test, two-tail, $P = 0.0001$, $n = 42$; Figure 1.16).

Cost of ejection did not differ significantly between robins and catbirds (16 mm:

Kruskal-Wallis test, $\chi^2 = 0.0085$, $df = 1$, $P = 0.9267$, $n = 45$; 29 mm: Kruskal-Wallis test, $\chi^2 = 0.4515$, $df = 1$, $P = 0.5016$, $n = 42$; 32 mm: Kruskal-Wallis test, $\chi^2 = 0.0000$, $df = 1$, $P = 1.000$, $n = 29$).

Method of ejection

Eighteen video-recordings of robins and catbirds showed that they ejected the model either by grasping its entire width (Figure 1.17; hereafter grasp-ejection) or ejected by pinching the edge of the cylinder (Figure 1.18; hereafter pinch-ejection). Robins grasped the entire width of real cowbird eggs ($n = 2$) and models 16-mm wide ($n = 2$; one ejection was observed but not video-recorded), but pinch-ejected models 29-mm wide ($n = 4$). Catbirds grasp-ejected 5 of 7 real cowbird eggs, but pinch-ejected all models 29-mm wide ($n = 3$).

Discussion

Video-recordings revealed that robins and catbirds used grasp-ejection (Figure 1.17) or pinch-ejection (Figure 1.18). Grasp-ejection of a model represents the host's ability to grasp-eject an egg the same width as the model, whereas pinch-ejection involves the host using the edge formed between the side and end-face of the cylinder to

Figure 1.16. Percentage of ejected models recovered within 3 m of American Robin and Gray Catbird nests according to model width (sample sizes above bars).

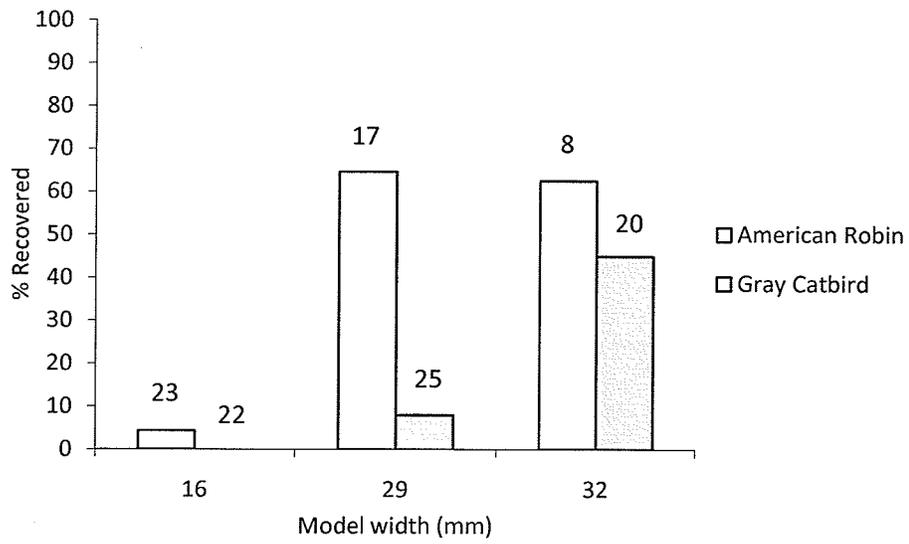


Figure 1.17. Video stills illustrating grasp-ejection by Gray Catbird (A) and American Robin (B).

A



B



Figure 1.18. Video stills illustrating pinch-ejection by Gray Catbird (A) and American Robin (B).



grasp the model and obviously is not a natural situation. Eggs do not afford hosts the option of pinch-ejection because they do not have edges and, thus, the host must be able to grasp the entire width of the egg between upper and lower mandible for grasp-ejection. In this experiment, I assumed that the only way robins and catbirds can eject the models is to grasp-eject them by their maximum widths. This turned out to be erroneous and, hence, interpretation of the results in terms of the hypotheses was impossible. Because not all of the ejections were video-recorded and robins and catbirds used two methods to eject models from their nests, it is not known whether the absence of a model at an active nest represents the host's ability to grasp-eject an egg of the same width as the model. However, knowing the widths at which robins and catbirds switched from grasp-ejection to pinch-ejection permitted the limit of grasp-ejection to be determined.

Video-recordings suggested that robins and catbirds used grasp-ejection for smaller objects and pinch-ejection for larger models. From these preliminary data, I predicted that robins and catbirds switched from grasp- to pinch-ejection at a model width between 16 mm and 29 mm. The width at which robins and catbirds switched from ejecting models by grasping their entire width (i.e., grasp-ejection) to using only part of the width (i.e., pinch-ejection), I assumed, was the limit width of grasp-ejection, because grasping the entire width of the model is the less complicated option for ejecting the model.

In Chapter 2, I present the results of a new experiment that involved augmenting the sample of video-recorded ejections already taken to determine the method of ejection used by robins and catbirds for models of different widths. Knowing the method of

ejection allowed me to determine the largest width robins and catbirds could grasp-eject, which ultimately allowed me to determine the smallest bill required by a bird to grasp-eject a cowbird egg.

Chapter 2: Limits of grasp-ejection in the American Robin and Gray Catbird: implications for the evolutionary lag and evolutionary equilibrium hypotheses

Brown-headed Cowbirds (hereafter cowbirds) lay their eggs in the nests of other species, the hosts, and let the hosts foster and feed their young until they become independent (Friedmann 1929). Avian brood parasites, like the cowbird, impose high costs on their hosts' fitness because hosts fledge fewer and inferior young because the parasite's eggs and chicks reduce the host's hatching success (Kattan 1998, McMaster and Sealy 1998, Sealy et al. 2002, Hoover 2003), and the parasitic chick may outcompete host chicks for parental care (Dearborn et al. 1998). Parasitism also compromises fledgling survival (Airola 1986, Payne and Payne 1998, Rasmussen and Sealy 2006). Despite these costs, most hosts accept parasitic eggs and young (Rothstein 1975, Peer and Sealy 2004). Acceptance seems maladaptive and, therefore, is one of the greatest enigmas in the study of avian brood-parasitic systems (Winfrey 1999). Adding to the enigma is that the appearance (i.e., color, pattern, and shape) of cowbird eggs differs sufficiently from the eggs of many accepters (Mermoz and Ornelas 2004), thus, providing hosts with a stimulus for the evolution of ejection behavior given the precedence of refined egg discrimination in some hosts such as the Brown Thrasher (Rothstein 1975, Haas and Haas 1998).

The evolutionary lag and evolutionary equilibrium hypotheses have been proposed to explain acceptance. The premise of the evolutionary lag hypothesis is that hosts accept foreign eggs because they have not been parasitized long enough or at frequencies sufficient to enable appropriate genetic variants to appear, be selected, and

spread within the population (Rothstein 1975, 1982, 1990; Davies and Brooke 1989). By contrast, evolutionary equilibrium posits that acceptance in certain hosts has been selected because the cost of rejection is greater than the cost of acceptance (Rohwer and Spaw 1988, Lotem and Nakamura 1998). Both hypotheses are founded on different physical abilities of hosts to reject parasitic eggs. In evolutionary lag, the adaptive response to parasitism is rejection by all hosts. By contrast, in equilibrium certain hosts may be constrained by their size to accept parasitic eggs because it is more costly for them to reject the parasitic egg than to accept and raise a cowbird (Rohwer and Spaw 1988). Because the physical ability of hosts is likely to vary between species, however, there is no reason to assume that either hypothesis can be applied to all cowbird hosts (Ortega 1998, Davies 1999). Knowing the minimum physical requirements for efficient rejection of cowbird eggs is essential for understanding whether equilibrium or lag best explains acceptance in each host species.

Methods of rejection such as egg burial, nest desertion, and egg ejection impose different costs on hosts and small hosts are thought to be constrained by small bills to more costly methods of rejection (Rohwer and Spaw 1988). Ejection is apparently the most easily evolved anti-parasite defense because it has a genetic basis, is efficient, and involves the same motor patterns that are used in foraging and nest sanitation (Rothstein 1975, Peer and Sealy 2004, Martín-Gálvez et al. 2006). As the basic motor patterns required for ejection are likely present in all hosts and because ejection behavior is heritable, why do most hosts accept cowbird eggs?

Hosts eject by either puncturing a cowbird eggshell with their bill and using the

hole to remove the egg from the nest (hereafter puncture-ejection) or removing the unbroken egg by grasping its entire width between the mandibles (hereafter grasp-ejection; Rohwer and Spaw 1988, Rohwer et al. 1989). Puncture-ejection is more costly than grasp-ejection because hosts are more likely to damage their own eggs (Lorenzana and Sealy 2001). The higher cost of puncture-ejection is in part due to the proportionally rounder shape and thicker shells of cowbird eggs, which according to the “puncture-resistance” hypothesis evolved to render puncture-ejection maladaptive for some hosts (Spaw and Rohwer 1987, Picman 1989, Antonov et al. 2006). Some blows may ricochet off the parasitic egg to the host’s own eggs, damaging the host’s eggs. Puncture-ejection may also cost in time and energy invested (Spaw and Rohwer 1987, Sealy 1996, Martín-Vivaldi et al. 2002). By contrast, grasp-ejection is nearly cost-free (Rohwer et al. 1989, Lorenzana and Sealy 2001, Underwood and Sealy 2006a).

By comparing bill lengths of accepters and grasp-ejecters, Rothstein (1975) suggested that hosts with tomial-length-to-egg-width ratios of 0.7 should be able to eject parasitic eggs. However, including both grasp-ejecters and puncture-ejecters in his calculation likely overestimated the ability of small hosts because bill length may be inconsequential to puncture-ejection (Rohwer and Spaw 1988). Because of the demonstrated inability of Rothstein’s (1975) ratio to identify hosts capable of grasp-ejection (Briskie and Sealy 1987), Rohwer and Spaw (1988) developed an index that more accurately identified hosts that can grasp-eject. Rohwer and Spaw’s (1988) grasp-index is the ratio of tomial length multiplied by the commissural breadth of the bill (i.e., bill width, measured in mm as the distance between the commissural points). By

applying the grasp-index to several cowbird hosts, they found that no hosts with grasp-indexes less than 200 mm^2 grasp-ejected parasitic eggs (Rohwer and Spaw 1988).

Since then, the discovery of grasp-ejecters with grasp-indexes far below 200 mm^2 have led others to suggest that bill length, instead of the grasp-index, better represents a host's ability to grasp-eject (Moksnes et al. 1991, Peer and Sealy 2004). Rothstein attributed the failure of the grasp-index to the inclusion of commissural width in the index, which, according to him, is unimportant to grasp-ejection because in grasp-ejection the egg is held at the tip of the bill. However, both Rothstein's (1975) and Rohwer and Spaw's (1988) approaches have shortcomings because factors other than physical ability have been correlated with the appearance of ejection behavior (Chapter 1).

Differential past parasitism pressure, population size (hence, a more variable gene pool), and taxonomic affiliations of the host species have also been suggested as possible reasons for the current pattern of accepters and ejecters (Rothstein 1975, Peer and Sealy 2004). Furthermore, the pattern of larger rejecters and smaller accepters has been suggested to have resulted from preferential parasitism of larger hosts in the past by cowbirds because larger species were superior foster parents because they provided more food to nestlings and defended their nests better (Rothstein 1975). It has also been suggested that larger hosts were parasitized more frequently in the past because their nests were easier to find (Rothstein 1975). Therefore, the propensity of hosts to reject may be attributable to differences in parasitism pressure hosts experienced in the past.

The problem of differential past parasitism plaguing previous studies was eliminated in the experiment presented in Chapter 1 by testing for the largest

grasp-ejectable egg width within a species. However, preliminary video, recorded to confirm the method of ejection, revealed that robins and catbirds grasp-ejected models and eggs 16-mm wide and pinch-ejected models 29-mm wide (see Figure 1.17 and 1.18 in Chapter 1). The use of two methods of ejection violated the assumptions required to interpret the results in terms of the hypotheses. Interpretation of the results was only possible if the method of ejection used for each model was known, but it was not.

The objective of this study was to determine the method of ejection (i.e., grasp- or pinch-ejection) and associated costs for models of different widths to determine at what width robins and catbirds switched methods, which I assumed represented the largest widths that they can grasp-eject (hereafter limit width). The limit width could then be standardized according to the species' tomial length to render the ratio applicable to hosts of any brood parasite. This ratio is important to the study of brood parasitism because it can predict which hosts are capable of grasp-ejection and which ones are constrained to more costly methods of rejection or even acceptance. However, costs associated with an increase in the egg-width-to-tomial-length ratio may prevent the appearance of grasp-ejection in some species, despite being physically capable. In this study, I tested the following hypotheses.

Hypotheses

- i) A minimum tomial length is required to grasp-eject a cowbird egg; all hosts with tomia shorter than the minimum length are constrained to accept cowbird eggs or reject through more costly methods.
- ii) Cost of grasp-ejection increases and distance cowbird eggs are carried from host nests decreases as egg-width-to-bill-length ratio increases.

Methods

During the spring of 2007, the limits of grasp-ejection were sought in robins and catbirds breeding at Delta, Manitoba (50°11' N, 98°19' W; see Chapter 1 for a complete description of the study species and study site). I determined the method robins and catbirds used to eject models of different widths by video-recording ejections of models 16-, 19-, 22-, 25-, 28-, and 29-mm wide (Table 2.1). Each data point consisted of a video-recorded ejection in which the method of ejection could be determined. Ejections video-recorded in 2006 were added to those taken in 2007. It is unlikely that the year of testing affects the method of ejection. Models used in this experiment were identical to the ones used in the experiment presented in Chapter 1 (see Chapter 1 for a complete description) except that all models had an identification number (2 mm x 2mm) placed on them that was used to identify the nest to which it had been added. I also determined the methods robins and catbirds used to eject real cowbird eggs because the only previously available information is anecdotal. This allowed me to determine their status as grasp-ejectors in a natural context.

I used a within-subject design to compare the effect of model width on the method of ejection because it offers several advantages over a between-subject design. A within-subject design requires relatively fewer participants and reduces problems of individual difference, which is of concern in between-subject designs (Gravetter and Forzano 2003). However, within-subject designs have disadvantages such as participant attrition and order effects (Gravetter and Forzano 2003). Potential order effects were minimized by randomizing treatment order at each nest. As will be seen in the

Table 2.1. Width, length, and mass (mean \pm SE) of models used in American Robin and Gray Catbird nests for video-recorded ejections.

Species	Model width	<i>n</i>	Width (mm)	Length (mm)	Mass (g)
American Robin					
	16 mm	12	15.94 \pm 0.02	16.59 \pm 0.14	6.63 \pm 0.08
	19 mm	9	19.29 \pm 0.02	19.72 \pm 0.10	6.22 \pm 0.23
	22 mm	10	21.87 \pm 0.03	22.36 \pm 0.15	6.44 \pm 0.03
	25 mm	10	24.98 \pm 0.06	25.16 \pm 0.05	6.35 \pm 0.05
	28 mm	6	28.17 \pm 0.05	29.06 \pm 0.11	6.47 \pm 0.10
	29 mm	4	29.50 \pm 0.05	30.41 \pm 0.09	6.33 \pm 0.06
Gray Catbird					
	16 mm	10	15.94 \pm 0.02	16.94 \pm 0.09	6.77 \pm 0.03
	19 mm	11	19.24 \pm 0.02	19.50 \pm 0.05	6.05 \pm 0.07
	22 mm	10	21.87 \pm 0.02	22.53 \pm 0.08	6.45 \pm 0.04
	25 mm	10	25.06 \pm 0.04	25.19 \pm 0.06	6.42 \pm 0.09
	28 mm	10	28.22 \pm 0.04	29.30 \pm 0.28	6.58 \pm 0.08
	29 mm	3	29.45 \pm 0.06	30.62 \pm 0.14	6.53 \pm 0.09

results, participant attrition was high and all model sizes were tested on 2 robin and 3 catbird nests only because of eggs hatching, depredation, or desertion by hosts. The high rate of participant attrition was addressed by analyzing the data with exact conditional logistic regression and stratifying the analysis according to “nest of ejection.”

Because of the within-subject design, with nest of ejection as the experimental unit, each nest was tested up to six times with a real cowbird egg and models of different widths (i.e., treatments). Each nest received a series of randomly selected treatments, but each nest was tested with a particular treatment only once. If the selected treatment had already been tested at a given nest, another model was randomly selected until a treatment that had not been tested for that nest was selected; this allowed for a random treatment order for each nest. Testing ended if ejections of a real cowbird egg and all model widths had been recorded at that nest. Testing also stopped when host eggs hatched or the nests were depredated or deserted.

The limit widths for robins and catbirds were standardized according to tomial length to render the estimate applicable to hosts of any brood parasite. Tomial length was represented as an interval because the exact tomial lengths of individuals in this experiment were not known. The upper and lower limits were 1.96 standard deviations above and below the mean tomial length for each species. Standard deviation is an estimate of the amount of variation in tomial lengths in the population sampled and 1.96 standard deviations above and below the mean encompasses approximately 95% of the tomial lengths we are expected to find within the population. As a result, maximum egg-width-to-tomial-length ratios (hereafter limit ratios) were also represented as intervals.

In addition to the method of ejection, the cost of ejection and distance hosts carried the models from the nests were measured. Cost of ejection was the number of eggs damaged or missing during the ejection. The distance robins and catbirds transported ejected models was measured to an arbitrary distance of 3 m from a point on the ground directly below the nest or beyond 3 m from a point on the ground directly below the nest. I measured distance dichotomously because of the difficulty of finding ejected models (e.g., I observed one robin drop a model 16-mm wide in water 20 m from the nest.).

Cameras similar to that described in Sabine et al. (2005) were set up 1-3 m from active nests in which models were inserted. Cameras consisted of camouflaged JVC™ 30GB Hard Drive Camcorders and Sony™ CCD-TRV308 NTSC Hi 8 cameras that were linked to Sony™ 160 GB DVD/HDD recorders. Motomaster Eliminator 1200W Powerboxes™ powered the cameras. All components, except for the Motomaster Eliminator 1200W Powerboxes™, were housed in water-resistant plastic containers to protect them from the elements. The cameras recorded continuously, without the need to change the batteries or recording media, for at least 8 hours.

Analysis

The data were analyzed with exact conditional logistic regression models because they consisted of a small number of samples (51 and 54 observations for robins and catbirds, respectively) within a small number of clusters (21 and 23 nests for robins and catbirds) with repeated binary responses (grasp- or pinch-ejection) tested under different experimental conditions (up to 6 different treatments; Luta et al. 1998). The logistic

regression model, the standard for analyzing binary outcome data (Kuss 2002), was used to describe the relationship between a binary outcome variable and one or more explanatory variables (Luta et al. 1998). The sample sizes obtained were not large enough to use asymptotic logistic regression models and, thus, the data were analyzed using exact (i.e., non-parametric) methods (Luta et al. 1998). Furthermore, because nests were treated repeatedly under different experimental conditions (i.e., model widths), the data were correlated and, thus, conditional logistic regression models with “nest of ejection” as a stratification variable were used (Luta et al. 1998). Unstratified versions of the exact logistic regression analyses were conducted, not as part of the main analyses, but as a means of assessing the effect of stratifying for nests (Luta et al. 1998).

Cox (1970) originally devised the theory for exact conditional logistic regression and Hirji et al. (1987) rendered the analysis computationally feasible by programming the technique for the SAS statistical software package. The “PROC LOGISTIC” procedure in the SAS statistical software package 9.1.3 was used to analyze the data using exact conditional logistic models. Asymptotic methods of analysis, such as general linear models, general estimating equations, and mixed-effect models, for analyzing small, sparse, or skewed data sets are often unreliable (Derr 2000).

Not all nests (i.e., clusters) were tested under all experimental conditions (i.e., model widths). Using terminology introduced by Rubin (1976), the data are considered to be missing completely at random because missing responses were independent of the treatments and any other covariate in the data set. Missing responses in this study were due to the inability to continue to test nests that had hatched, had been depredated, or were deserted. Because the missing responses are missing at random, the use of exact

logistic regression models, conditioning on the nests, is appropriate (Rubin 1976, Luta et al. 1998).

Results

I recorded 51 and 54 ejections of models at 21 and 23 nests by robins and catbirds, respectively (Table 2.2), and 12 and 17 ejections of real cowbird eggs by robins and catbirds, respectively (Table 2.3). Robins grasp-ejected all 12 real cowbird eggs and 82.4% ($n = 51$) of the models. Robins pinch-ejected the others. Catbirds grasp-ejected 82.4% ($n = 17$) of the real cowbird eggs and puncture-ejected the others. Catbirds grasp-ejected 57.4% ($n = 54$) of the models and pinch-ejected the others.

The probabilities that robins pinch-ejected (exact conditional logistic regression: $\beta = 1.6190$, $P = 0.0004$) and catbirds pinch-ejected models (exact conditional logistic regression: $\beta = 2.0201$, median unbiased estimate, $P = 0.0010$, Figure 2.1) increased significantly with model width. No host eggs were damaged in 12 and 14 observed grasp-ejections of real cowbird eggs by robins and catbirds, respectively. Catbirds did not damage their own eggs in any of the three observed puncture-ejections of real cowbird eggs. The probability that robins damaged their own eggs while grasp-ejecting a model did not vary significantly with width (exact conditional logistic regression: $\beta = 0.2812$, median unbiased estimate, $P = 0.67$, $n = 39$, Table 2.4). Robins damaged their own eggs in 1 of 39 model grasp-ejections. For catbirds, there was no increase in the cost of grasp-ejecting models as width increased (Table 2.4). Catbirds did not damage their own eggs while grasp-ejecting models.

Model width did not affect the probability that robins would drop models within

Table 2.2. Frequency of grasp-ejection by American Robins and Gray Catbirds according to model width video-recorded in 2006 and 2007.

Species	Model width	<i>n</i>	Grasp-ejected	Pinch-ejected	% Grasp-ejected
American Robins					
	16 mm	12 ^a	12	0	100
	19 mm	9	9	0	100
	22 mm	10	9	1	90
	25 mm	10	8	2	80
	28 mm	6	4	2	68
	29 mm	4	0	4	0
Gray Catbirds					
	16 mm	10	9	1	91
	19 mm	11	9	2	82
	22 mm	10	9	1	90
	25 mm	10	4	6	40
	28 mm	10	0	10	0
	29 mm	3	0	3	0

^a One ejection was observed but not video-recorded in 2006.

Table 2.3. Method of ejection of real Brown-headed Cowbird eggs by American Robins and Gray Catbirds video-recorded in 2006 and 2007.

Species	<i>n</i>	Punctured	Grasped
Gray Catbird	17	3	14
American Robin	12	0	12

Figure 2.1. Frequency of grasp-ejection by American Robins (A) and Gray Catbirds (B) according to model width video-recorded in 2006 and 2007 (sample sizes above bars).

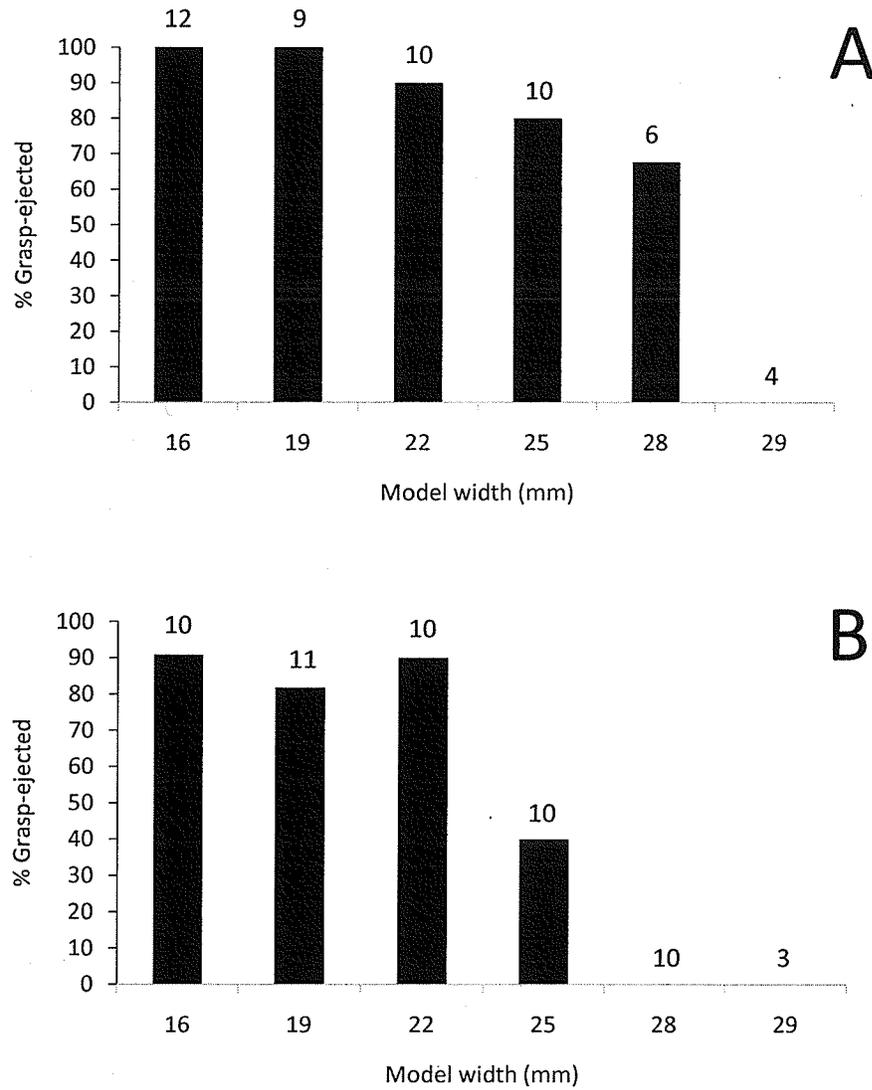


Table 2.4. Number of instances where host eggs were damaged during grasp-ejections.

Species	Model width	Ejections with damage	Total ejections
American Robin	16 mm	0	10
	19 mm	0	8
	22 mm	0	9
	25 mm	1	8
	28 mm	0	4
Gray Catbird	16 mm	0	9
	19 mm	0	9
	22 mm	0	9
	25 mm	0	4

3 m of the nest (exact conditional logistic regression: $\beta = 0.7910$, median unbiased estimate, $P = 0.33$, $n = 39$; Figure 2.2). By contrast, larger models were dropped by catbirds within 3 m more frequently than smaller models (exact conditional logistic regression: $\beta = 1.5981$, median unbiased estimate, $P = 0.0370$, $n = 31$; Figure 2.2).

Exact conditional analyses, stratified and unstratified for nest of ejection, yielded similar parameter estimates for the effect of model size on the method of ejection for robins and for catbirds (Table 2.5). Similarly, exact conditional logistic regression analyses, stratified and unstratified for nest of ejection, yielded similar parameter estimates for the effect of model width on the cost of grasp-ejection for robins (exact conditional logistic regression stratified for nest of ejection: $\beta = 0.2812$, median unbiased estimate, $P = 0.6667$, $n = 39$; exact conditional logistic regression not stratified for nest of ejection: $\beta = 0.8406$, $P = 0.6154$, $n = 39$). No statistical analyses were conducted to test the effect of model width on the cost of grasp-ejection for catbirds because damage to host eggs was not recorded for any width. Stratified and unstratified exact conditional analyses testing the effect of model width on the percentage of models recovered within 3 m from the nest also yielded similar results for robins and catbirds (Table 2.6).

The largest width that robins grasped was 28.2 mm, which is the smaller of the two measurements taken to represent the mean width of the cylinder. This feat represented a limit ratio between 0.96 and 1.10 given that approximately 95% (i.e., 1.96 standard deviations) of robin bill lengths are between 25.60 mm and 29.50 mm ($n = 97$; Underwood 2003). Linear extrapolation of the egg-width-to-bill-length ratio to the mean width of a cowbird egg (mean \pm SE: 16.4 ± 0.07 mm, $n = 113$; S. G. Sealy, unpublished data) predicted that a tomial length between 14.91 mm and 17.08 mm is required to

Figure 2.2. Percentage of grasp-ejected models recovered within 3 m of American Robin (A) and Gray Catbird (B) nests according to model width (sample sizes above bars).

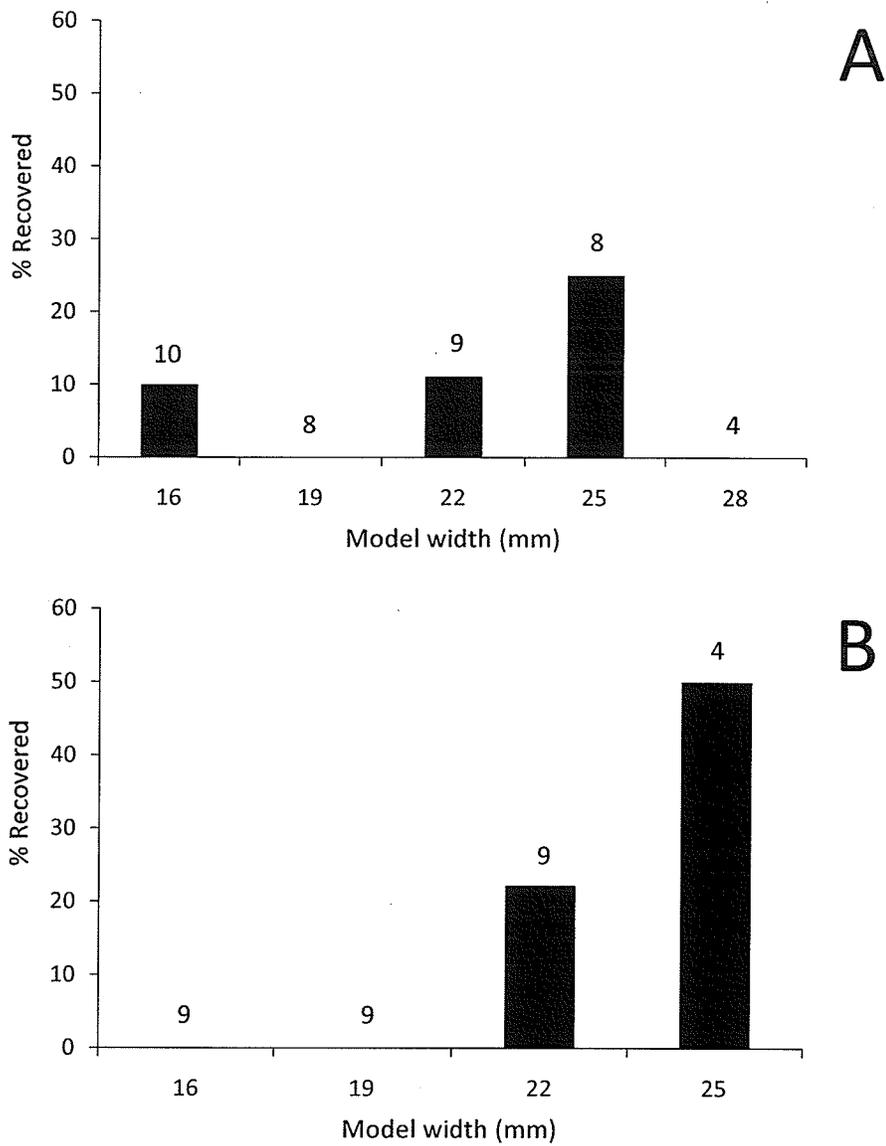


Table 2.5. Exact conditional logistic regression analysis parameter estimates, stratified and unstratified according to nest of ejection, for the effect of model width on the method of ejection.

Species	<i>n</i>	Stratified		Unstratified	
		β	P	β	P
American Robin	51	2.0201 ^a	0.0010	1.0753	0.0002
Gray Catbird	54	1.6190	0.0004	1.3261	< 0.0001

^a Median unbiased estimate.

Table 2.6. Exact conditional logistic regression analysis parameter estimates, stratified and unstratified according to nest of ejection, for the effect of model width on the percentage of models recovered within 3 m of nest.

Species	<i>n</i>	Stratified		Unstratified	
		β	P	β	P
American Robin	39	0.7910 ^a	0.3333	0.1894	0.7708
Gray Catbird	31	1.5981	0.0370	1.8414	0.0184

^a Median unbiased estimate.

grasp-eject a cowbird egg. This measurement is conservative because a robin's ability to grasp-eject eggs between 28.2 mm and 29.4 mm was not tested.

The largest width that catbirds grasped using the entire width was 25.1 mm, which is the smaller of the two measurements taken to represent the mean width of the model. This feat represented a limit ratio between 0.97 and 1.10 given that approximately 95% (i.e., 1.96 standard deviations) of catbird bill lengths are between 22.73 mm and 25.94 mm ($n = 90$; Underwood 2003). Linear extrapolation of this ratio to the mean width of a cowbird egg revealed a tomial length between 14.91 mm and 16.91 mm is required to grasp-eject cowbird eggs. This measurement is conservative because a catbird's ability to grasp-eject eggs between 25.1 mm and 27.9 mm was not tested.

Discussion

The results of my study support the hypothesis that grasp-ejection of parasitic eggs requires a bill of a minimum length and species whose bills are shorter than this length are relegated to rejecting parasitic eggs through more costly methods such as puncture-ejection, desertion/burial, or they accept the eggs. Only partial support was gained for the hypothesis that the distance ejected parasitic eggs are carried decreases as the egg-width-to-bill-length ratio increases. The prediction that the cost of grasp-ejection increases as the egg-width-to-bill-length ratio increases was not supported.

Robins and catbirds grasp-ejected models up to 28.2 mm and 25.1 mm wide, respectively, suggesting that the minimum tomial length required to grasp-eject cowbird eggs without risk to their own eggs lies between 14.91 mm and 17.08 mm. The results

provide contradictory evidence on whether the distance grasp-ejected models are carried from the nest increases as the egg-width-to-bill-length ratio increases.

Method of ejection of real cowbird eggs

Video-recorded ejections of real cowbird eggs revealed that robins and catbirds use grasp-ejection almost exclusively and, as a result, are suitable species to use to test the limits of grasp-ejection. Robins grasp-ejected all real cowbird eggs. By contrast, three of the four previously published observations of robins ejecting cowbird eggs suggest that they puncture-eject real cowbird eggs (Friedmann 1929:185, Nice 1944, Briskie et al. 1992, J. V. Briskie *in* Sealy and Neudorf 1995). Among catbirds, grasp-ejection was used most frequently (i.e., 14 of 17 ejections), whereas puncture-ejection was relatively rare (i.e., 3 of 17 ejections). Previous studies observed grasp-ejection in catbirds (Hauber 1998, Lorenzana and Sealy 2001), but I am the first to document puncture-ejection in this species.

Robins and catbirds did not damage any of their own eggs when ejecting real cowbird eggs, whether by puncture- or grasp-ejection. In two previous studies, catbirds incurred the same losses of 0.02 eggs on average per ejection when ejecting artificial cowbird eggs (Rothstein 1976, Lorenzana and Sealy 2001). Previous studies on robins also found that they incur very low ejection costs. Rothstein (1976) recorded 0.03 damaged or missing eggs per ejection of model eggs for robins. Similarly, S. G. Sealy (*in* Lorenzana and Sealy 2001) recorded 0.08 damaged or missing eggs per ejection by robins. Rohwer et al. (1989) did not record any damage to host eggs in two ejections of real cowbird eggs by robins. The slightly higher cost of ejection recorded in previous

studies may be due to partial depredation of eggs or, in catbirds, the use of artificial cowbird eggs, which prevented puncture-ejecters in the population from revealing themselves (Martín-Vivaldi et al. 2002). These factors were controlled in the present study, however, because video-recordings permitted monitoring of partial depredations and determination of whether ejection was by puncturing or grasping. It is also possible that the small sample sizes precluded the detection of any cost.

Catbirds puncture-ejected three cowbird eggs at no costs, which suggests that puncture-ejection may not be as costly as previously thought, at least in larger hosts. Puncture-ejection has also been found to be adaptive in the only four other hosts that have been observed to puncture-eject cowbird eggs: Baltimore Orioles, Bullock's Orioles, Cedar Waxwings (*Bombycilla cedorum*), and Warbling Vireos (Rothstein 1976, Rothstein 1977, Rohwer et al. 1989, Røskaft et al. 1993, Sealy and Neudorf 1995, Sealy 1996). Despite being adaptive in hosts larger than the Warbling Vireo, puncture-ejection may not be selected for in smaller hosts because the cost they incur may be greater if they are not strong enough to puncture the eggs efficiently (Spaw and Rohwer 1987, Sealy 1996).

Limits of grasp-ejection

Robins and catbirds grasp-ejected models (see Chapter 1: Figure 1.17) up to 28.2- and 25.1-mm wide, respectively, beyond which they pinch-ejected them (see Chapter 1: Figure 1.18). These limit widths were proportional to the mean length of their tomia. Thus, their maximum ejectable-egg-width-to-tomial-length ratios were the same, which supports Rothstein's (1975) suggestion that the ability to grasp-eject eggs is highly

correlated with the hosts' tomial length. However, because I do not know the tomial length of the individual in each observation, my prediction of the minimum tomial length required to grasp-eject a cowbird egg are only as good as our estimate of the variation in tomial length in robin and catbird populations. This is why my estimate is represented as an interval of limit ratios within which the true limit ratio exists. With this in mind, the largest model widths that robins and catbirds were able to grasp-eject represented a limit ratio between 0.95 and 1.11. This is a conservative estimate, however, because we did not test the ability of robins and catbirds to grasp-eject a continuous series of model widths, but instead tested them with widths that occurred at intervals (i.e., 16 mm, 19 mm, 22 mm, 25 mm, 28 mm and 29 mm). As a result, the limit width each species can grasp-eject may be higher because there is a gap between widths tested, between the largest model they grasp-ejected and the next larger model they pinch-ejected, that was not tested.

Applying the limit ratio in robins and catbirds to the width of a cowbird egg suggests that host species with tomial lengths above 17.08 mm can grasp-eject cowbird eggs and hosts with bill lengths below 14.91 mm cannot grasp-eject them. The ability of hosts with tomial lengths between 14.91 mm and 17.08 mm is not known, but information can be gained from the responses of species with tomial lengths between these limits to cowbird eggs.

My estimate of the minimum tomial length required to grasp-eject a cowbird egg corresponds to the responses of cowbird hosts that have been tested and for which tomial lengths are available (Appendix 1). Most hosts that have been tested and have tomial lengths above 17.08 mm eject cowbird eggs at high frequencies (Appendix 1). Of the hosts with bill lengths shorter than 14.91 mm, ejections have been recorded in only four

of them at frequencies less than 20% (Appendix 1). Interestingly, three of the four species (i.e., Lark Bunting, Dickcissel, and Song Sparrow) with tomial lengths shorter than 14.91 mm for which ejection has been recorded nest on the ground, suggesting that perhaps they roll the eggs out of the nest. There is, however, a published observation of a Song Sparrow grasp-ejecting a conspecific egg, which represents, according to Rothstein's ratio (1975), a tomial-length-to-egg-width ratio of 1.26. Because of the results of the present study and Briskie and Sealy's (1987) demonstration, it is unlikely that this was a case of grasp-ejection or that the ejection was performed by an individual with an unusually large bill. Ejections have also been recorded for the Yellow Warbler, but rarely (Sealy 1995), which suggests that grasp-ejection by individuals with long bills, puncture-ejection, partial depredation, or ejection by other methods may account for egg removal (M. Kuehn, pers. comm.).

Because of the resolution of our prediction, we cannot predict whether Least Flycatchers are physically capable of grasp-ejecting parasitic eggs. This species mean (a measure of dispersion was not provided) tomial length falls within the upper and lower limits of the interval that encompasses the minimum tomial length required to grasp-eject a cowbird egg. However, Briskie and Sealy's (1987) finding that a cowbird egg does not fit in a Least Flycatcher's bill suggests that the minimum tomial length required for grasp-ejection is probably longer than 15.2 mm.

The estimated variability in tomial lengths in Northern Cardinals (*Cardinalis cardinalis*) and the *swainsoni* subspecies of Warbling Vireo suggest that at least some individuals within the population have tomial lengths that are long enough to grasp-eject

parasitic eggs. *Swainsoni* has ejected two model cowbird eggs in eight tests, which suggests that at least some individuals in the population have tomia long enough to grasp-eject parasitic eggs, whereas the rest are constrained by small bill sizes to accept. Alternatively, the low frequency of ejection in *swainsoni* has been suggested to be due to its relatively recent history with cowbirds (Sealy 1996, Sealy et al. 2000).

The validity of the approach presented for determining the minimum requirements for grasp-ejection is supported by the fact that there are no hosts with tomia shorter than 17.08 mm known to grasp-eject cowbird eggs. By contrast, Rohwer and Spaw's (1988) estimate based on the grasp-index failed to discriminate grasp-ejecters from puncture-ejecters because species with grasp-indexes less than 200 m^2 have since been discovered to be able to grasp-eject (e.g., *gilvus* subspecies of Warbling Vireo; Sealy 1996, Underwood and Sealy 2006a). In addition to incorporating commissural width into their index for grasp-ejection (Moksnes et al. 1991, S. I. Rothstein *in* Peer and Sealy 2004), one of the problems with Rohwer and Spaw's (1988) estimate is that it assumes that the smallest species physically capable of grasp-ejection have evolved grasp-ejection behavior. This was based on the size distribution of cowbird hosts known to accept versus grasp-eject. Rohwer and Spaw's (1988) estimate is probably biased by differential past parasitism pressures among hosts and the state of knowledge about which species grasp-eject cowbird eggs. The approach introduced in the present study is not affected by biases imposed by past parasitism pressures because it tests the limits of grasp-ejection within species. With this approach, we can predict which hosts can grasp-eject before the behavior has evolved or that researchers have discovered it.

Knowing the tomial length of a host species and the width of the parasite's egg, my estimate can be applied to any host species of any brood parasite to determine whether it is physically capable of grasp-ejection. As such, my estimate corroborates the method of ejection used by different host species of the cuckoo. Five video-recorded ejections of model eggs 15.0 ± 0.7 SE mm wide by European Blackbirds showed that they invariably grasp-eject, representing an egg-width-to-tomial length ratio of 0.51 given a tomial length of 29.6 ± 1.3 SD mm (Moksnes et al. 1991, Soler et al. 2002). Blackcaps and Chaffinches invariably puncture-eject model eggs 15.0 ± 0.7 SE mm wide in five and three video-recroded ejections, respectively (Soler et al. 2002). These feats represented egg-width-to-bill-length ratios of 0.97 and 1.09 for Blackcaps and Chaffinches, respectively. Interestingly, both of these ratios are within the interval of ratios for which we cannot predict whether they have the ability to grasp-eject. Given Briskie and Sealy's (1987) demonstration with the Least Flycatcher, it is improbable that Chaffinches can grasp-eject, but Blackcaps likely can grasp-eject. Additionally, cuckoo eggs are larger than the model eggs Soler et al. (2002) used. Thus, using the width of a real cuckoo egg (i.e., 17.23 mm, $n = 100$, Witherby et al. 1943) to calculate the egg-width-to-tomial-length ratio suggests ratios of 0.58, 1.12, and 1.25 for the Blackbird, Blackcap, and Chaffinch, respectively. Therefore, it is probable that Blackcaps and Chaffinches evolved puncture-ejection in response to foreign eggs because they were unable to grasp-eject them. Honza et al. (2007) also showed that Blackcaps consistently use puncture-ejection when repeatedly parasitized. The only other cuckoo host for which the method of ejection has been documented is the Great Reed Warbler (*Acrocephalus arundinaceus*), which puncture-ejects (Lotem et al. 1992), and its tomia are likely too

short to grasp-eject a cuckoo egg. As discussed in Chapter 1, puncture-ejection, despite being more costly, is adaptive in cuckoo hosts because the cost of acceptance is high.

Rejection is selected in cuckoo hosts at almost any cost because the cost of acceptance is so high (Davies 2000). In contrast to cowbirds, the physical inability of hosts to eject parasitic eggs efficiently does not explain acceptance in hosts for which the cost of raising a parasite is higher than the cost of ejection, such as in the cuckoo. Instead, acceptance in cuckoo hosts may be explained by an evolutionary equilibrium between the low probability of parasitism and the high probability of committing recognition errors, due to highly refined host-egg-mimicry in the cuckoo, or incurring ejection costs (Davies and Brooke 1988, Davies and Brooke 1989, Marchetti 1992, Davies et al. 1996, Soler et al. 2002).

Future directions

Several experiments are required to refine the estimate of the minimum tomial length required by hosts to grasp-eject cowbird eggs. To obtain a more precise estimate of the minimum tomial length required to grasp-eject a parasitic egg, robins and catbirds should be tested with model widths between the largest size they grasp-ejected and the next larger size they could not grasp-eject. However, because the bill lengths of the individuals ejecting the models are not known, our estimate is only as precise as our estimate of the variation in tomial lengths in robin and catbird populations. According to Underwood's (unpublished data) measurements of the tomial lengths of robins and catbirds, approximately 95% of robins have tomial lengths between 25.60 mm and 29.50 mm and approximately 95% of catbirds have tomia between 22.73 mm and 25.94 mm.

Because of variation in tomial length among individuals of the same species, our estimates can only be precise to within approximately 2.5 mm. But what about the approximately 5% of individuals whose tomial lengths that fall outside our estimate of the variation in tomial lengths of the population? It is unlikely that individuals with tomial lengths larger and smaller than those bounded by two standard deviations of the mean affected the results of this study because of the large sample sizes involved, random assignment of models, and number of treatments. To provide more precise estimates of the minimum bill lengths required to grasp-eject a cowbird egg, observations of models varying in width being grasp-ejected by individuals for which the length of the tomia are known are necessary.

The texture and shape of the models compared with cowbird eggs may have rendered their manipulation easier than cowbird eggs in that the texture of the models was not as smooth as the shells of real cowbird eggs. It is also possible that the cylindrical shape of the models, as opposed to an egg shape, rendered model manipulation easier. Experiments testing the effect of model shape and texture on the limit width are required to refine my estimate of the egg-width-to-tomial-length ratio. The effect of model shape should be tested by recording the limits of grasp-ejection of catbirds and robins ejecting spherical or egg-shaped models and comparing to the limits found for grasp-ejecting cylindrical models. The effect of texture could be tested by video-recording robins and catbirds ejecting real eggs with widths that approximate the limit widths for grasp-ejection (e.g., *Coturnix* quail eggs).

Is the relationship between the limit width and tomial length linear as assumed in this study? Elucidation of this relationship requires testing the limit width of more hosts

that have different tomial lengths than robins and catbirds. An ideal subject to test the limits of grasp-ejection is the *gilvus* subspecies of the Warbling Vireo, which as the smallest known grasp-ejecter, has a much smaller tomial length than either the robin or catbird (Underwood and Sealy 2006a).

An important limitation of the estimate derived in the present study is that the role of bill shape and cranial kinesis in grasping eggs was not investigated. Future work should focus on the role of bill shape and mechanics of cranial kinesis in grasping eggs so that our estimates of the egg-width-to-tomial-length ratio can be more precise.

Comparisons between hosts of the maximum egg-width-to-bill-length ratios are required to better understand the anatomical and morphological factors that affect a bird's ability to grasp-eject eggs. For example, if grasp-ejecter hosts with hooked bills are found to be able to grasp-eject egg widths larger relative to their tomial length than grasp-ejecter hosts with straight bills, the importance of a hooked bill could then be modeled to provide better estimates of which hosts are capable of grasp-ejection and which hosts are not. Studies of the jaw anatomy of a sample of cowbird hosts may reveal factors that, in addition to tomial length, correlate with a host's ability to grasp-eject cowbird eggs.

The interaction between brood parasites and their hosts has been described as an "arms race" (Krüger 2007). Anti-parasite adaptations in the host select for better adaptations in the parasite and, these, in turn, select for better anti-parasite adaptations in the host. Under this scenario, a parasite would have to increase the size of its eggs to prevent hosts from grasp-ejecting them. In response to these larger eggs, hosts would evolve longer bills to be able to eject them and, in turn, parasites would evolve even larger eggs to counter grasp-ejection. Yet this does not seem to happen because costs

other than that of parasitism or rejection exert pressure on host bill length and parasite egg size. The primary selective pressure on bill size and shape of hosts is for feeding (Grant and Grant 1993), whereas, the main selective forces on parasite egg size include host egg mimicry (Payne 1974, Krüger and Davies 2002, 2004) and the length of incubation (Kattan 1995). Both of the main selective forces on egg size are selecting for smaller egg size in parasites. However, the larger size of the cowbird egg relative to host eggs may also allow the cowbird egg to hatch before the host eggs by disrupting the incubation of host eggs (McMaster and Sealy 1998). In addition, cowbird eggs have a faster rate of embryonic growth relative to egg volume, suggesting that egg size may not be the only factor affecting the length of the incubation period (McMaster and Sealy 1998). Because selection pressures maintain bill and egg dimensions within a narrow range, hosts with short bills may not only be physically constrained but may be evolutionarily constrained to accept the eggs of parasites and, as a result, are not likely to evolve larger bills to be able to efficiently grasp-eject a parasite's eggs nor are parasites likely to evolve larger eggs.

Even without a change in the overall size of their eggs, parasites can prevent some hosts from grasp-ejecting their eggs by maximizing the width of their eggs by evolving rounder eggs. Cowbird eggs are generally rounder (i.e., a lower egg width-to-length ratio) than host eggs (Picman 1989, Underwood and Sealy 2006b). A round egg has been suggested to have been selected to increase egg strength and, along with thicker eggshells, to prevent hosts from puncture-ejecting them (Rohwer and Spaw 1988, Picman 1989). But a round egg, which has a greater width compared to a more pointed egg shape of a given volume, may prevent certain hosts from grasp-ejecting them. The greater width

provided by the shape of a cowbird egg probably allows cowbirds to exploit hosts with larger tomial lengths than they would be able to if their egg was ovoid in shape. The present study suggests that hosts with tomia shorter than 14.91 mm cannot grasp-eject a cowbird egg. However, if cowbirds did not evolve round eggs, they may only be able to exploit hosts with tomia that are much shorter than 14.91 mm. Studies investigating the influence of the cost of parasitism on bill-size, as well as egg shape and size, are warranted.

Two species that would lend themselves nicely to this study are the Warbling Vireo and Northern Cardinal because they both have tomial lengths near the minimum length required for grasp-ejection and they show variability among individuals in their response to cowbird eggs (Rothstein 1975, Sealy 1996, Sealy et al. 2000). More interestingly, different populations of the Warbling Vireo differ in response to cowbird eggs and have different tomial lengths. The *gilvus* subspecies of Warbling Vireo, which occurs from the Rocky Mountains to northeastern North America has a longer tomium and grasp-ejects cowbird eggs at a high frequency (Underwood and Sealy 2006a; Appendix 1). By contrast, *swainsoni*, which occurs from the Rocky Mountains to the Pacific Ocean, has a shorter tomium and rejects infrequently (Sealy et al. 2000; Appendix 1). The *gilvus* subspecies has likely suffered from cowbird parasitism because it has occurred in sympatry with cowbirds longer than *swainsoni*. Cowbirds were historically limited to the Great Plains, but since 1900, they have extended their range and as a result, they are now widespread across North America. But it is possible that *swainsoni* suffered from parasitism before the cowbird's range extension since 1900 because cowbirds were historically found from the Rocky Mountains to the Sierra Nevada and Cascade Range

(Rothstein 1994). Therefore, it would be interesting to know whether the ejection behavior has evolved in *gilvus* because it has been in contact with cowbirds longer than *swainsoni* or whether *swainsoni* is morphologically constrained to accept cowbird eggs. It would also be interesting to know whether past parasitism pressure selected for longer bills in *gilvus*, and whether the cost of parasitism will select for longer bills in *swainsoni*. This may be unlikely, however, because *gilvus* has been observed to puncture- as well as grasp-eject cowbird eggs, which suggests that *swainsoni* can puncture-eject as well (Sealy 1996, Underwood and Sealy 2006a).

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Appendix 1. Cowbird egg ejection frequency by host species for which the tomial length has been measured. Species are grouped according to their ability to grasp-eject cowbird eggs as suggested by limit ratio estimated in Chapter 2. Data are from studies where nests were experimentally parasitized with host eggs present and 5 days considered as the acceptance criterion, unless otherwise noted. (Adapted from Underwood 2003).

Species	Tomial length (mm \pm SD) ^a	<i>n</i>	% ejected (<i>n</i>)	Reference
<i>Capable of grasp-ejection</i>				
Crissal Thrasher (<i>Toxostoma crissale</i>)	39.1 \pm 3.4	5	100 (9)	Finch 1982
Brown Thrasher	31.7 \pm 1.4	5	96.3 (26)	Rothstein 1975
			57.8 ^b (64)	Haas and Haas 1998
Florida Scrub-Jay (<i>Aphelocoma coerulescens</i>)	31.6 \pm 0.6	5	92.3 ^c (26)	Fleischer 2000
			93.3 (15)	Fleischer and Woolfenden 2004
Blue Jay (<i>Cyanocitta cristata</i>)	30.7 \pm 1.0	5	100 (25)	Rothstein 1975
Eastern Meadowlark (<i>Sturnella magna</i>)	28.5 \pm 1.9	5	35.7 ^d (14)	Peer et al. 2000
American Robin	27.55 \pm 1.0 ^e	97	82.6 (46)	Rothstein 1975
			96 (25)	Briskie et al. 1992
			66.7 (18)	Briskie et al. 1992
Cassin's Kingbird (<i>Tyrannus vociferans</i>)	26.1 \pm 0.4	5	100 (unk)	Rothstein in Peer and Sealy 2000
Eastern Kingbird	25.8 \pm 1.4	5	100 (33)	Rothstein 1975
			98.7 (88)	Sealy and Bazin 1995
Gray Catbird	24.34 \pm 0.82 ^e	90	94.3 (53)	Rothstein 1975
			96 (94)	Lorenzana 1999
Sage Thrasher	23.9 \pm 0.6	5	90.9 (11)	Rich and Rothstein 1985
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	22.0 \pm 1.2	5	100 (21)	Rothstein 2001
Bullock's Oriole	21.21 \pm 0.79 ^e	51	100 ^f (20)	Rothstein 1977

Baltimore Oriole	20.58 ± 1.20 ^e	106	100 (16)	Sealy and Neudorf 1995
Eastern Phoebe	20.2 ± 0.5	5	0 (50)	Rothstein 1975
Cedar Waxwing	19.15 ± 0.80 ^e	106	42.4 ^f (33)	Rothstein 1975
			27.6 ^f (58)	Rothstein 1976
Red-winged Blackbird	19.1 ± 0.9	5	3.3 ^f (92)	Rothstein 1975
Yellow-breasted Chat (<i>Icteria virens</i>)	19.1 ± 0.5	5	9.1 (11)	Burhans and Freeman 1997
Warbling Vireo <i>gilvus</i> subspecies	17.21 ± 0.61 ^e	65	96.7 (30)	Sealy 1996, Sealy et al. 2000
<i>Part of the population is capable of grasp-ejection</i>				
Northern Cardinal (<i>Cardinalis cardinalis</i>)	17.0 ± 1.2	5	14.3 (7)	Rothstein 1975
Warbling Vireo <i>swainsoni</i> subspecies	16.19 ± 0.55 ^e	69	25 (8)	Sealy et al. 2000
<i>Unknown</i>				
Least Flycatcher	15.2	26	0 ^g (27)	Briskie and Sealy 1987
<i>Not capable of grasp-ejection</i>				
Lark Bunting (<i>Calamospiza melanocorys</i>)	14.2 ± 0.9	5	20 (5)	Sealy 1999
Dickcissel	13.8 ± 0.9	5	11.1 ^d (9)	Peer et al. 2000
Song Sparrow	13.5 ± 0.5	5	11.1 (9)	Rothstein 1975
Yellow Warbler	13.4 ± 1.1	5	0 (16)	Rothstein 1975
			0 (3)	Burgham and Picman 1989
			0 (29)	Briskie et al. 1992
			5.1 ^h (158)	Sealy 1995
Lark Sparrow	12.8 ± 0.6	5	0 ^d (2)	Peer et al. 2000
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	12.5 ± 0.9	5	0 (2)	Sealy, unpublished data
Chestnut-collared Longspur (<i>Calcarius ornatus</i>)	12.1 ± 0.5	5	0 (23)	Davis et al. 2002
Vesper Sparrow	12.0 ± 0.5		0 (3)	Rothstein 1975
			0 ^d (4)	Peer et al. 2000
Chipping Sparrow	11.3 ± 0.5	5	0 (19)	Rothstein 1975

Grasshopper Sparrow	11.1 ± 0.1	5	0 ^d (10)	Peer et al. 2000
Clay-colored Sparrow	10.0 ± 0.0	5	0 (67)	Hill and Sealy 1994

^a All measurements for tomial length are from Rohwer and Spaw 1988, unless otherwise noted.

^b For some nests, only a 3-day acceptance criterion was used.

^c A 12-day acceptance criterion was used.

^d A 5-day acceptance criterion was not used. Nests were checked until an egg was rejected or the host eggs hatched.

^e T. J. Underwood, unpublished data.

^f Percent ejection includes artificial eggs damaged by pecking that were not ejected. (If real eggs were used, these likely would have been ejected by puncture-ejection.) Artificial eggs were solid plaster or wood and could not be puncture-ejected.

^g A 3-day acceptance criterion was used.

^h Data adjusted because some tests were conducted before host egg laying occurred.