

**PROXIMATE AND ULTIMATE INFLUENCES ON EGG RECOGNITION AND
REJECTION BEHAVIOUR IN RESPONSE TO AVIAN BROOD PARASITISM**

BY

TODD J. UNDERWOOD

A Thesis presented to
the Faculty of Graduate Studies
in partial fulfillment of the requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department of Zoology
University of Manitoba
Winnipeg, Manitoba

© Todd J. Underwood, December 2003

**THE UNIVERSITY OF MANITOBA
FACULTY OF GRADUATE STUDIES

COPYRIGHT PERMISSION**

**PROXIMATE AND ULTIMATE INFLUENCES ON EGG RECOGNITION AND
REJECTION BEHAVIOUR IN RESPONSE TO AVIAN BROOD PARASITISM**

BY

TODD J. UNDERWOOD

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree**

Of

DOCTOR OF PHILOSOPHY

Todd J. Underwood © 2003

Permission has been granted to the Library of the University of Manitoba to lend or sell copies of this thesis/practicum, to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film, and to University Microfilms Inc. to publish an abstract of this thesis/practicum.

This reproduction or copy of this thesis has been made available by authority of the copyright owner solely for the purpose of private study and research, and may only be reproduced and copied as permitted by copyright laws or with express written authorization from the copyright owner.

I hereby declare that I am the sole author of this thesis.

I authorize the University of Manitoba to lend this thesis to other institutions or individuals for the purpose of scholarly research.

Todd J. Underwood

I further authorize the University of Manitoba to reproduce this thesis by photocopying or by other means, in whole or in part, at the request of other institutions or individuals for the purpose of scholarly research.

Todd J. Underwood

ABSTRACT

I examined proximate mechanisms and ultimate causes of egg rejection behaviour in several potential hosts of avian brood parasites. First, I studied the influence of egg characteristics on egg rejection in Brown-headed Cowbird (*Molothrus ater*) hosts. I tested Rothstein's (1982b) prediction that hosts with eggs more similar to a parasite's egg, Warbling Vireos (*Vireo gilvus*), would be less tolerant of foreign eggs than hosts with less similar eggs, Baltimore Orioles (*Icterus galbula*). The responses of vireos to foreign eggs supported this prediction, but oriole responses were inconclusive. I also found that egg shape significantly influenced rejection in American Robins (*Turdus migratorius*) and Gray Catbirds (*Dumetella carolinensis*), but the rounder cowbird egg did not appear to elicit rejection. Second, I addressed why hosts accept parasitism. I examined the influence of ultraviolet (UV) light on egg recognition in 11 cowbird hosts and tested the UV matching hypothesis. Eggs of rejecters and accepters differed significantly from cowbird eggs in UV reflectance, providing another parameter for egg recognition. However, cowbird reflectance did not vary significantly by host and was not significantly correlated with that of host clutches. Thus, UV matching does not explain acceptance. Using plaster eggs and video documentation, I also identified the method of egg ejection in the two smallest ejecters of cowbird eggs as tests of the evolutionary equilibrium and lag hypotheses. Warbling Vireos grasp-ejected cowbird eggs with negligible cost, supporting the evolutionary lag hypothesis. Most Baltimore Orioles did not grasp-eject and the depth of their nests did not prevent grasp-ejection. Based on observations of ejection, I suggest that ejecters use both grasp- and puncture-ejection. Therefore, puncture-ejection may place stronger selection on the strength of cowbird eggs

than previously believed. Finally, I examined whether Black-billed Magpies (*Pica hudsonia*) have retained egg rejection phylogenetically through their congener, Eurasian Magpies (*P. pica*), which reject Old World cuckoo eggs. Magpies rejected all non-mimetic eggs and half of mimetic eggs and little support for conspecific parasitism influencing egg rejection was found. Thus, magpies appear to have retained egg rejection in the absence of parasitism.

ACKNOWLEDGMENTS

I am indebted to three people, Robyn Underwood, Celia Bodnar (McLaren), and Spencer G. Sealy, without whose assistance this project would not have been possible. My wife, Robyn, was always by my side providing support and assistance. She took time off from her own research to help me in the field and was an excellent assistant not only for her nest finding and egg painting abilities, but also for taking care of those other tasks in life (i.e. laundry!) that helped reduce my stress. My friend and colleague, Celia, has always been there to discuss research and to offer advice and assistance on all of my various projects. She also took time out of her own field season to help me find and climb to nests. My sample size would also have been one nest less if she wasn't crazy enough to stand unsupported on the top rung of a 12-meter tower to reach a Warbling Vireo nest! My advisor, Spencer, has always been there to offer encouragement and advice, and to entertain my interest in yet another side project. He also didn't allow my cautious respect of unstable structures to stop us from reaching the odd nest by climbing to nests I wouldn't.

Throughout the course of my research, I received technical and statistical assistance from several people and I thank them all. The guidance provided by the members of my committee, R. Baydack, S. Forbes and L. Graham, was much appreciated. J. Hare and R. Currie offered insightful statistical advice. I benefited from various discussions about my research with C. Bodnar, W. Brown, D. Campobello, K. Ellison, J. Hare, S. G. Sealy, and R. Underwood. K. Ellison, H. McGaha, J. Hare, and T. McLain helped to transfer images from videotapes. M. Sowa of the Institute for Biodiagnostics introduced me to spectrophotometry. G. Manche of Ocean Optics spent

hours on the phone to help me work out the bugs with the spectrophotometer. R. Stewart also provided some initial guidance with the spectrophotometer. D. Vanderwel and R. Vakili provided helpful advice on reflectance calculations. C. and M. Bodnar were indispensable in analyzing reflectance data.

I was fortunate to have the expert assistance of several people in the field. Some of these were paid for their work but many volunteered their assistance after their own work was done for the day. These assistants were: A. Andruschak, C. Bodnar, K. Jacobs, D. Jeske, M. Kasumovich, S. Lelievre, J. Lorenzana, E. Prigoda, S. G. Sealy, K. Shonk, R. Stewart, R. Underwood, B. van Poorten, and I. Whetter. I am grateful to them all for helping me get through the long days in the field when we had many towers to climb.

Finally, I thank those who granted access to property, facilitated logistical aspects of my work, and provided funding. M. Harris for always having the answers to departmental questions. The staff of the Delta Marsh Field Station provided excellent food, accommodations and vehicles that sometimes ran. I thank S. Larivière for providing lab space at the Delta Marsh Wetlands and Waterfowl Research Station. The Portage Country Club, Delta Marsh Wetlands and Waterfowl Research Station and the many private landowners at Delta Marsh and in Winnipeg who kindly allowed access to their land. A University of Manitoba Graduate Fellowship, the Roger Evans Memorial Scholarship, and the George Lubinsky Memorial Scholarship provided personal funding for this project. Research funding was provided by awards from the Natural Sciences and Engineering Research Council of Canada and the University of Manitoba Research Grants Program to S. G. Sealy. Research for this thesis was conducted under permits

from the Canadian Wildlife Service and was approved of by the animal care committee of the University of Manitoba.

TABLE OF CONTENTS

<i>ABSTRACT</i>	<i>i</i>
<i>ACKNOWLEDGMENTS</i>	<i>iii</i>
<i>TABLE OF CONTENTS</i>	<i>vi</i>
<i>LIST OF FIGURES</i>	<i>ix</i>
<i>LIST OF TABLES</i>	<i>xi</i>
GENERAL INTRODUCTION	1
CHAPTER 1. PARAMETERS OF COWBIRD EGG RECOGNITION IN WARBLING VIREOS AND BALTIMORE ORIOLES	6
<i>INTRODUCTION</i>	6
<i>METHODS</i>	11
<i>General</i>	11
<i>Warbling Vireos</i>	13
<i>Baltimore Orioles</i>	18
<i>Analysis</i>	23
<i>RESULTS – WARBLING VIREOS</i>	26
<i>Parameters of cowbird egg recognition</i>	27
<i>Cost of ejection and ejection errors</i>	31
<i>Conspecific egg recognition</i>	31
<i>Mechanism of egg recognition</i>	31
<i>Videotaped egg-ejection behaviour</i>	33
<i>RESULTS – BALTIMORE ORIOLES</i>	36
<i>Parameters of cowbird egg recognition</i>	37
<i>DISCUSSION</i>	42
<i>Warbling Vireos</i>	42
<i>Baltimore Orioles</i>	47
<i>Summary</i>	50
CHAPTER 2. THE ROLE OF EGG SHAPE IN EGG RECOGNITION IN AMERICAN ROBINS AND GRAY CATBIRDS	52
<i>INTRODUCTION</i>	52
<i>METHODS</i>	57
<i>Analysis</i>	65
<i>RESULTS</i>	66
<i>DISCUSSION</i>	76
<i>Summary</i>	80

CHAPTER 3. THE POTENTIAL INFLUENCE OF ULTRAVIOLET LIGHT REFLECTANCE IN EGG RECOGNITION BY HOSTS OF THE BROWN-HEADED COWBIRD	81
<i>INTRODUCTION</i>	81
<i>METHODS</i>	86
<i>Analysis</i>	89
<i>RESULTS</i>	93
<i>Comparison of host eggs to cowbird eggs</i>	93
<i>Cowbird eggs laid among different host species</i>	96
<i>DISCUSSION</i>	101
<i>Summary</i>	104
 CHAPTER 4. GRASP-EJECTION OF COWBIRD EGGS BY WARBLING VIREOS AND BALTIMORE ORIOLES	 105
<i>INTRODUCTION</i>	105
<i>METHODS</i>	112
<i>General</i>	112
<i>Grasp-ejection tests</i>	113
<i>Grasp-index measurements</i>	115
<i>Baltimore Oriole nest dimensions</i>	116
<i>Statistical analysis</i>	117
<i>RESULTS</i>	117
<i>Grasp-ejection tests</i>	117
<i>Grasp-index measurements</i>	121
<i>Baltimore Oriole nest dimensions</i>	121
<i>DISCUSSION</i>	125
<i>Summary</i>	132
 CHAPTER 5. EGG RECOGNITION IN THE ABSENCE OF A CURRENT SELECTION PRESSURE OF BROOD PARASITISM.....	 134
<i>INTRODUCTION</i>	134
<i>METHODS</i>	137
<i>General</i>	137
<i>Conspecific egg recognition – Black-billed Magpies</i>	140
<i>Analysis</i>	142
<i>RESULTS</i>	142
<i>General egg recognition – Black-billed Magpies</i>	142
<i>General egg recognition – American Crows</i>	146
<i>Conspecific egg recognition – Black-billed Magpies</i>	147
<i>DISCUSSION</i>	149
<i>Summary</i>	154

LITERATURE CITED 155
APPENDICES 185

LIST OF FIGURES

Figure 1.1. TV antenna tower guyed with ropes used to access Warbling Vireo and Baltimore Oriole nests. Use of this tower allowed access to nests up to 12 m high.	12
Figure 1.2. Egg treatments used in experiments concerning Warbling Vireo parameters of egg recognition. Top row contains, from left to right, the three large egg treatments (cb-spotted, white, and vireo-spotted), the three equal egg treatments (cb-spotted, white, and vireo-spotted), and the two small egg treatments (cb-spotted and white). For comparison, bottom row shows a real Brown-headed Cowbird egg (left) and a real Warbling Vireo egg (right).	16
Figure 1.3. Egg treatments used in experiments concerning Baltimore Oriole parameters of egg recognition. Top row contains two real oriole eggs (left and middle) and a real cowbird egg (right). Bottom row contains, from left to right, white-equal-brown-spotted, gray-equal-black-spotted, gray-equal-brown-scrawled, gray-equal-black-scrawled, gray-small-black-scrawled, gray-small-black-spotted, and white-small-brown-spotted egg treatments. Several egg treatments are missing from this photograph.	21
Figure 1.4. Survival curves for experimental eggs added to Warbling Vireo nests in relation to egg parameters (A - spot pattern, B - egg size, and C - nest stage).	30
Figure 1.5. Warbling Vireo at nest 1998-31 ejecting a real Brown-headed Cowbird egg.	35
Figure 1.6. Survival curves for experimental eggs added to Baltimore Oriole nests in relation to egg parameters (A - ground colour, B - maculation colour, and C - nest stage).	40
Figure 1.7. Survival curves for experimental eggs added to Baltimore Oriole nests in relation to egg parameters (A - maculation and B - size).	41
Figure 2.1. Experimental objects added to American Robin (A) and Gray Catbird (B) nests to examine the influence of shape on egg recognition. From left to right (A, bottom row and B, top row), shapes are control, pointed, rounded, sphere, cylinder, rectangle, and cube. In A, top row, from left to right, are a real robin egg, a control egg after a 5-day acceptance, and a real cowbird egg. In B, bottom row, from left to right, are a real catbird egg and a real cowbird egg.	63
Figure 2.2. Response of American Robins and Gray Catbirds to experimental objects added to their nests as measured by proportion of eggs ejected. For robins, n = 14 for most objects, except for control eggs (n = 13) and rounded eggs (n = 15). For catbirds, n = 14 for most objects, except for spheres (n = 15), rectangles (n = 15) and rounded eggs (n = 13).	69
Figure 2.3. Survival curves by nest stage for objects added to American Robin (A) and Gray Catbird (B) nests.	72
Figure 2.4. Survival curves for experimental objects added to American Robin nests.	73
Figure 2.5. Survival curves for experimental objects added to Gray Catbird nests.	74
Figure 2.6. Survival curves for egg-shaped and odd-shaped objects added to American Robin (A) and Gray Catbird (B) nests.	75
Figure 3.1. Equipment setup for egg reflectance measurements. Fiber optic probe held at 45° angle to an egg by probe holder.	90

Figure 3.2. Mean UV reflectance (\pm SE) of the cap and side of Brown-headed Cowbird (BHCO) eggs and the eggs of 11 host species. Host species included: Least Flycatcher (LEFL), Eastern Kingbird (EAKI), Warbling Vireo (WAVI), Red-eyed Vireo (REVI), American Robin (AMRO), Gray Catbird (GRCA), Yellow Warbler (YWAR), Song Sparrow (SOSP), Red-winged Blackbird (RWBL), Baltimore Oriole (BAOR), and Orchard Oriole (OROR).	95
Figure 3.3. Mean UV reflectance (\pm SE) of Brown-headed Cowbird (BHCO) eggs laid in the nests of five different host species at Delta Marsh. Host species included: Red-eyed Vireo (REVI), Yellow Warbler (YWAR), Song Sparrow (SOSP), Red-winged Blackbird (RWBL), and Orchard Oriole (OROR).	99
Figure 3.4. Relationship between UV reflectance of Brown-headed Cowbird (BHCO) eggs and the UV reflectance of the host clutch in which they were laid: A, cap; B, side.	100
Figure 4.1. Variation in Baltimore Oriole nests illustrating their considerable structural variability in shape and size, especially in relation to nest depth and the diameter of the nest opening (figure from Nickell 1958).	111
Figure 4.2. Male Warbling Vireo (sex identified by song just prior to ejection) at nest 1999-75 grasp-ejecting a plaster model cowbird egg.	119
Figure 4.3. Plaster model cowbird eggs from experiments with Warbling Vireos (A) and Baltimore Orioles (B). For each photograph, the top row contains ejected eggs that were recovered near the nests and the bottom row contains eggs that were accepted and subsequently removed from nests.	120
Figure 4.4. Nest dimensions (means \pm SE) for Baltimore Orioles that ejected (n = 9) or accepted (n = 21) plaster cowbird eggs.	124
Figure 5.1. Experimental egg treatments added to Black-billed Magpie and American Crow nests. Eggs are (from left to right) real magpie egg, artificial magpie egg (mimetic), artificial egg (non-mimetic), artificial crow egg (mimetic), and real crow egg.	139

LIST OF TABLES

Table 1.1. Mean measurements (mm \pm SE) of experimental eggs used in Warbling Vireo experiments in comparison to those of Warbling Vireo and Brown-headed Cowbird eggs from Delta Marsh, Manitoba.	14
Table 1.2. Mean measurements (mm \pm SE) of experimental eggs used in Baltimore Oriole experiments in comparison to those of Baltimore Oriole and Brown-headed Cowbird eggs from Delta Marsh, Manitoba.	19
Table 1.3. Responses of Warbling Vireos to experimental eggs that varied in two egg parameters.	28
Table 1.4. The influence of egg parameters and nest stage on the response of Warbling Vireos to foreign eggs over time.	29
Table 1.5. Influence of egg parameters on costs of experimental egg ejection and ejection errors by Warbling Vireos.	32
Table 1.6. Experimental cowbird-spotted eggs ejected from Warbling Vireo nests as a function of host clutch size.	34
Table 1.7. Response of Baltimore Orioles to experimental eggs that varied in four parameters.	38
Table 1.8. The influence of egg parameters and nest stage on the response of Baltimore Orioles to foreign eggs over time.	39
Table 2.1. Objects experimentally added to nests to determine the influence of shape on egg recognition in previous studies.	55
Table 2.2. Mean (\pm SE) measurements (mm), volume (cm ³) and mass (g) of objects used in shape experiments on American Robins.	59
Table 2.3. Mean (\pm SE) measurements (mm), volume (cm ³) and mass (g) of objects used in shape experiments on Gray Catbirds.	61
Table 2.4. Comparison of egg shape indices (shape = length/width) between Brown-headed Cowbirds and two ejecters, American Robins and Gray Catbirds.	67
Table 2.5. Frequency of rejection of egg-shaped and odd-shaped objects by American Robins and Gray Catbirds.	71
Table 3.1. Hosts of the Brown-headed Cowbird experimentally determined to be capable of detecting ultraviolet light.	85
Table 3.2. Rejecter and accepter species of Brown-headed Cowbird eggs for which egg reflectance measurements were made at Delta Marsh.	88
Table 3.3. Comparison of the UV reflectance of the cap and side of eggs from three closely related pairs of accepter and rejecter species.	92
Table 3.4. Analysis of variance examining the influence of species and incubation stage on UV reflectance of the cap of Brown-headed Cowbird eggs and the eggs of 11 cowbird hosts.	94
Table 3.5. Analysis of variance examining the influence of species and incubation stage on UV reflectance of the side of Brown-headed Cowbird eggs and the eggs of 11 cowbird hosts.	97
Table 3.6. Analysis of variance examining the influence of host species and incubation stage on the UV reflectance of Brown-headed Cowbird eggs.	98

Table 4.1. Cost of ejection in hosts of the Brown-headed Cowbird. Cost is the number of host eggs damaged or missing per cowbird egg ejected.	109
Table 4.2. Grasp-index measurements (mean \pm SE) for Warbling Vireos, Baltimore Orioles and a few other grasp-ejecters and puncture-ejecters.....	122
Table 4.3. Baltimore Oriole nest dimensions (mean \pm SE) where individuals damaged their own eggs during an ejection attempt compared to those where no damage occurred.....	126
Table 5.1. Percent of experimental eggs ejected by Black-billed Magpies and American Crows.	144
Table 5.2. Time to ejection (days) of experimental eggs by Black-billed Magpies by nest stage. P is the significance value for Mann-Whitney U test, two-tailed.	145

GENERAL INTRODUCTION

Most hosts of obligate brood parasites produce fewer of their own offspring while raising parasitic young. The potential cost to hosts varies depending on the species of brood parasite. Hosts of Common Cuckoos (*Cuculus canorus*) and some other Old World cuckoos face a complete loss of their current clutch when parasitized because cuckoo nestlings evict all of the host's eggs and/or nestlings (Wyllie 1981). Similarly, nestling Striped Cuckoos (*Tapera naevia*) and honeyguides (*Indicator spp.*) eliminate host chicks in the nest but do so by attacking them with sharply hooked bills (Friedmann 1955, Morton and Farabaugh 1979). By contrast, the young of other brood parasites, such as cowbirds (*Molothrus spp.*) and Great Spotted Cuckoos (*Clamator glandarius*), are reared in the nest with host young. For these hosts, the cost of parasitism is incurred through host egg removal (Sealy 1992, Tewksbury et al. 2002) or host egg destruction by parasites (Soler et al. 1997, Peer and Sealy 1999, Massoni and Reboresda 2002), incubation interference (Sealy et al. 2002), nestling competition (Soler et al. 1995a, 1996; Dearborn 1998, Dearborn et al. 1998, Lichtenstein and Sealy 1998), and an increased risk of nest predation (Dearborn 1999). Ultimately, these costs reduce fledgling production in parasitized nests (Payne 1997, Ortega 1998, Lorenzana and Sealy 1999), and possibly decrease fledgling survival (Payne and Payne 1998) and future adult reproductive success (Dearborn et al. 1998). These costs of parasitism place strong selection pressures on hosts to evolve defences against brood parasitism.

Host defences occur either before or after the nest has been parasitized.

Defending the nest to prevent parasitism is the most efficient defence against parasitism because it may prevent all costs of parasitism, but its effectiveness is equivocal (Sealy et

al. 1998). After a nest has been parasitized, egg rejection is a very effective and common defence against parasitism (Rothstein 1975a, Davies and Brooke 1989a), although nestling rejection has recently been identified as an alternative defence in one host of Australian cuckoos (*Chrysococcyx* spp.; Langmore et al. 2003). Egg-rejection behaviour involves ejecting a parasitic egg from the nest (Rothstein 1975a, Davies and Brooke 1989a), deserting the parasitized nest (Graham 1988, Hosoi and Rothstein 2000), or burying the parasitic egg under new nest material (Sealy 1995). Of the methods of egg rejection, only egg ejection has been conclusively demonstrated to require egg recognition (Rothstein 1975a, 1982a, 1982b). Recent evidence also suggests that egg ejection may be maintained in the absence of selection from brood parasitism (Rothstein 2001). Nest desertion may be stimulated by a reduction in clutch size when host egg removal occurs (Hill and Sealy 1994) or by detecting a parasite at the nest (Strausberger and Burhans 2001; but see Burhans 2000). However, the cue that elicits egg burial is unknown (Sealy and Lorenzana 1998).

Host defences select for additional adaptations by parasites to counter these defences, which in turn favour the evolution of new host defences (Davies and Brooke 1998). These reciprocal patterns of adaptation and counteradaptation between brood parasites and their hosts has provided one of the best examples of coevolution (Rothstein 1990). The most well studied relationship is that of the Common Cuckoo and its hosts (Davies 2000). Many cuckoo hosts reject non-mimetic eggs (Davies and Brooke 1988, Moksnes 1992), which selected for host egg mimicry by the cuckoo (Brooke and Davies 1988, Moksnes and Røskoft 1995). To counter host egg mimicry, hosts have produced clutches of eggs with low intraclutch variability and high interclutch variability, which

makes it easier for the host to reject a cuckoo egg and more difficult for a cuckoo to match a host egg (Stokke et al. 1999, 2002). This cycle of reciprocal adaptations could continue on with a coevolutionary arms race (Dawkins and Krebs 1979) or one side might “win” the race with a host forced to accept parasitism or the cuckoo forced to switch to a new host and begin the cycle again (Davies 2000).

Regardless of the well-developed rejection behaviour of some species and the coevolutionary relationships between some hosts and parasites, many hosts do not appear to behave adaptively and accept the reproductive costs of brood parasitism (Rothstein 1982a). This paradigm remains one of the most challenging questions in brood parasitism research. Two major opposing theories have been proposed to explain egg acceptance: the evolutionary lag hypothesis and the evolutionary equilibrium hypothesis (Rothstein and Robinson 1998). The evolutionary lag hypothesis proposes egg-rejection behaviour is an adaptive response to parasitism that most host species have yet to evolve or have not evolved because they lack the appropriate genetic variability (Rothstein 1975a, 1990; Davies and Brooke 1989b). In contrast, the equilibrium hypothesis explains egg acceptance as an adaptive response because the costs incurred while rejecting a parasite’s egg outweigh the cost of accepting the egg, especially for small hosts (Rohwer and Spaw 1988, Lotem and Nakamura 1998). Recently, a third hypothesis was proposed that suggested acceptance of non-mimetic eggs by hosts was due to host egg matching in the ultraviolet portion of the spectrum, which birds are capable of detecting but humans are not (Cherry and Bennett 2001). All three hypotheses use both proximate mechanisms and ultimate causes to explain the acceptance of parasitism.

Many questions remain unanswered concerning egg-recognition and rejection behaviour in response to brood parasitism. The parameters used by hosts to recognize Brown-headed Cowbird (*M. ater*) eggs have only been thoroughly investigated in two species, American Robins (*Turdus migratorius*) and Gray Catbirds (*Dumetella carolinensis*). The ability of hosts to retain egg recognition in the absence of current selection is only beginning to be understood, and the explanation for egg acceptance by most hosts remains unclear. In this thesis, I investigated both proximate and ultimate questions as they relate to egg-recognition and rejection behaviour in hosts to better understand how the egg characteristics of hosts and parasites influence egg recognition and to examine why hosts accept the costs of parasitism. In Chapters 1 and 2, I examined the influence of proximate factors relating to the characteristics of Brown-headed Cowbird and host eggs that elicit egg rejection in four host species. The influence of these characteristics on egg rejection provides an understanding of the potential conflicting selection pressures that may be placed on the appearance of a parasite's egg at the beginning of a coevolutionary arms race. In Chapters 3 and 4, I investigated the influence of proximate mechanisms and ultimate causes of egg acceptance in Brown-headed Cowbird hosts by testing the ultraviolet egg matching hypothesis in 11 host species and testing the evolutionary equilibrium and lag hypotheses by determining the method of egg ejection in two small rejecters of Brown-headed Cowbird eggs. Finally, in Chapter 5, I investigated the retention of egg recognition and ejection in the absence of current brood parasitism on two North American corvids whose relatives are hosts of Old World Cuckoos. Throughout this thesis, egg terminology follows Underwood and Sealy

(2002). Ground colour represents the base colour of the eggshell and maculation is the superficial pigmentation on top of the ground colour, such as spots or scrawls.

CHAPTER 1. PARAMETERS OF COWBIRD EGG RECOGNITION IN WARBLING VIREOS AND BALTIMORE ORIOLES

INTRODUCTION

Egg recognition in birds has evolved in response to selection pressures associated with nesting in dense colonies, nest usurpation and brood parasitism (Underwood and Sealy 2002). However, egg recognition appears to be most refined and studied as an adaptation to counter obligate brood parasitism. Only a small number of species have been identified as being able to recognize conspecific eggs (Underwood and Sealy 2002, Lyon 2003) and some of these eject only a small proportion, usually < 10 %, of conspecific eggs (e.g. Peer and Sealy 2000a, Welbergen et al. 2001). By contrast, many species recognize and eject eggs laid by obligate brood parasites, especially non-mimetic eggs, i.e. those that do not match host eggs closely (Rothstein 1975a, Moksnes et al. 1991, Davies and Brooke 1998, Soler et al. 1999; Appendix 1, 2, 3).

Hosts of most obligate brood parasites (hereafter brood parasite or parasitism) usually incur large reproductive costs when parasitized (Payne 1997, Ortega 1998, Lorenzana and Sealy 1999, General Introduction). Selection thus favours several defences against parasitism in addition to egg ejection. These include nest defence (Sealy et al. 1998), egg burial (Sealy 1995) and nest desertion (Hosoi and Rothstein 2000). Nest defence can remove all costs of parasitism by preventing parasitism, but its effectiveness is equivocal (Sealy et al. 1998). Of the remaining defences that occur after parasitism, only egg ejection requires a host to recognize a brood parasite's egg. Nest desertion may only be a response to clutch reduction when a parasite removes a host egg (Hill and Sealy

1994) or it may be stimulated by the detection of a parasite at the nest (Strausberger and Burhans 2001; but see Burhans 2000), whereas the cue eliciting egg burial remains unknown (Sealy and Lorenzana 1998).

Species that eject a parasite's egg may recognize foreign eggs in one of two ways: recognition of their own eggs, i.e. true egg recognition, or recognition of the discordant egg (Rothstein 1982a). Results of experiments by Rensch (1925) were interpreted as evidence that European passerines recognized foreign eggs by discordancy. However, Rothstein (1970) re-examined Rensch's data and showed that his experiments were poorly controlled and did not support discordancy as the mechanism of egg recognition. Evidence in support of true egg recognition comes from experiments on numerous Brown-headed Cowbird (*Molothrus ater*) hosts (Rothstein 1975b, 1977, 1982a; Sealy and Bazin 1995, Peer and Sealy 2001) and a few hosts of Old World cuckoos (Victoria 1972, Moksnes 1992, Lotem et al. 1995, Lahti and Lahti 2002). These experiments revealed that foreign eggs were ejected regardless of whether there were equal numbers of host and foreign eggs or whether host eggs were in the minority.

A host's ability to recognize its own eggs is believed to develop through a learning process in young birds (Victoria 1972, Rothstein 1974). Experiments on two cowbird ejectors, Gray Catbirds (*Dumetella carolinensis*) and Bullock's Orioles (*Icterus bullockii*), showed that individuals with no or minimal exposure to their own eggs before finding a cowbird egg in their nests were more likely to accept the cowbird egg than individuals exposed to their own eggs first (Rothstein 1974, 1978). Based on these results, Rothstein (1974, 1978) suggested that first-time breeders learn the appearance of their eggs during a sensitive period during which they imprint on the first egg or eggs in a

clutch. Additional evidence for egg learning comes from experiments on a host of the Common Cuckoo (*Cuculus canorus*). Juvenile female Great Reed Warblers (*Acrocephalus arundinaceus*) accepted more cuckoo eggs than adult females (Lotem et al. 1992, 1995; but see Amundsen et al. 2002). Young females also accepted more non-mimetic eggs when exposure to their own eggs was minimized, but there was no evidence of an increase in egg recognition after experiencing the first egg of a clutch and the frequency of egg rejection by young females did not increase between first and second nestings (Lotem et al. 1995). Lotem et al. (1992, 1995) suggested that the length of the learning period is related to the variability of host eggs and the risk of committing recognition errors. For cuckoo hosts, egg variability and the risk of recognition errors may be high because the probability of parasitism is low. By contrast, for many cowbird hosts, parasitic eggs do not match host eggs and the risk of recognition errors is low because the probability of parasitism is high. Therefore, a prolonged learning period may be required for cuckoo hosts, whereas imprinting on a single egg may be sufficient for cowbird hosts (Lotem et al. 1992, 1995).

Compared to the mechanism of egg recognition, the individual egg characteristics used by ejecter species to distinguish foreign eggs from their own has received little attention, especially for cowbird hosts. The egg characteristics of Brown-headed Cowbird hosts vary widely in ground colour (blue to white), maculation (immaculate to heavily spotted or scrawled), and size (smaller than to larger than a cowbird egg). Thus, it is expected that the characteristics used by ejecters to identify foreign eggs will vary. Rothstein (1982b) placed artificial eggs of different characteristics, size (for robins only), spot pattern and ground colour, in nests of American Robins (*Turdus migratorius*) and

Gray Catbirds to determine which parameters elicited egg ejection. Robins ejected only those eggs that differed in at least two of the three characteristics tested, whereas catbirds ejected foreign eggs based solely on their white ground colour. Based on these results, Rothstein (1982b) predicted that ejecters with eggs more similar to cowbird eggs will tolerate foreign eggs less to maximize ejection of cowbird eggs and minimize mistakenly ejecting their own eggs. Thus, ejecters with eggs similar to cowbird eggs should eject foreign eggs based on fewer differences between the two egg types. Since Rothstein's initial work, the parameters of cowbird egg recognition by ejecter species have received little attention.

In this study, I determined which egg parameters Warbling Vireos (*Vireo gilvus*) and Baltimore Orioles use to identify and eject cowbird eggs. Warbling Vireos and Baltimore Orioles both eject nearly 100 % of experimental cowbird eggs (Rothstein 1977, Sealy and Neudorf 1995, Sealy 1996, Appendix 1) making them excellent species to examine the parameters used for egg recognition. Warbling Vireos are unique because they are the smallest ejecter of cowbird eggs and because they exhibit geographic variation in their response to parasitism. The eastern subspecies (*V. g. gilvus*) is an ejecter and the western subspecies (*V. g. swainsoni*) appears to be an accepter (Sealy 1996, Sealy et al. 2000). I tested Rothstein's (1982b) prediction that ejecter species with eggs similar to cowbird eggs will be less tolerant of foreign eggs than ejecter species with eggs substantially different from cowbird eggs. Warbling Vireo eggs are more similar to cowbird eggs than Baltimore Oriole eggs are to cowbird eggs. Cowbird eggs have a white ground colour and are heavily spotted with mostly brown spots that are somewhat concentrated on the large end of the egg (Lowther 1993). Warbling Vireo eggs are

similar to cowbird eggs in their white ground colour, but differ in two parameters. Vireo eggs are smaller in size and have fewer spots that are sparsely distributed about the large end of the egg (Gardali and Ballard 2000). Baltimore Oriole eggs differ from cowbird eggs in four parameters: size, ground colour, type of maculation, and colour of maculation. By contrast to cowbird eggs, oriole eggs are grayish-blue in ground colour, larger, scrawled rather than spotted, and most scrawls are black (Rising and Flood 1998). The eggs of vireos and orioles also differ in ground colour, size, maculation, and maculation colour. I predicted that: i) Warbling Vireos would be less tolerant of foreign eggs than American Robins; and ii) Baltimore Orioles would tolerate foreign eggs more than American Robins. In addition, for Warbling Vireos, I examined the mechanism of egg recognition and the influence of egg characteristics on the cost of ejection and recognition errors. Finally, I tested the hypothesis that the size and spot pattern of foreign eggs would affect the cost of ejection and probability of committing recognition errors. Ejection in small cowbird hosts may be limited by bill size (Rohwer and Spaw 1988). These small hosts may damage their own eggs while ejecting cowbird eggs, which may force them to accept parasitism and create an evolutionary equilibrium (Rohwer and Spaw 1988, Lotem and Nakamura, Chapter 4). Cuckoo hosts face another cost because they make more recognition errors when ejecting eggs with a higher degree of mimicry (Davies and Brooke 1988).

METHODS

General

Fieldwork was conducted at Delta Marsh, Manitoba (50° 11' N, 98° 23' W) on the properties of the Delta Marsh Field Station (University of Manitoba), Delta Waterfowl and Wetlands Research Station, Portage Country Club, private cottage owners and on the Bell Estate. This area is characterized by a narrow dune-ridge forest, which separates Lake Manitoba from the extensive Delta Marsh (see MacKenzie 1982, Mackenzie et al. 1982 for a detailed description of the study site and Sealy 1980 for a map of the area). I located and monitored nests from May to July for Warbling Vireos in 1998 and 1999 and for Baltimore Orioles in 1999 and 2000. Because both species nest high in the canopy, e.g. Warbling Vireo nests average 8.6 m high (n = 156; unpublished data), I used a TV antenna tower guyed with ropes to climb to most nests (Figure 1.1).

Experimental egg additions at Warbling Vireo and Baltimore Oriole nests followed the same general procedure. A single foreign egg of one of the treatments was added to a nest during laying or incubation. Because I did not know the exact day of incubation for most nests at the time of parasitism, I added eggs throughout the incubation period. Egg treatments were randomly assigned to nests and each nest was tested only once. I inspected each nest daily to determine whether the experimental egg was ejected and to determine the length of time until ejection. I followed Rothstein's (1975a) criterion for determining egg acceptance. If an experimental egg was still present in the nest and the nest was still active after 5 days, I assumed that the egg was accepted. The time until egg ejection was considered because the length of time for a response to be elicited provides additional information regarding the influence of a given

Figure 1.1. TV antenna tower guyed with ropes used to access Warbling Vireo and Baltimore Oriole nests. Use of this tower allowed access to nests up to 12 m high.



parameter on a host's tolerance to foreign eggs (Rothstein 1982b).

Because some cowbird hosts respond to parasitism differently according to nest stage (Rothstein 1976, Sealy 1995), I examined the influence of nest stage on the response of Warbling Vireos and Baltimore Orioles to experimental eggs. Nest stage at the time of parasitism was determined as laying, early incubation, or late incubation by recording egg laying between daily nest inspections, backdating from the hatching or fledging date, or by candling a host egg with a foam tube candler (Lokemoen and Koford 1996). Instead of considering only two nest stages (laying and incubation) as most previous egg recognition studies have (e.g. Rothstein 1976, Sealy 1996), I used three nest stages (two incubation stages) because of the long incubation period of Warbling Vireos (Gardali and Ballard 2000). The laying stage was defined as the day the first egg was laid through the day the penultimate egg was laid. Nests parasitized on the last day of laying or incubated 1-6 days were considered in early incubation and those incubated ≥ 7 days were in late incubation. For Baltimore Orioles, the onset of incubation is believed to occur on the day the last or penultimate egg is laid (Rising and Flood 1998), whereas the onset of incubation is unknown for Warbling Vireos (Gardali and Ballard 2000).

Warbling Vireos

Experimental eggs were added to Warbling Vireo nests without the removal of a host egg as Brown-headed Cowbirds do not remove a host egg from every parasitized nest (Sealy 1992) and no difference in a host's response to experimental parasitism has been found whether or not a host egg is removed at the time of parasitism (Rothstein 1975a, Davies and Brooke 1988). In total, I added foreign eggs of eight different treatments to Warbling Vireo nests (Table 1.1, Figure 1.2). The experimental egg

Table 1.1. Mean measurements (mm \pm SE) of experimental eggs used in Warbling Vireo experiments in comparison to those of Warbling Vireo and Brown-headed Cowbird eggs from Delta Marsh, Manitoba.

Egg Type	Length	Width	n
large-cowbird-spotted ^a	21.68 \pm 0.25	16.66 \pm 0.18	14
large-white	21.04 \pm 0.34	16.59 \pm 0.21	13
large-vireo-spotted	21.50 \pm 0.30	16.62 \pm 0.15	13
total large	21.42 \pm 0.17	16.62 \pm 0.10	40
equal-cowbird-spotted ^b	19.19 \pm 0.17	13.72 \pm 0.14	13
equal-white	19.16 \pm 0.24	13.95 \pm 0.13	13
equal-vireo-spotted	19.62 \pm 0.20	13.89 \pm 0.08	13
total equal	19.32 \pm 0.12	13.85 \pm 0.07	39
small-spotted ^c	15.41 \pm 0.20	11.20 \pm 0.13	8
small-white	15.31 \pm 0.15	11.16 \pm 0.15	8
total small	15.36 \pm 0.12	11.18 \pm 0.09	16
Warbling Vireo ^d	19.69 \pm 0.14	14.09 \pm 0.13	20
Brown-headed Cowbird ^e	21.10 \pm 0.10	16.44 \pm 0.07	113

^a Real Brown-headed Cowbird eggs were used to create the large treatments.

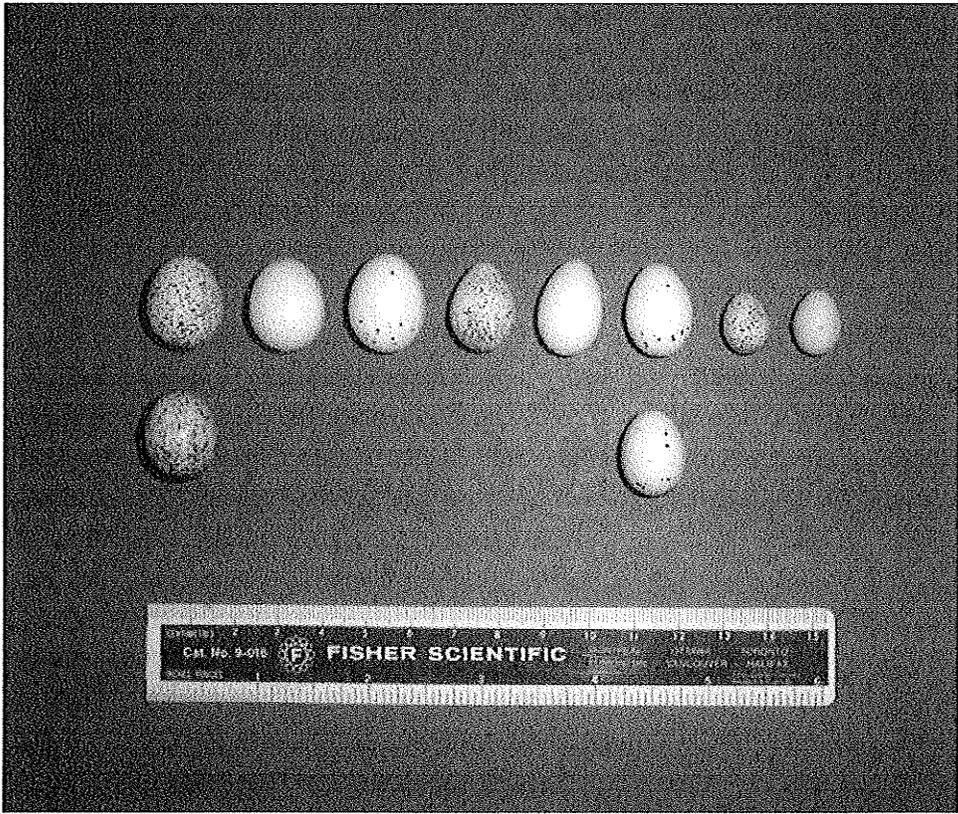
^b Real Barn Swallow (*Hirundo rustica*) eggs were used to create the equal treatments.

^c Real Zebra Finch (*Taeniopygia guttata*) eggs were used to create the small treatments.

^d Eggs were measured at Delta Marsh in 1998. The range of these eggs was 18.9-21.0 mm for length and 13.1-15.1 mm for width.

^e Measurements from eggs found in Yellow Warbler (*Dendroica petechia*) and Red-winged Blackbird (*Agelaius phoeniceus*) nests at Delta Marsh in 1988 (Sealy unpublished data). The range of these eggs was 18.1-23.3 mm for length and 14.3-18.8 mm for width.

Figure 1.2. Egg treatments used in experiments concerning Warbling Vireo parameters of egg recognition. Top row contains, from left to right, the three large egg treatments (cb-spotted, white, and vireo-spotted), the three equal egg treatments (cb-spotted, white, and vireo-spotted), and the two small egg treatments (cb-spotted and white). For comparison, bottom row shows a real Brown-headed Cowbird egg (left) and a real Warbling Vireo egg (right).



treatments varied in size and spot pattern. Three size categories of eggs (large, equal and small) were used with sizes relative to that of a Warbling Vireo egg. There were three spot patterns for each size category (cowbird-spotted, vireo-spotted and immaculate-white), except the small size eggs, which only had two spot patterns. In 1998, only two spotting patterns of experimental eggs were used (cowbird-spotted and immaculate-white), whereas only two egg sizes were used in 1999 (large and equal). I used real eggs of other species to create all egg treatments (see Table 1.1 for specific egg information) because Warbling Vireos were believed to be capable only of puncture-ejecting cowbird eggs (Sealy 1996; but see Chapter 4). To remove a potential bias from paint applied to eggs, all egg treatments were painted with non-toxic acrylic paints (Folk Art Acrylic Paint by Plaid®; colours and product numbers to follow). Eggs of all treatments were first painted with a base coat of white (Wicker White 901). The cowbird-spotted treatments then received numerous brown spots (Coffee Bean 940) to match the heavily-spotted pattern of maculation on real cowbird eggs. The vireo-spotted treatments received diffuse brown spots (Coffee Bean 940) focused around the base of the egg to match the sparse pattern of spots on Warbling Vireo eggs. A toothbrush dipped in brown paint was used to spatter the eggs with realistic spots. I used real Brown-headed Cowbird eggs, Warbling Vireo and Baltimore Oriole eggs from the study area as models when painting experimental eggs (see below for description of eggs used in Baltimore Oriole experiments).

Two experimental procedures were conducted in addition to experiments in 1998 and 1999 on the parameters of egg recognition. In 1998, nests that received the large-cowbird-spotted treatment (i.e. a real cowbird egg painted over to match the appearance

of a cowbird egg) were videotaped for one hour after egg addition to record ejection behaviour. Where possible, I determined whether males were responsible for ejection. I identified males based on whether they sang before ejection because there is no evidence that female Warbling Vireos of the eastern subspecies sing (Howes-Jones 1985a, b; personal observation). In 2000, Warbling Vireos were tested for their ability to recognize conspecific eggs. Single Warbling Vireo eggs were switched between pairs of vireo nests that were as close as possible to the same stage of laying or incubation (e.g. Lanier 1982, Lorenzana and Sealy 2001). Once switched, all eggs in a clutch were numbered with a non-toxic black marker, including the switched egg. Numbers on switched eggs were varied sequentially for each additional nest to remove any potential bias of using the same number (i.e. one that provided a large mark). Nests were monitored daily to determine whether the conspecific egg was accepted. After 5 days, a switched egg was considered accepted if it was still present and undamaged. Accepted eggs were moved back into their original nests to prevent any negative effects of hatching asynchrony caused by the differential incubation stages of switched eggs.

Baltimore Orioles

In 1999, I added foreign eggs of eight different treatments to Baltimore Oriole nests (see Table 1.2, Figure 1.3). The experimental eggs varied in three parameters: size and type and colour of maculation. Two sizes of eggs (large and equal) were used with sizes relative to the size of a Baltimore Oriole egg. Each size category had two maculation types: spotted like a cowbird egg or scrawled like an oriole egg. The two maculation types had two colours: brown like most spots on a cowbird egg or black like the scrawls on an oriole egg. I used real eggs of other species to create all egg treatments

Table 1.2. Mean measurements (mm \pm SE) of experimental eggs used in Baltimore Oriole experiments in comparison to those of Baltimore Oriole and Brown-headed Cowbird eggs from Delta Marsh, Manitoba.

Egg Type	Length	Width	n
w-small-black-scrawled ^{a, b}	21.22 \pm 0.30	16.48 \pm 0.10	6
w-small-black-spotted	22.14 \pm 0.59	16.62 \pm 0.19	6
w-small-brown-scrawled	21.85 \pm 0.24	16.39 \pm 0.15	6
w-small-brown-spotted	21.45 \pm 0.55	16.58 \pm 0.26	6
g-small-black-scrawled	21.06 \pm 0.22	16.62 \pm 0.25	6
g-small-black-spotted	21.76 \pm 0.21	16.54 \pm 0.25	6
g-small-brown-scrawled	21.36 \pm 0.41	16.25 \pm 0.25	6
g-small-brown-spotted	20.88 \pm 0.40	16.41 \pm 0.35	6
total small	21.46 \pm 0.14	16.49 \pm 0.08	48
w-equal-black-scrawled ^c	23.37 \pm 0.53	15.78 \pm 0.25	6
w-equal-black-spotted	23.25 \pm 0.36	16.40 \pm 0.32	6
w-equal-brown-scrawled	23.58 \pm 0.27	16.02 \pm 0.13	6
w-equal-brown-spotted	22.95 \pm 0.13	15.65 \pm 0.27	6
g-equal-black-scrawled	23.50 \pm 0.44	16.06 \pm 0.24	6
g-equal-black-spotted	23.05 \pm 0.55	16.27 \pm 0.22	6
g-equal-brown-scrawled	23.49 \pm 0.42	16.15 \pm 0.15	6
g-equal-brown-spotted	23.08 \pm 0.62	16.14 \pm 0.17	6
total equal	23.28 \pm 0.15	16.06 \pm 0.08	48
Baltimore Oriole ^d	23.28 \pm 0.15	16.06 \pm 0.08	48

Brown-headed Cowbird ^e	21.10 ± 0.10	16.44 ± 0.07	113
-----------------------------------	--------------	--------------	-----

^a w = white ground colour and g = gray ground colour.

^b Brown-headed Cowbird eggs were used to create the small treatments.

^c Baltimore Oriole eggs were used to create the equal treatments.

^d Measurements of oriole eggs are the same as those used for all equal-sized treatments.

The range for these eggs was 21.1-25.5 mm for length and 14.7-17.2 mm for width.

^e Measurements from eggs found in Yellow Warbler and Red-winged Blackbird nests at Delta Marsh in 1988 (Sealy unpublished data). The range for these eggs was 18.1-23.3 mm for length and 14.3-18.8 mm for width.

Figure 1.3. Egg treatments used in experiments concerning Baltimore Oriole parameters of egg recognition. Top row contains two real oriole eggs (left and middle) and a real cowbird egg (right). Bottom row contains, from left to right, white-equal-brown-spotted, gray-equal-black-spotted, gray-equal-brown-scrawled, gray-equal-black-scrawled, gray-small-black-scrawled, gray-small-black-spotted, and white-small-brown-spotted egg treatments. Several egg treatments are missing from this photograph.



and the control (see Table 1.2 for specific egg information) because Baltimore Orioles were believed only to be capable of puncture-ejection (Rothstein 1977, Sealy and Neudorf 1995; but see Chapter 4). All egg treatments were painted with non-toxic, acrylic paints (Folk Art Acrylic Paint by Plaid®; colours and product numbers to follow) to remove any potential bias of painted versus unpainted treatments. Eggs of these treatments were first painted with a base coat of white (Wicker White 901). Spotted eggs received numerous spots of either brown (Coffee Bean 940) or black (Licorice 938) to match the heavily-spotted pattern on real cowbird eggs. Scrawled patterns of either brown (Coffee Bean 940) or black (Licorice 938) were painted on scrawled egg treatments with a fine-tipped paintbrush.

In 2000, I added another parameter to experimental eggs, ground colour, which created eight additional egg treatments to Baltimore Oriole nests (Table 1.2). These treatments had the same egg characteristics as treatments added in 1999 (Table 1.2), except they were painted with the blue-gray ground colour (a 1:1:1:2 mixture of Tapioca 903, Basil 645, Porcelain Blue 765, and Wicker White 901) of oriole eggs (Figure 1.3). The same egg treatments as used in 1999, with a white ground colour, were added to increase the sample size for these treatments. Also in 2000, I used a TreeTop Peeper II (Sandpiper Technologies, Inc.) extendable video nest inspection camera to monitor oriole nests. This video system allowed high oriole nests (up to 12 m high) to be checked from the ground, removing the need for the time-intensive use of the TV antenna tower to inspect nests.

In both years, I removed one oriole egg at the time of experimental egg addition and used those eggs to create the equal-sized egg treatments (see Table 1.2). I only

parasitized oriole nests when they had a minimum of three eggs to prevent possible desertions due to partial clutch reduction (e.g. Hill and Sealy 1994).

Analysis

The effect of egg characteristics on a host's ability to recognize a foreign egg was examined by analyzing the binomial (accept or eject) response and, separately, by considering the time until experimental egg ejection. I used logistic regression to analyze the binomial response data using the CATMOD procedure in SAS (Stokes et al. 2000). I used a full model to examine the interactions of all variables. In the absence of significant interactions, the main effects of egg characteristics and nest stage were examined in a single model. In each data set, because observations for some treatment combinations were zero or lacking (with nest stage), values of one acceptance and one ejection were added to all cells prior to analysis. Data are presented as untransformed values. In addition, I compared the overall ejection frequencies in response to eggs that varied in the number of parameters they differed from host eggs. To test the response by number of parameters, I used a 2 x 2 Fisher exact test for Warbling Vireos and a 4 x 2 Fisher exact test (Schlotzhauer and Littell 1997) for Baltimore Orioles because sample sizes were small and expected values were less than five for these data.

The time-to-ejection data were examined using survivorship analysis, the LIFETEST procedure in SAS (Everitt and Der 1996), which examined the daily proportion of eggs "alive" (i.e. accepted) over the 5-day test period. I used Log-rank and Wilcoxon-rank tests to compare the survival of eggs differing in egg characteristics or the stage of the nest at the time of parasitism. The Wilcoxon-rank test places more weight on the earlier portion of the survival curve, whereas the Log-rank test places more weight on

the later portion of the survival curve. When multiple comparisons were made, Bonferoni-corrected alpha values were used.

For Warbling Vireos, where each egg parameter included treatments with characteristics both above and below that of host eggs (e.g. large, equal and small eggs), I determined whether egg characteristics influenced the cost of ejection and the number of recognition errors. The cost of ejection was measured as the number of host eggs damaged (i.e. with a puncture or large crack) or missing when an experimental egg was ejected. Recognition errors occur when a host ejects one of its own eggs in the absence of parasitism (Marchetti 1992) or when a host ejects one of its own eggs instead of the foreign egg in a parasitized nest (Davies and Brooke 1988). Røskaft et al. (2002) defined the latter type of errors as “rejection errors” because they may be interpreted as an ejection cost or as a recognition error. I examined only the influence of egg characteristics on ejection errors because I did not monitor unparasitized nests to document true recognition errors, which are extremely difficult to identify even in control nests. I assumed any host egg missing from nests where an experimental egg was accepted to be an ejection error. However, this assumption likely overestimates errors slightly because of the potential for egg losses from partial clutch depredation, egg removal by cowbirds, and the removal of damaged host eggs that is unrelated to parasitism (Rothstein 2001). Another potential bias in distinguishing between cost and errors occurred when nests were experimentally parasitized during the laying stage. At a few nests, vireos appeared to skip a day in their laying sequence. These apparent skips may also represent eggs laid that went missing as an ejection cost (i.e. a host egg damaged during an ejection attempt and then removed) or error because Warbling Vireos

are not known to skip a day in laying, although much of their life history remains poorly studied (Gardali and Ballard 2000). To account for this potential bias, I analyzed these data both with and without the skips as missing eggs. Because ejection costs and errors always involved a single host egg per nest, I examined differences in the frequency of damaged or missing host eggs by experimental egg parameters instead of using the mean number of damaged or missing host eggs. I used 3 x 2 Fisher exact tests (Schlotzhauer and Littell 1997) to examine the influence of each egg parameter due to small sample sizes and the presence of expected values less than five. The influence of egg characteristics on the cost of ejection and recognition errors was not examined in Baltimore Orioles because nest inspections with the video camera system may not have detected some damaged eggs and egg treatments did not provide characteristics above and below those of host eggs.

Egg addition experiments also provided data to examine the mechanism of egg recognition, i.e. true egg recognition or discordancy, in Warbling Vireos. I compared data from nests that were experimentally parasitized with a cowbird-spotted egg (highly divergent from vireo eggs) to determine whether vireos recognized a foreign egg only when it was in the minority or when there was an equal number of foreign and host eggs in the nest. I used a Fisher exact test to compare the number of acceptances and ejections at nests where there was an equal number of foreign and host eggs to nests where host eggs were in the minority (i.e. ≥ 2 host eggs present). The mechanism of egg recognition in Baltimore Orioles was not examined because oriole nests were parasitized only when host eggs were in the majority. Unless specified otherwise, all statistical tests were two-tailed and I used a significance level of $\alpha = 0.05$.

RESULTS – WARBLING VIREOS

I found 83 Warbling Vireo nests in 1998 and 80 in 1999. However, I recorded experimental results on 51 nests in 1998 and 48 nests in 1999. The remaining nests were either too high to reach (up to 20 m), found during the nestling stage, or failed (due to predation or inclement weather) before or during an experiment. In 1998 and 1999, two nests were depredated after experimental parasitism and the eggs in one nest hatched on day 4 of acceptance (described below). One depredation occurred on day 1 before any result (partial or complete) could be recorded, whereas the other depredation occurred on day 3 of acceptance of an equal-vireo-spotted egg. Inclusion of the partial acceptances in the analyses as complete 5-day acceptances did not change the significance of any of the statistical comparisons. Therefore, these were not included in the final analyses. In 2000, Warbling Vireo eggs were switched between eight nests. One of these was depredated on day 1 of the switch, whereas all others survived the 5-day test period.

The results from two nests were excluded from analysis. Nest 1998-34 was excluded from analysis due to the following events. The nest was experimentally parasitized and videotaped on 9 June 1998 when it had one vireo egg. The adult vireos were not seen at the nest during the one-hour video nor were they seen at the nest again. Two days later both eggs were gone and the nest lining was pulled up. This nest was probably deserted prior to experimental parasitism. Nest 1998-51 was excluded from analysis because the experimental egg (small-white egg) disappeared on day 4 when the vireo eggs hatched. After excluding these nests and the depredated nests, my data represent responses of Warbling Vireos to foreign eggs at 97 nests.

Parameters of cowbird egg recognition

Warbling Vireos ejected 100 % of cowbird-spotted eggs regardless of size, whereas only 46 % of each size of vireo-spotted eggs and 50 to 62 % of immaculate-white eggs were ejected (Table 1.3). There were no significant interactions ($P > 0.8$) in the full logistic regression model. Therefore, only results from the main effects model were reported. Only spot pattern significantly influenced a vireo's probability of ejecting a foreign egg (logistic regression, $\chi^2 = 14.04$, $df = 2$, $P = 0.0009$). There was no significant effect of egg size (logistic regression, $\chi^2 = 0.55$, $df = 2$, $P = 0.759$) and nest stage (logistic regression, $\chi^2 = 2.18$, $df = 2$, $P = 0.337$). In addition, Warbling Vireos did not differ significantly in their response to foreign eggs that varied in only one parameter (28/40 or 70 % ejected) versus two parameters (35/44 or 80 % ejected; Fisher exact test, $P = 0.328$).

Foreign egg survival followed trends similar to the acceptance/ejection response. Spot pattern had a significant effect on egg survival (Table 1.4, Figure 1.4A), whereas size of experimental eggs and nest stage had no significant effect (Table 1.4; Figure 1.4B and 4C). Within spot pattern, survival of cowbird-spotted eggs was significantly lower than that of white eggs (Log-rank test, $\chi^2 = 33.03$, $df = 1$, $P < 0.001$; Wilcoxon-rank test, $\chi^2 = 33.03$, $df = 1$, $P < 0.001$; Figure 1.4A) and vireo-spotted eggs (Log-rank test, $\chi^2 = 30.04$, $df = 1$, $P < 0.001$; Wilcoxon-rank test, $\chi^2 = 30.04$, $df = 1$, $P < 0.001$; Figure 1.4A), but there was no significant difference in survival between white eggs and vireo-spotted eggs (Log-rank test, $\chi^2 = 0.80$, $df = 1$, $P = 1.0$; Wilcoxon-rank test, $\chi^2 = 0.26$, $df = 1$, $P = 1.0$; Figure 1.4A). Thus, the spot pattern of cowbird eggs appears to be the most

Table 1.3. Responses of Warbling Vireos to experimental eggs that varied in two egg parameters.

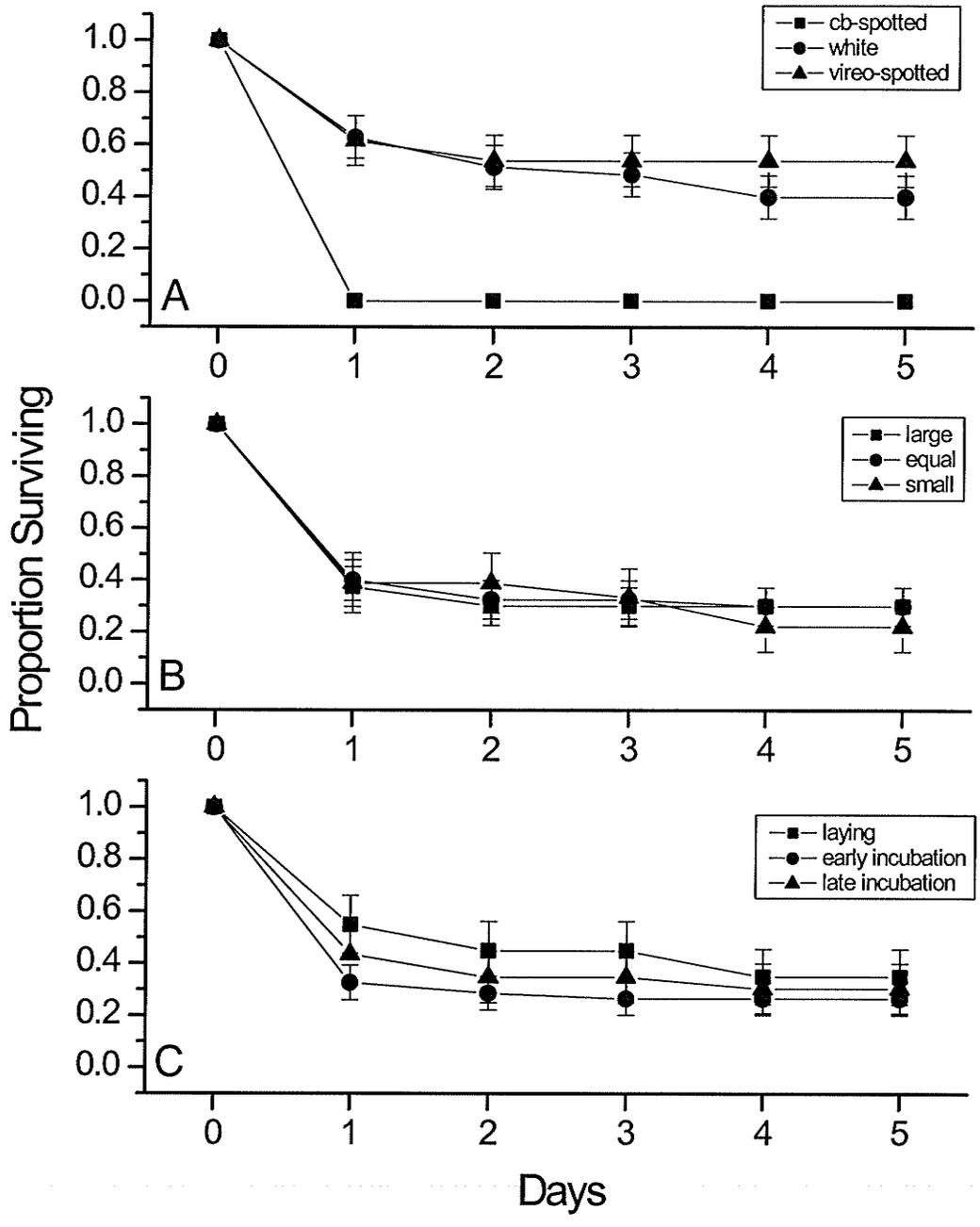
Egg Parameters		Response		
Size	Spot Pattern	Eject	Accept	% Ejected
large	cb-spotted	14	0	100
	immaculate	8	5	62
	vireo-spotted	6	7	46
equal	cb-spotted	14	0	100
	immaculate	8	5	62
	vireo-spotted	6	7	46
small	cb-spotted	9	0	100
	immaculate	4	4	50
Total		69	28	71

Table 1.4. The influence of egg parameters and nest stage on the response of Warbling Vireos to foreign eggs over time.

Test	Chi-square (df = 2)	P
Size (n = 97)		
Log-rank	0.26	0.877
Wilcoxon-rank	0.05	0.975
Spot Pattern (n = 97)		
Log-rank	38.06	<0.0001
Wilcoxon-rank	37.35	<0.0001
Nest Stage (n = 91) ^a		
Log-rank	0.85	0.655
Wilcoxon-rank	2.20	0.333

^a Sample size for nest stage was smaller than those for egg parameters because stage was not determined at all nests.

Figure 1.4. Survival curves for experimental eggs added to Warbling Vireo nests in relation to egg parameters (A - spot pattern, B - egg size, and C - nest stage).



important egg parameter used in foreign egg recognition by Warbling Vireos, while size had no significant influence.

Cost of ejection and ejection errors

Over all egg parameters, Warbling Vireos infrequently damaged eggs or made ejection errors (Table 1.5). There was no significant difference in the frequency of damaged or missing eggs at nests where vireos ejected eggs that varied in spot pattern (Fisher exact test, $P = 1.0$) or size (Fisher exact test, $P = 0.596$). Including skips in the egg-laying sequence as missing eggs did not change the trends for spot pattern (Fisher exact test, $P = 0.635$) or egg size (Fisher exact test, $P = 0.835$). The occurrence of ejection errors also was not significantly different at nests where accepted eggs varied in spot pattern (Fisher exact test, $P = 1.0$) or egg size (Fisher exact test, $P = 1.0$). These trends also remained the same for spot pattern (Fisher exact test, $P = 1.0$) and egg size (Fisher exact test, $P = 0.341$) when skips in the egg-laying sequence were included as missing eggs.

Conspecific egg recognition

All seven conspecific eggs experimentally switched with one of their own eggs were accepted. There was no significant difference in response to conspecific eggs based on nest stage (Fisher exact test, $P = 1.0$; $n = 2$ during laying vs. $n = 5$ during incubation).

Mechanism of egg recognition

Warbling Vireos ejected all cowbird-spotted eggs from their nests. There was no significant difference in response to parasitism based on whether host eggs were in the majority or whether there was an equal number of host and foreign eggs (Fisher exact

Table 1.5. Influence of egg parameters on costs of experimental egg ejection and ejection errors by Warbling Vireos.

Egg Parameter	Cost for Ejections			Errors for Acceptances		
	Eggs Missing	n	Cost per Ejection	Eggs Missing	n	Errors per acceptance
Size						
large	1	28	0.04	0	12	0.00
equal	1 (2) ^a	28	0.04 (0.07) ^a	1 (2) ^a	12	0.08 (0.17) ^a
small	1	13	0.08	0 (1) ^a	4	0.00 (0.25) ^a
Spot Pattern						
cowbird	2	37	0.05	0	0	0.00
immaculate	1 (2) ^a	20	0.05 (0.10) ^a	0 (1) ^a	14	0.00 (0.07) ^a
vireo	0	12	0.00	1 (2) ^a	14	0.07 (0.14) ^a
Total	3	69	0.04 (0.06) ^a	1 (3) ^a	28	0.04 (0.11) ^a

^a Includes as missing eggs those that appeared only as a skip in the vireo's laying sequence.

test, $P = 1.0$; Table 1.6). This supports true egg recognition as the mechanism used by Warbling Vireos to recognize foreign eggs.

Videotaped egg-ejection behaviour

I videotaped seven nests where a cowbird egg (large-cowbird-spotted treatment) was added to vireo nests. However, only five of these captured the vireos' behaviour after experimental parasitism because two nests were obscured. Warbling Vireos ejected cowbird eggs an average of $4.7 \text{ mins} \pm 1.1 \text{ SE}$ after egg addition. Four of the five vireos ejected cowbird eggs without sitting on the nest. The remaining vireo sat on the nest a few minutes before ejecting the cowbird egg, although it looked into the nest upon first arrival (see full description of ejection at nest 98-38 below). Thus, only visual cues were available for egg recognition in four ejections, whereas in one ejection both visual and tactile cues were available.

Two additional observations were captured that identify important aspects of ejection behaviour by Warbling Vireos. At nest 1998-31, a Warbling Vireo grasp-ejected the experimental cowbird egg (Figure 1.5). At 0835 Central Daylight Time (CDT), I flushed the male vireo from the nest and inserted a cowbird egg. Five minutes later, a vireo perched on the rim and looked into the nest. It probed the eggs for approximately 3 seconds and then lifted the cowbird egg out of the nest and flew away. A frame-by-frame examination of the videotape showed the cowbird egg was held between the vireo's widely stretched mandibles (Figure 1.5), indicating grasp-ejection. This observation led to a test of the hypothesis that Warbling Vireos are capable of grasp-ejection (see Chapter 4).

Table 1.6. Experimental cowbird-spotted eggs ejected from Warbling Vireo nests as a function of host clutch size.

Host Clutch Size ^a	# Ejected	# Accepted	Number of Nests
1	5	0	5
2	4	0	4
3	6	0	6
4	21	0	21
5	1	0	1
≥ 2 (total)	32	0	32

^a Number of host eggs at the time of parasitism.

Figure 1.5. Warbling Vireo at nest 1998-31 ejecting a real Brown-headed Cowbird egg.



In another video, the male Warbling Vireo at nest 1998-38 ejected a cowbird egg added to this nest. Three minutes after egg addition a vireo landed above the nest, looked in and then settled on the nest. Several seconds later, it began singing, which identified this individual as a male. After four minutes of sitting on the nest, the vireo got up on the rim of the nest and probed into the nest. A few seconds later, it flew away from the nest with the cowbird egg. The method of ejection could not be determined due to the direction the vireo flew from the nest. In a video from another experiment (Chapter 4), a second male Warbling Vireo ejected a plaster cowbird egg added to nest 1999-75. Five minutes after egg addition, a vireo landed on the nest branch and, after probing inside the nest twice, it sang, which identified it as a male. The vireo continued to probe or peck inside the nest and sang intermittently until finally ejecting the cowbird egg at 0938 CDT. These two observations provide the first documentation of male Warbling Vireos ejecting cowbird eggs.

In 1998, one of five real cowbird eggs was ejected by a male Warbling Vireo and, in 1999, one of four model cowbird eggs was ejected by a male. Thus, a minimum of 22 % of ejections were by males. Unfortunately, because I relied on song to distinguish between males and females this represents a lower estimate of the proportion of ejections by males. Only those birds that sang prior to ejecting could be reliably sexed by this method.

RESULTS – BALTIMORE ORIOLES

Sixty-one Baltimore Oriole nests were found in 1999 and 75 in 2000. Experimental results were recorded at 40 nests in 1999 and 56 nests in 2000. The other

nests were either too high to access (up to 20 m or higher), found during the nestling stage, or failed (due to predation or inclement weather) before or during an experimental parasitism. In 1999 and 2000, two nests were depredated after experimental parasitism. One was depredated on day 1 before any result could be recorded, whereas the other was depredated on day 4 of an acceptance. Inclusion or exclusion of this partial acceptance in the analyses as a complete 5-day acceptance did not change the significance of any of the statistical comparisons. However, this result was included in the analyses to maintain an equal sample size of six for each egg treatment. Therefore, my data represent responses to foreign eggs at 96 nests.

Parameters of cowbird egg recognition

Baltimore Orioles ejected 91 % of all experimental eggs added to their nests, although there were no strong trends apparent in these data (Table 1.7). There were no significant interactions ($P > 0.2$) in the full logistic regression model. Therefore, only results from the main effects model were reported. There was no significant effect of nest stage (logistic regression, $\chi^2 = 0.69$, $df = 2$, $P = 0.709$) or any egg characteristic: ground colour (logistic regression, $\chi^2 = 0.01$, $df = 1$, $P = 0.938$), size (logistic regression, $\chi^2 = 0.66$, $df = 1$, $P = 0.415$), maculation (logistic regression, $\chi^2 = 1.12$, $df = 1$, $P = 0.291$), or maculation colour (logistic regression, $\chi^2 = 0.02$, $df = 1$, $P = 0.892$). In addition, there was no significant difference in ejection frequency of eggs that varied in one parameter (22/24 or 92 % ejected), two parameters (34/36 or 94 % ejected), three parameters (22/24 or 92 % ejected), or four parameters (6/6 or 100 % ejected; Fisher exact test, $P = 1.0$).

The lack of any strong trends was also apparent in the time to ejection data. Survival of experimental eggs was not significantly affected by most of the egg

Table 1.7. Response of Baltimore Orioles to experimental eggs that varied in four parameters.

Egg Parameters				Response		
Ground	Size	Maculation	Maculation	Eject	Accept	%
Colour			Colour			Ejected
gray	small	Scrawled	black	6	0	100
		Scrawled	brown	5	1	83
		Spotted	black	6	0	100
		Spotted	brown	6	0	100
	equal	Scrawled	black	3	3	50
		Scrawled	brown	6	0	100
		Spotted	black	6	0	100
		Spotted	brown	6	0	100
white	small	Scrawled	black	6	0	100
		Scrawled	brown	5	1	83
		Spotted	black	6	0	100
		Spotted	brown	6	0	100
	equal	Scrawled	black	4	2	67
		Scrawled	brown	5	1	83
		Spotted	black	6	0	100
		Spotted	brown	5	1	83
Total			87	9	91	

Table 1.8. The influence of egg parameters and nest stage on the response of Baltimore Orioles to foreign eggs over time.

Test	Chi-square	P
Ground Colour (n = 96)	df = 1	
Log-rank	0.03	0.873
Wilcoxon-rank	0.05	0.823
Size (n = 96)	df = 1	
Log-rank	2.97	0.085
Wilcoxon-rank	2.14	0.143
Maculation (n = 96)	df = 1	
Log-rank	5.49	0.019
Wilcoxon-rank	2.53	0.112
Maculation Colour (n = 96)	df = 1	
Log-rank	0.04	0.835
Wilcoxon-rank	0.03	0.852
Nest Stage (n = 88) ^a	df = 2	
Log-rank	0.65	0.722
Wilcoxon-rank	1.28	0.527

^a Sample size for nest stage was smaller than those for egg parameters because nest stage was not determined at all nests.

Figure 1.6. Survival curves for experimental eggs added to Baltimore Oriole nests in relation to egg parameters (A - ground colour, B - maculation colour, and C - nest stage).

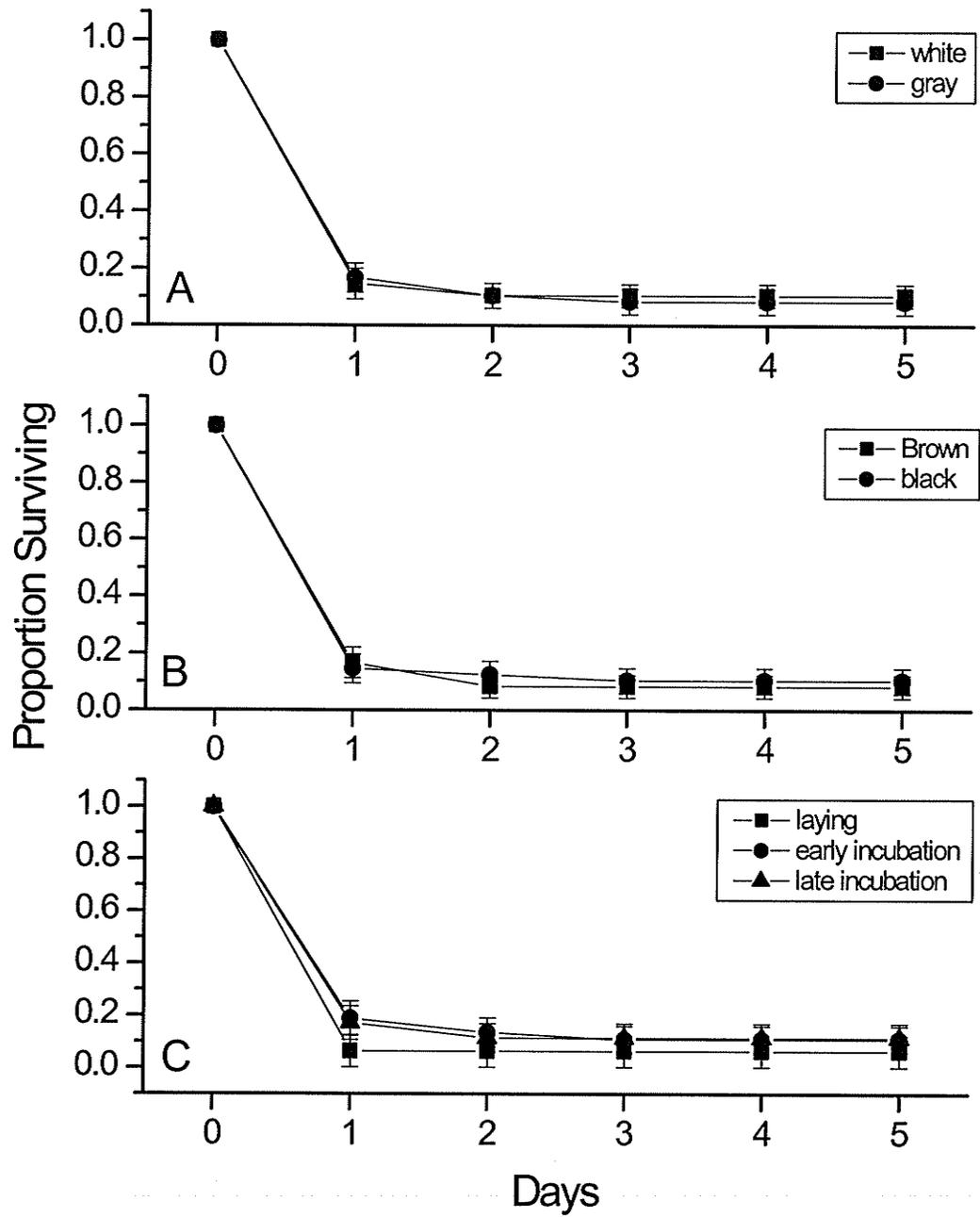
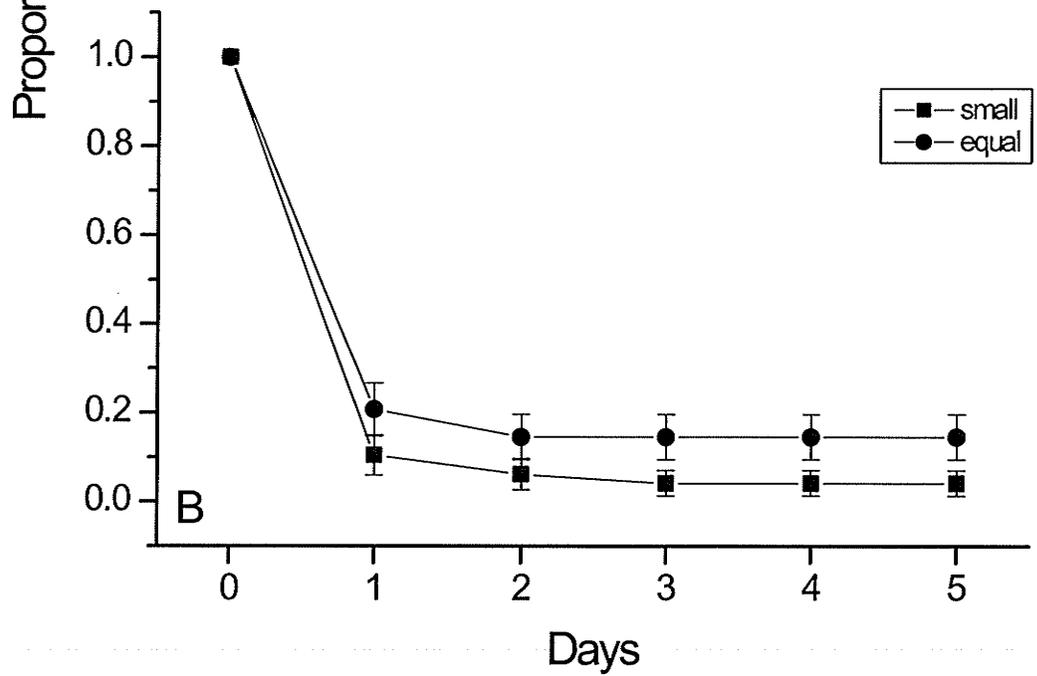
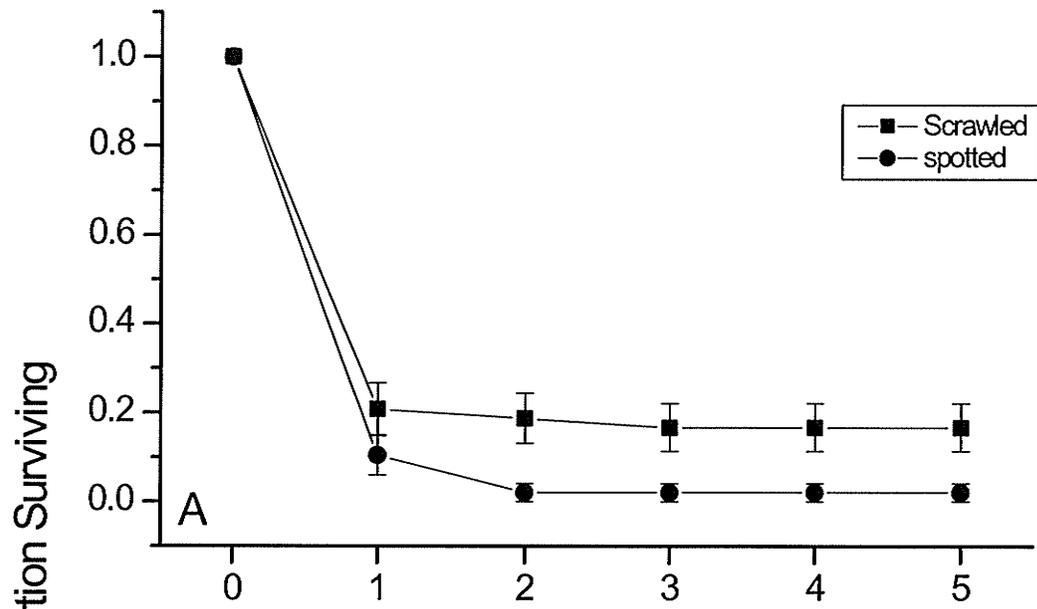


Figure 1.7. Survival curves for experimental eggs added to Baltimore Oriole nests in relation to egg parameters (A - maculation and B - size).



parameters or nest stage (Table 1.8, Figures 1.6 and 1.7). However, maculation type had a significant effect on egg survival that was more pronounced over the early portion of the survival curve (Table 1.8, Figure 1.7). Egg size also showed a trend that approached significance in its affect on egg survival, especially over the later portion of the survival curve (Table 1.8, Figure 1.7).

DISCUSSION

Warbling Vireos

Warbling Vireos ejected foreign eggs based only on spot pattern. Foreign eggs that differed in two parameters were not more likely to be ejected than those that differed in only a single parameter. Warbling Vireos appear to be less tolerant of foreign eggs than were American Robins, which required a difference in at least two parameters before ejecting a foreign egg (Rothstein 1982b). However, vireos showed a level of tolerance similar to that of Gray Catbirds, which require only a difference in ground colour to elicit ejection (Rothstein 1982b). How quickly cowbird eggs are ejected has also been used as a measure of tolerance (Rothstein 1982b). Warbling Vireos ejected 100 % of the cowbird-like egg treatment, a large-cowbird-spotted egg, within 24 hours and, for those nests videotaped, all five eggs were ejected within 10 minutes. By comparison, American Robins and Gray Catbirds ejected only 58 % and 77 % of artificial cowbird eggs, respectively, within 24 hours (Rothstein 1982b). Thus, the egg-recognition abilities of Warbling Vireos in comparison to American Robins support Rothstein's (1982b) prediction that ejecter species whose eggs are more similar in appearance to cowbird eggs should be less tolerant of foreign eggs.

However, unlike American Robins, vireos responded only to spot pattern and not to a difference in either spot pattern or size as would be predicted by egg recognition in robins. In addition, only eggs with the heavily-spotted pattern of a cowbird egg were ejected more quickly than eggs with vireo-like spot patterns. Immaculate eggs survived at levels similar to vireo-spotted eggs. Warbling Vireos did not eject foreign eggs based on size, despite Brown-headed Cowbird eggs averaging about 40 % larger in volume (Johnsgard 1997). Lack of a response to size where a considerable difference in size exists is surprising because size has been found to be a parameter important for egg recognition in other cowbird and cuckoo hosts (Marchetti 2000, Mason and Rothstein 1986, Rothstein 1982b).

The reliance on the cowbird-like spot pattern only and not size for foreign egg recognition may be related to the reliability of this parameter in distinguishing a foreign egg from a vireo egg. Rothstein (1982b) found that robins and catbirds appeared to be most responsive to the egg parameters that most reliably differentiated cowbird eggs, i.e. white ground colour in both species and also size for robins. Furthermore, Rothstein (1982b) interpreted the need for stimulus summation, the use of two parameters, in robins, and lack of response to maculation in catbirds as a method of preventing ejection errors due to natural variability in their own eggs. Both species sometimes lay spotted eggs and robins occasionally lay white or lighter eggs (Rothstein 1982b). For Warbling Vireos, egg size may not be a reliable cue. Although Brown-headed Cowbird eggs are considerably larger than vireo eggs, the ranges of length and width of eggs of both species overlap (Table 1.1). If vireos used size alone to identify cowbird eggs, they would risk occasionally ejecting their own eggs due to natural variation in size. By

contrast, most *Vireo* species lay eggs that are sparsely spotted (Baicich and Harrison 1997) and at least five species are known occasionally to lay immaculate or nearly immaculate eggs (Bent 1950). To my knowledge, there are no records of *Vireo* eggs showing variation toward a more heavily-spotted pattern. Therefore, the heavily-spotted pattern of a cowbird egg likely is the most reliable cue for recognizing a foreign egg with no need for stimulus summation and responding to immaculate eggs may risk an ejection error.

Differences in egg-recognition behaviour exhibited by other ejecters also may explain the lack of an effect of size on egg recognition in Warbling Vireos. Both American Robins and Rufous Horneros (*Furnarius rufus*) are believed to use tactile perception to detect differences in the size of eggs. Mason and Rothstein (1986) found that Rufous Horneros ejected Shiny Cowbird (*M. bonariensis*) eggs that were $\geq 12\%$ less in width than their own eggs regardless of the pattern of spotting on the eggs. They suggested that differences in size were detected through touch because the dark interiors of hornero nests rendered visual detection unlikely. Similarly, Rothstein (1982b) found that smaller eggs elicited the quickest ejections of foreign eggs by robins and suggested that this rapidity was due to the use of both visual and tactile stimuli. By contrast, Warbling Vireos apparently eject cowbird eggs solely on the basis of visual cues. Sealy (1996) observed several instances of ejection of experimental cowbird eggs by Warbling Vireos. Female vireos always looked into the nest and attempted to eject the cowbird egg without settling on the nest to incubate. Sitting on a parasitized clutch may allow a host to use tactile stimuli through their brood patch to identify the presence of a foreign egg by size (larger or smaller). In only one observed ejection attempt, a male Warbling Vireo

settled on its nest before attempting to eject (Sealy 1996). These results were confirmed in this study. Most vireos ejected the cowbird egg before settling on the nest. Only at one nest did the male vireo eject the egg after settling on the nest. Thus, most vireos identified the cowbird egg by sight and, in most cases, rapid ejection of the cowbird egg precluded the possibility of using tactile cues. The different behaviour of male Warbling Vireos may be due to a lack of experience in ejecting cowbird eggs, as has been suggested for male Baltimore Orioles (Sealy and Neudorf 1995), and not the use of different stimuli than females.

Warbling Vireos damaged relatively few of their own eggs while ejecting foreign eggs. There was no difference in the frequency of damage when eggs of different patterns or sizes were ejected, which reveals that the larger and thicker-shelled cowbird eggs were not more difficult to eject than smaller and thinner-shelled eggs. This indicates that the Warbling Vireos' small size is not a constraint against ejecting cowbird eggs, which is counter to the assumptions of the evolutionary equilibrium hypothesis (Rohwer and Spaw 1988). Warbling Vireos also rarely ejected their own egg instead of the foreign egg. Foreign egg characteristics or their similarity to host eggs did not influence the frequency of ejection errors. The lack of ejection errors in vireos is not surprising because they rely on spot pattern to detect foreign eggs, a cue that appears to be very reliable. Ejection errors in cuckoo hosts tend only to occur when a host is confronted with highly mimetic eggs (Davies and Brooke 1988, Davies et al. 1996), but some cuckoo hosts also rarely commit ejection errors even when responding to conspecific eggs (Lahti and Lahti 2002, Stokke et al. 2002). Therefore, the occurrence of

ejection errors in Brown-headed Cowbird hosts is less likely because cowbird eggs do not closely match eggs of most ejecters, including Warbling Vireos.

Warbling Vireos recognized their eggs through true egg recognition. All highly non-mimetic eggs were ejected regardless of whether foreign or host eggs were in the minority. True egg recognition has been found in all species of ejecters tested to date (Underwood and Sealy 2002). Unfortunately, the ages of the vireos in this study were unknown and, therefore, I could not address the role of experience or egg learning on the development of egg recognition and ejection.

Despite their intolerance of foreign eggs and rapid ejection of cowbird eggs, Warbling Vireos did not recognize conspecific eggs, which is not surprising because it has been documented in only a few species of passerines (Underwood and Sealy 2002). There is also no evidence for the occurrence of conspecific parasitism in any *Vireo* species (Yom-Tov 2001). This supports the hypothesis that egg recognition in Warbling Vireos has evolved in response only to interspecific brood parasitism from cowbirds. However, similar to other ejecters (Rothstein 1982b), Warbling Vireos did not evolve recognition of only a cowbird egg type (a larger, heavily-spotted egg), but recognize their own eggs and eject those that differ in the most reliable parameter, spot pattern.

In addition to recording ejection behaviour, videotapes confirmed ejection by male Warbling Vireos. Males ejected cowbird eggs at about 20 % of nests. Previously, Sealy (1996) observed males at two different Warbling Vireo nests attempt without success to eject cowbird eggs, but his other observations implicated ejection only by females. Ejection by males has also been observed in two other Brown-headed Cowbird hosts, Gray Catbirds and Baltimore Orioles (Sealy and Neudorf 1995). Only a few

anecdotal observations of ejection by catbirds exist, but Sealy and Neudorf (1995) documented male involvement in 3 of 14 cowbird egg ejections, a proportion similar to the one recorded for Warbling Vireos. Sealy and Neudorf (1995) predicted that species where males incubate or are more involved at the nest are the most likely to have evolved egg recognition and ejection by males. Ejection by male Warbling Vireos provides support for this prediction because males also incubate (Gardali and Ballard 2000). Recent experiments on a few species of Common Cuckoo hosts also support this prediction. Soler et al. (2002) found that in species where males were involved in incubation both sexes recognized and ejected model cuckoo eggs, but in species where males were not involved in incubation, only females recognized and ejected model cuckoo eggs. Previously, females have often been assumed to be solely capable of ejection because in many species they are responsible for most activities at the nest (e.g. Rothstein 1975c). However, in Brown-headed Cowbird hosts, determining which sex ejects has been difficult because most ejecters are not sexually dimorphic (Sealy and Neudorf 1995). Indeed, only two species of 18 ejecter species (Appendix 1), Baltimore and Bullock's Orioles, are strongly sexually dimorphic. Thus, the involvement of males in cowbird egg ejection may have been underestimated. Nevertheless, ejection by males has theoretical implications because ejection by both sexes should increase the spread of the ejecter trait in a population (Rothstein 1975c, Kelly 1987, Sealy and Neudorf 1995).

Baltimore Orioles

None of the four egg parameters significantly influenced egg ejection by Baltimore Orioles. Egg ejection also was not influenced by the number of parameters that a foreign egg differed from a host egg in. Only maculation had a significant effect

on the time until ejection of foreign eggs and size had a strong trend toward an effect on time until ejection. Overall no strong trends emerged in the responses of orioles to foreign eggs because they rejected nearly all experimental eggs. Therefore, these mostly non-significant results should be interpreted with caution.

Surprisingly, Baltimore Orioles appeared to be somewhat less tolerant to foreign eggs than American Robins. Stimulus summation was not required for ejection by orioles as is required by other species whose eggs differ from a parasite's egg in a number of parameters (Rothstein 1982b, Lahti and Lahti 2002). Similar to experiments with real cowbird eggs (Sealy and Neudorf 1995), orioles ejected 100 % of cowbird-like eggs demonstrating less tolerance to cowbird eggs than American Robins and Gray Catbirds (Rothstein 1982b), but the same tolerance as Warbling Vireos. This suggests that the egg-recognition abilities of orioles do not support Rothstein's (1982b) prediction that ejecter species with eggs more divergent in appearance compared to cowbird eggs should be more tolerant of foreign eggs.

Both maculation and size appeared to have an influence on egg recognition in orioles, but a combination of these parameters was not necessary. Interestingly, Bullock's Orioles (*I. bullockii*), closely related to Baltimore Orioles, accepted a few House Finch (*Carpodacus mexicanus*) eggs that differ mainly in size from oriole eggs (Rothstein 1978). Based on these results and those from experimental cowbird parasitism, Rothstein (1978) suggested that size was not important and that ground colour and maculation were more important for egg recognition in Bullock's Orioles. As Rothstein (1978) pointed out for Bullock's Orioles and my results suggest for Warbling Vireos, size is not likely to be a reliable cue for cowbird egg recognition because the

ranges of oriole and cowbird egg dimensions overlap (Table 1.2). Therefore, a size trend here is surprising. Maculation appears to be a much more reliable cue for separating the scrawled eggs of orioles from the heavily-spotted eggs of cowbirds. Baltimore Oriole eggs are only known to vary toward being unmarked (Bent 1958), which would enforce the difference in maculation of oriole and cowbird eggs.

The lack of strong trends in the response of Baltimore Orioles to experimental eggs was somewhat perplexing. This was likely due to the small sample sizes and possibly a response by the orioles to the artificiality of the eggs. The lowest frequency of ejection of experimental eggs was 50 % for the gray-oriole-black-scrawled egg treatment, which was the control oriole-like egg. The majority of other treatments were ejected at frequencies of ≥ 80 % (Table 1.7). If ground colour is important for egg recognition in orioles as Rothstein (1978) suggested, a mismatch in the oriole-like ground colour of experimental eggs may have strongly influenced the response by orioles. Alternatively, Baltimore Orioles may be very intolerant of foreign eggs and capable of recognizing even conspecific eggs. Because of the lack of significant trends, comparisons between the recognition abilities of Baltimore Orioles and other ejectors can only be considered tentative. Additional experimental work on Baltimore Oriole egg recognition would be needed before any solid comparisons can be made. However, the low variability in response to foreign eggs by Baltimore Orioles would require very large sample sizes to yield statistically significant trends. Even the relative abundance of orioles at Delta Marsh would not make such work feasible. Future research should focus on testing the ability of Baltimore Orioles to recognize conspecific eggs.

Summary

Warbling Vireos were less tolerant of foreign eggs than American Robins and showed a tolerance similar to that of Gray Catbirds, which supports Rothstein's (1982b) prediction that ejecter species whose own eggs are more similar to cowbird eggs in appearance should be more intolerant of foreign eggs. Surprisingly, the egg-recognition abilities of orioles do not appear to support Rothstein's (1982b) prediction that ejecter species with more divergent eggs compared to cowbird eggs should be more tolerant of foreign eggs, but these results should be interpreted with caution. As the parameters used for egg recognition by cowbird egg ejecters become known for more species, we begin to understand the selective pressures placed on a generalist parasite's egg type at the beginning of a coevolutionary arms race. Selection by various ejecter species may act in opposite directions on a parasitic egg. Species with immaculate or sparsely-spotted eggs, Warbling Vireos and American Robins (Rothstein 1982b), provide selection against maculation, whereas species with heavily-spotted eggs, Yellow-breasted Chats (*Icteria virens*; Burhans and Freeman 1997) and possibly Brown Thrashers (*Toxostoma rufum*), provide selection for maculation. By comparison, species with a different type of maculation such as Baltimore Orioles may provide selection for scrawls instead of spots. These selective forces are similar to those that have driven host egg mimicry by Common Cuckoos. For example, discrimination by Reed Warblers (*A. scirpaceus*) has produced a cuckoo egg with a greenish ground colour and green or brown spots that matches Reed Warbler eggs (Davies and Brooke 1988), whereas discrimination by Redstarts (*Phoenicurus phoenicurus*) has produced an immaculate-blue cuckoo egg that matches Redstart eggs (Moksnes et al. 1995, Rutilia et al. 2002). However, before host

discrimination could drive the evolution of a mimetic egg in Brown-headed Cowbirds, host specialization on a single host species or small group of species with a similar egg type would be required. Experiments on the parameters of egg recognition required by other ejectors of cowbird eggs will reveal the full extent of divergent selection pressures placed on the appearance of cowbird eggs.

CHAPTER 2. THE ROLE OF EGG SHAPE IN EGG RECOGNITION IN AMERICAN ROBINS AND GRAY CATBIRDS

INTRODUCTION

Various selection pressures have influenced the shapes of birds' eggs. Because greater egg volume may increase reproductive success (Williams 1994), egg shape in some species or individuals appears to reflect the largest volume that will pass through a finite pelvis (Smart 1991, Encabo et al. 2002) or that will allow an optimal arrangement of eggs for a given clutch size to facilitate proper incubation (Andersson 1978, Barta and Székely 1997; but see Walters 2000, Encabo et al. 2001, Johnson et al. 2001). The spherical shape of some eggs increases strength to resist breakage by incubating parents (Barta and Székely 1997) and egg puncturing by conspecifics, i.e. Marsh Wrens (*Cistothorus palustris*; Picman et al. 1996), and hosts of obligate brood parasites (see below and Chapter 4). Common Murres (*Uria aalge*) lay pyriform eggs that roll in an arc, which prevents them from falling off the edge of cliff nests (Tschanz et al. 1969). The necessity to turn eggs during incubation (Deeming 1991) and the requirements for certain physiological conditions for embryonic development may influence egg shape (Smart 1991). In addition, egg shape is related to female age and body mass or size (Warham 1990, Olsen et al. 1994, Encabo et al. 2002) and may be limited by the morphology of the oviduct or pelvis (Warham 1990, Smart 1991). Thus, for a given species, egg shape likely is a compromise between the physical constraints of eggshell formation and the selection pressures for incubation efficiency and survival.

The eggshells of obligate brood parasites are stronger than those of their non-parasitic relatives (Spaw and Rohwer 1987, Rahn et al. 1988, Picman 1989, Brooker and Brooker 1991, Picman and Pribil 1997). The strong shells of brood parasites' eggs appear to be an adaptation to increase puncture resistance for discriminating hosts and may force an evolutionary equilibrium with hosts (Spaw and Rohwer 1987, Chapter 4; but see Blankespoor et al. 1982, Rothstein 1990, Brooker and Brooker 1991 for alternative hypotheses). Increased strength in most species is due to a thicker eggshell (Hoy and Ottow 1964, Blankespoor et al. 1982, Spaw and Rohwer 1987, Rahn et al. 1988, Picman 1989, Brooker and Brooker 1991) or a higher eggshell density (Picman and Pribil 1997). However, an additional aspect of eggshell strength in cowbirds (*Molothrus spp.*) and cuckoos in the genus *Clamator* is the more spherical shape of their eggs (Hoy and Ottow 1964, Picman 1989, Brooker and Brooker 1991). Cowbirds are the only species whose egg shapes in comparison to their hosts has been investigated in detail. Picman (1989) found that the eggs of five cowbird species were significantly rounder than those of 50 common host species of the Brown-headed Cowbird (*M. ater*). This subtle difference in egg shape between the eggs of some brood parasites and their hosts may provide an additional parameter for egg recognition by hosts that can recognize and reject foreign eggs. Thus, the shape of a brood parasite's egg may represent a compromise of conflicting selection pressures from host discrimination, the need for strength to resist punctures, and the ability of the embryo to hatch (Picman 1997, Honza et al. 2001).

The influence of egg parameters, such as size, ground colour and maculation on egg recognition have been thoroughly addressed for a few species that reject parasitic

eggs (Rothstein 1982b, Chapter 1), but the influence of shape has not been fully investigated in rejecter species. Rothstein (1982b) suggested that shape was not a factor in egg recognition, citing examples (e.g. Poulsen 1953, Tschanz 1959) that dealt mainly with experiments on gulls (*Larus* spp.) and other waterbirds. Shape had little influence on egg recognition in most of these species (Poulsen 1953, Tschanz 1959), but most also have limited ability to recognize their eggs (Underwood and Sealy 2002) and are not subject to brood parasitism. In addition, Herring Gulls (*Larus argentatus*) showed some ability to differentiate between egg-shaped and odd-shaped objects and those with rounded versus sharp edges (Baerends and Drent 1982). Subsequent studies on hosts of brood parasites have provided some evidence to suggest that shape may play a role in egg recognition.

Alvarez et al. (1976) examined the influence of shape on egg recognition in Eurasian Magpies (*Pica pica*), the primary host of the Great Spotted Cuckoo (*C. glandarius*) in Europe (Soler 1990). Eurasian Magpies are known to reject non-mimetic and mimetic eggs, but the frequency of rejection varies geographically (Alvarez and Arias de Reyna 1974, Soler et al. 1999). Alvarez et al. (1976) added three wooden models that varied in shape to magpie nests (Table 2.1), whereas volume, mass and colour pattern were similar to real magpie eggs. Conspecific magpie eggs were added to other nests as a control. Magpies rejected all three wooden models sooner than the control eggs and spherical and cubical models were rejected sooner than the egg-shaped model. Thus, magpies recognize and reject odd-shaped objects and their discrimination against spherical models suggests they may respond to the more spherical shape of a cuckoo egg.

Table 2.1. Objects experimentally added to nests to determine the influence of shape on egg recognition in previous studies.

Alvarez et al. (1976)	Ortega and Cruz (1988)	Ortega et al. (1993)
(real) conspecific eggs	pom-pom	Dowel
artificial host egg	smooth bead ^{a, b}	bead w/ filled hole
sphere	bumpy bead ^a	bead w/hole ^b
cube	oblong shape ^{a, b}	Star
	Star	

^a These objects had holes through them. Objects with holes may elicit the same response as broken eggs (e.g. Kemal and Rothstein 1988).

^b There were two sizes of these objects, large and small.

Ortega and Cruz (1988) examined the role of shape in egg acceptance by Red-winged Blackbirds (*Agelaius phoeniceus*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), species known to accept Brown-headed Cowbird eggs (Rothstein 1975a, 1982a), although only the former is parasitized regularly. Several odd-shaped objects (Table 2.1) were added to blackbird nests. Red-winged Blackbirds rejected 98 % of these objects and Yellow-headed Blackbirds rejected 100 % of odd-shaped objects. However, both species accepted a significant proportion of real and artificial eggs of various colours and sizes. Only small eggs elicited a few ejections, but the proportion was non-significant.

The role of shape in egg recognition by Red-winged Blackbirds was investigated further by Ortega et al. (1993). Additional odd-shaped models (Table 2.1) were placed in Red-winged Blackbird nests. In contrast to Ortega and Cruz (1988), some odd-shaped models were accepted. Dowels and beads with filled holes were accepted, whereas stars and beads with holes were ejected. Ortega et al. (1993) suggested that beads with holes were ejected because they were perceived as damaged eggs. Simulated broken eggs are ejected by Red-winged Blackbirds and several other species (Kemal and Rothstein 1988, Sealy and Lorenzana 1998). Thus, Red-winged Blackbirds may respond only to shapes that differ from an egg shape, such as stars.

These studies suggest that shape may play a role in egg-recognition behaviour. One ejector of cuckoo eggs and two accepters of cowbird eggs used shape as a cue to recognize and reject odd-shaped objects from their nests. However, all three studies tested shapes that differed drastically from real eggs and did not examine differences in actual shape and how they may influence egg recognition. Ability to recognize objects

shaped like a star or cube may represent a manifestation of nest-sanitation behaviour whereby individuals remove fecal sacs or debris from the nest (Rothstein 1975a, Ortega and Cruz 1988, Moskát et al. 2003). Nest sanitation is the most likely explanation for non-egg object recognition in Red-winged Blackbirds and Yellow-headed Blackbirds (Ortega and Cruz 1988) because large-scale clutch manipulations have shown that they cannot recognize their own eggs (Rothstein 1982a, Sealy unpublished data). In addition, Ortega and Cruz (1988) and Ortega et al. (1993) did not control for differences in object volume or mass and used objects with holes that may have been perceived as broken eggs (Ortega et al. 1993; see Kemal and Rothstein 1988). Therefore, further work is needed to understand fully the role of shape in egg recognition in hosts of brood parasites.

In this study, I examined the effect of subtle variations in egg shape, reflective of the more spherical shape of cowbird eggs, on egg-recognition behaviour in American Robins (*Turdus migratorius*) and Gray Catbirds (*Dumetella carolinensis*). Both of these species eject cowbird eggs (Rothstein 1975a) and possess true egg recognition, i. e. recognize their own egg types (Rothstein 1982a). In addition, the responses of robins and catbirds to egg-shaped models were compared to several odd-shaped objects.

METHODS

Fieldwork was conducted at Delta Marsh, Manitoba (50° 11' N, 98° 23' W), on the properties of the University of Manitoba Field Station, Delta Waterfowl and Wetlands Research Station, Portage Country Club, private cottage owners and on the Bell Estate (see MacKenzie 1982, Mackenzie et al. 1982 for description of the study site and Sealy 1980 for a map of the area). From May to July 2000, I located and monitored American

Robin and Gray Catbird nests, which were concentrated throughout the dune-ridge forest that separates the extensive Delta Marsh from Lake Manitoba.

I added a series of objects to nests that differed only in shape from the host eggs for catbirds, but differed in shape and ground colour for robins (Tables 2.2, 2.3; Figure 2.1A and B). Ground colour, volume and mass of these objects were controlled by matching them to the characteristics of real robin (except ground colour) and catbird eggs. I did not expect robins to reject objects that differed only in shape because robins require a difference in at least two parameters before rejecting a foreign egg (Rothstein 1982b). Thus, objects with a white ground colour were used for robin experiments to provide a second parameter. Objects were added to nests that ranged from the shape of an artificial robin or catbird egg, the control, and differed along a gradient to odd-shaped objects (Tables 2.2, 2.3; Figure 2.1A and B). All objects were made of wood or plaster and painted with non-toxic, acrylic paints (Folk Art Acrylic Paint by Plaid®; colours and product numbers to follow). A final coat of non-toxic, acrylic varnish (Liquitex® Acrylic Matte Medium) was applied to all objects to eliminate any potential difference in the gloss of objects made of wood or plaster. Objects added to robin nests were painted white (Wicker White 901). For catbird experiments, objects were painted blue-green (a 5:5:1 mixture of Teal 405, Green 408, and True Blue 401) to match the colour of catbird eggs. Egg-shaped objects were made of plaster cast from silicone molds following Rothstein's (1970) technique. Plaster molds for the control eggs for each species were made from a real robin egg and a real catbird egg. Other plaster molds were made from eggs of other species that matched the dimensions of the rounded eggs and from objects created from modeling clay. As artificial plaster eggs were slightly heavier than real eggs

Table 2.2. Mean (\pm SE) measurements (mm), volume (cm^3) and mass (g) of objects used in shape experiments on American Robins.

Object	n	Length	Width	Volume ^a	Mass
host egg ^b	304 ^c	28.76 \pm 0.08	20.52 \pm 0.04	6.1 \pm 0.03	6.2 \pm 0.04
control	16	28.86 \pm 0.05	20.09 \pm 0.02	5.9 \pm 0.01	6.2 \pm 0.14
pointed	14	34.65 \pm 0.02	18.09 \pm 0.03	5.7 \pm 0.02	6.3 \pm 0.10
rounded	19	25.52 \pm 0.03	21.08 \pm 0.02	5.7 \pm 0.01	6.5 \pm 0.08
sphere	14		22.47 \pm 0.02	5.9 \pm 0.02	6.6 \pm 0.07
cylinder	16	29.02 \pm 0.08	16.05 \pm 0.02	5.9 \pm 0.02	6.5 \pm 0.04
rectangle ^d	16	27.42 \pm 0.06	14.62 \pm 0.04	5.9 \pm 0.02	6.6 \pm 0.05
			14.64 \pm 0.04		
cube ^d	18	18.00 \pm 0.02	18.01 \pm 0.03	5.8 \pm 0.02	6.2 \pm 0.03
			18.04 \pm 0.02		

^a Volume of egg-shaped objects was calculated from the equations $\text{Volume} = K_v * LB^2$ (Hoyt 1979), where K_v is a species-specific constant, L is length, and B is breadth or width. For robins, $K_v = 0.504$, but K_v for odd egg shapes is not known. The K_v for robins was used for these because this most closely approximated the correct egg shape out of all species whose K_v is known. Volume of odd-shaped objects was calculated using the equations: sphere $V = 4/3\pi r^3$, cylinder $V = \pi r^2 h$, rectangle and cube $V = LWH$.

^b American Robin measurements are from eggs in nearly all experimental nests in 2000. Ranges were 24.19-33.21 mm for length, 18.04-22.21 mm for width, 4.5-7.7 cm^3 for volume and 4.2-8.4 g for mass.

^c For mass, $n = 300$.

^d The two widths shown represent width and height of the rectangular and cubic objects.

Table 2.3. Mean (\pm SE) measurements (mm), volume (cm^3) and mass (g) of objects used in shape experiments on Gray Catbirds.

Object	N	Length	Width	Volume ^a	Mass
host egg ^b	406	23.62 \pm 0.05	17.55 \pm 0.03	3.7 \pm 0.02	3.7 \pm 0.02
control	18	24.47 \pm 0.02	17.23 \pm 0.02	3.7 \pm 0.01	4.1 \pm 0.05
pointed	15	29.39 \pm 0.04	15.53 \pm 0.03	3.6 \pm 0.02	3.8 \pm 0.07
rounded	18	22.18 \pm 0.04	18.17 \pm 0.02	3.7 \pm 0.01	4.0 \pm 0.05
sphere	16		19.09 \pm 0.02	3.6 \pm 0.01	4.1 \pm 0.03
cylinder	15	23.60 \pm 0.05	14.53 \pm 0.02	3.9 \pm 0.01	4.0 \pm 0.05
rectangle ^c	18	24.07 \pm 0.07	12.47 \pm 0.03	3.7 \pm 0.02	3.9 \pm 0.03
			12.46 \pm 0.03		
cube ^c	17	15.75 \pm 0.02	15.74 \pm 0.02	3.9 \pm 0.01	3.8 \pm 0.04
			15.74 \pm 0.02		

^a Volume of egg-shaped objects was calculated from the equations $\text{Volume} = K_v * LB^2$ (Hoyt 1979), where K_v is a species-specific constant, L is length, and B is breadth or width. For robins, $K_v = 0.504$, but K_v for catbirds and odd egg shapes is not known. The K_v for robins was used for these because this most closely approximated the correct egg shape out of all species whose K_v is known. Volume of odd-shaped objects was calculated using the equations: sphere $V = 4/3\pi r^3$, cylinder $V = \pi r^2 h$, rectangle and cube $V = LWH$.

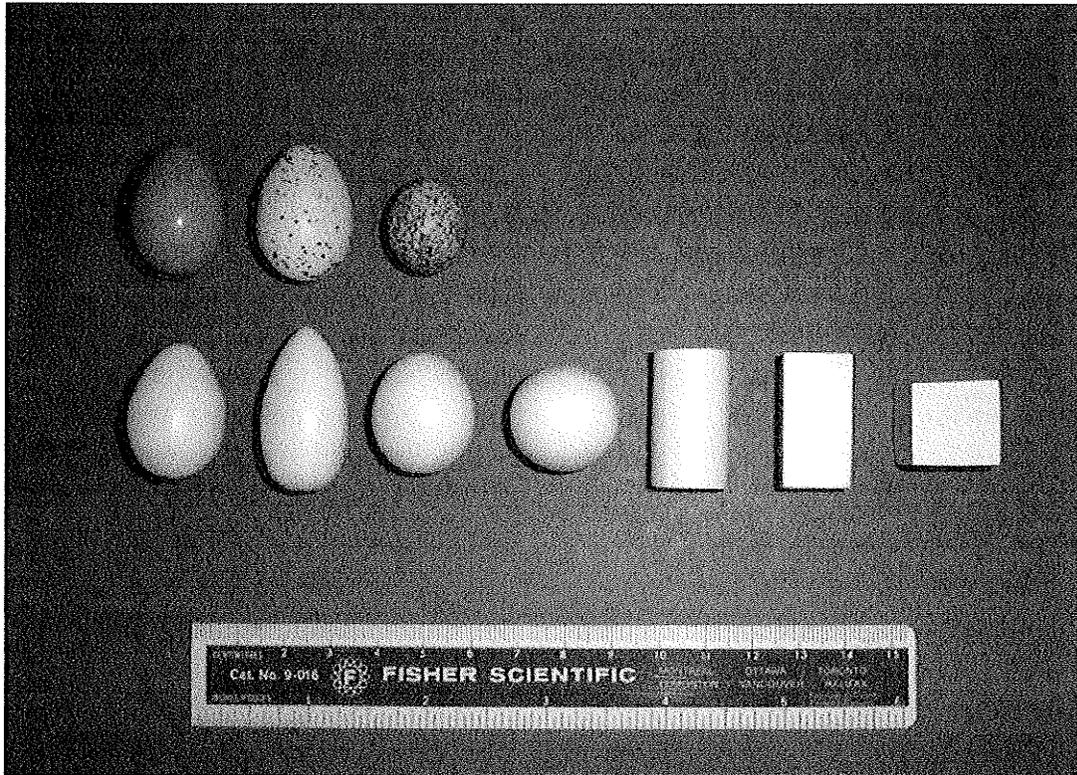
^b Gray Catbird measurements are from eggs in nearly all experimental nests in 2000.

Ranges were 20.83-26.58 mm for length, 15.17-19.03 mm for width, 2.8-4.6 cm³ for volume and 2.5-4.7 g for mass.

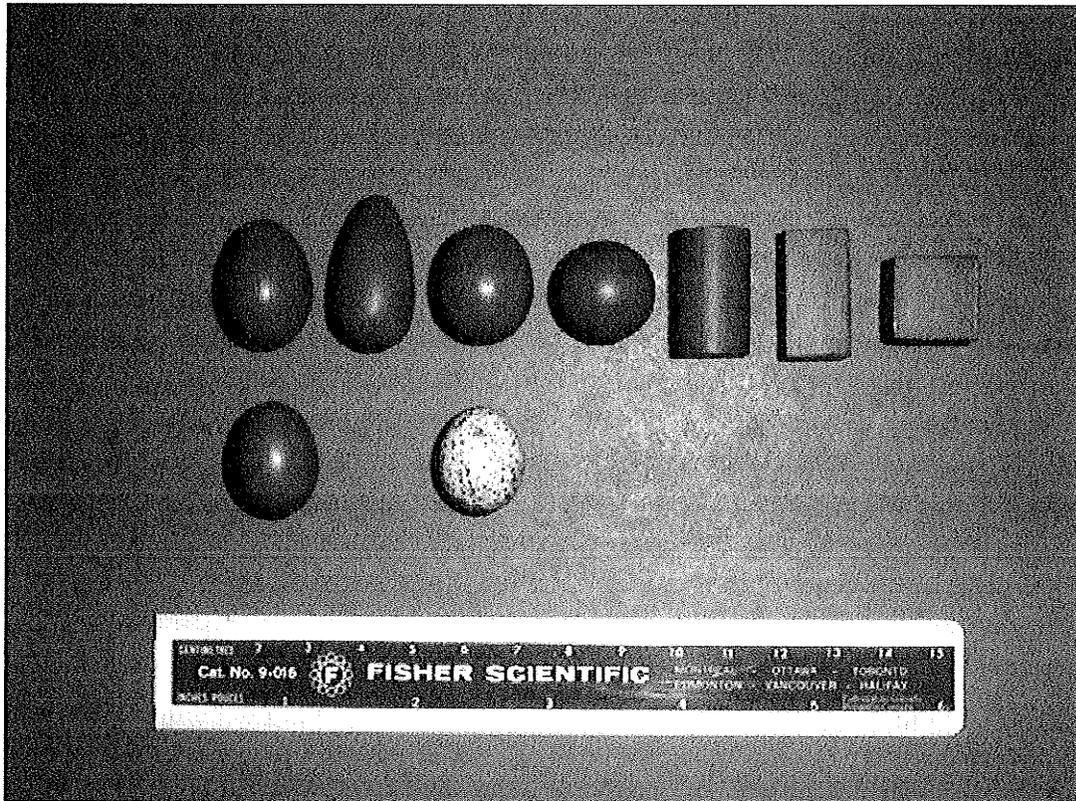
^c The two widths shown represent width and height of the rectangular and cubic objects.

Figure 2.1. Experimental objects added to American Robin (A) and Gray Catbird (B) nests to examine the influence of shape on egg recognition. From left to right (A, bottom row and B, top row), shapes are control, pointed, rounded, sphere, cylinder, rectangle, and cube. In A, top row, from left to right, are a real robin egg, a control egg after a 5-day acceptance, and a real cowbird egg. In B, bottom row, from left to right, are a real catbird egg and a real cowbird egg.

A



B



of the same size (Rothstein 1975a), I added pieces of styrofoam to the plaster during the molding process to adjust the mass of egg-shaped objects. Odd-shaped objects were made of wood and were lighter than real eggs of a similar size. Therefore, I adjusted the mass of wooden objects by inserting steel balls into a hole drilled through each object. Latex wood putty was used to seal in the balls and patch the hole. The resulting mass and volume of experimental objects were similar to the means of real robin and catbird eggs and well within the range of measurements of these two species (Tables 2.2, 2.3). Most hosts accept or reject artificial eggs made of plaster or wood at similar frequencies to real eggs (Rothstein 1975a, Peer et al. 2000).

A single object was added to a robin or catbird nest during laying or incubation. I experimentally parasitized nests throughout the incubation period because the exact day of incubation was not known for all nests at the time of object addition. However, a few nests were avoided that were close to or at the pipping stage. Objects were assigned to nests randomly within each replicate of objects. To maintain similar sample sizes for each object type, individual objects were put back into the pool to be available for experimental parasitism when a nest with that object type was depredated. I monitored nests daily to determine whether the object was rejected and to determine the length of time until rejection. After 5 days, if the undamaged object was still in the nest and the nest was active, an acceptance was recorded. The response to parasitism by nest stage was considered because some hosts respond to cowbird parasitism differently depending on the stage of their nest (Rothstein 1976, Sealy 1995). I determined the nest stage at the time of parasitism by recording egg laying between nest checks or by candling host eggs with a foam tube candler (Lokemoen and Koford 1996). The egg-laying stage was

defined as the day the first egg was laid through the day the penultimate egg was laid, whereas the incubation stage was considered to have begun on the day the last egg was laid. Where possible, all host eggs in a clutch were measured and weighed. Host egg data were used to compare the shape of cowbird and host eggs and to ensure that the volume and mass of eggs from Delta Marsh were similar to those of experimental objects.

Analysis

I used Picman's (1989) simple shape index ($\text{shape} = \text{length}/\text{width}$) to determine whether Brown-headed Cowbird eggs were more spherical than American Robin and Gray Catbird eggs. Measurements of cowbird eggs were from those laid in Yellow Warbler (*Dendroica petechia*), Song Sparrow (*Melospiza melodia*), Red-winged Blackbird, and Brewer's Blackbird (*Euphagus cyanocephalus*) nests at Delta Marsh (Sealy unpublished data, 1988 and 1992). American Robin and Gray Catbird egg measurements were from nests used in the shape experiments. I used the mean shape of the eggs of each clutch for robins and catbirds. Shape index data were log-transformed to meet the assumptions of normality. I used a one-factor analysis of variance (ANOVA) to compare the shape index of cowbirds, robins and catbirds. When significant species differences in shape index were found, I used orthogonal contrasts to compare the shape index of each host species to the cowbird. Probability values were adjusted using Bonferroni corrections for making these two comparisons.

I examined the influence of object shape on the response of hosts by analyzing the binomial (accept or reject) response and, separately, by considering the time until experimental object rejection. The influence of shape on the frequency of object

rejection was tested using a G test or a 7 x 2 Fisher exact test (Schlotzhauer and Littell 1997) where any cell frequencies were less than five. These tests were two-tailed. I further examined the influence of shape by using a 2 x 2 Fisher exact test for each species to compare the frequency of rejection of egg-shaped (rounded eggs, pointed eggs and spheres) and odd-shaped (cubes, rectangles and cylinders) objects. These tests were one-tailed because I predicted that more odd-shaped objects would be rejected than egg-shaped objects.

The time-to-rejection data were examined using survivorship analysis, the LIFETEST procedure in SAS (Everitt and Der 1996), which examined the daily proportion of eggs accepted or "alive" over the 5-day test period. The influence of shape on egg recognition was examined by comparing the survival of objects differing in shape. The influence of nest stage at the time of parasitism was also examined. I further examined the influence of shape by comparing the survival of egg-shaped and odd-shaped objects using Log-rank and Wilcoxon-rank tests to compare survival curves. The Wilcoxon-rank test places more weight on the earlier portion of the survival curve, whereas the Log-rank test places more weight on the later portion of the survival curve.

RESULTS

The egg shape index of Brown-headed Cowbirds, American Robins and Gray Catbirds differed significantly (ANOVA $F_{2, 362} = 98.56$, $P < 0.0001$). Cowbird eggs were significantly more spherical than catbird eggs ($F_1 = 53.86$, $P < 0.001$) and robin eggs ($F_1 = 191.00$, $P < 0.001$; Table 2.4).

Table 2.4. Comparison of egg shape indices (shape = length/width) between Brown-headed Cowbirds and two ejecters, American Robins and Gray Catbirds.

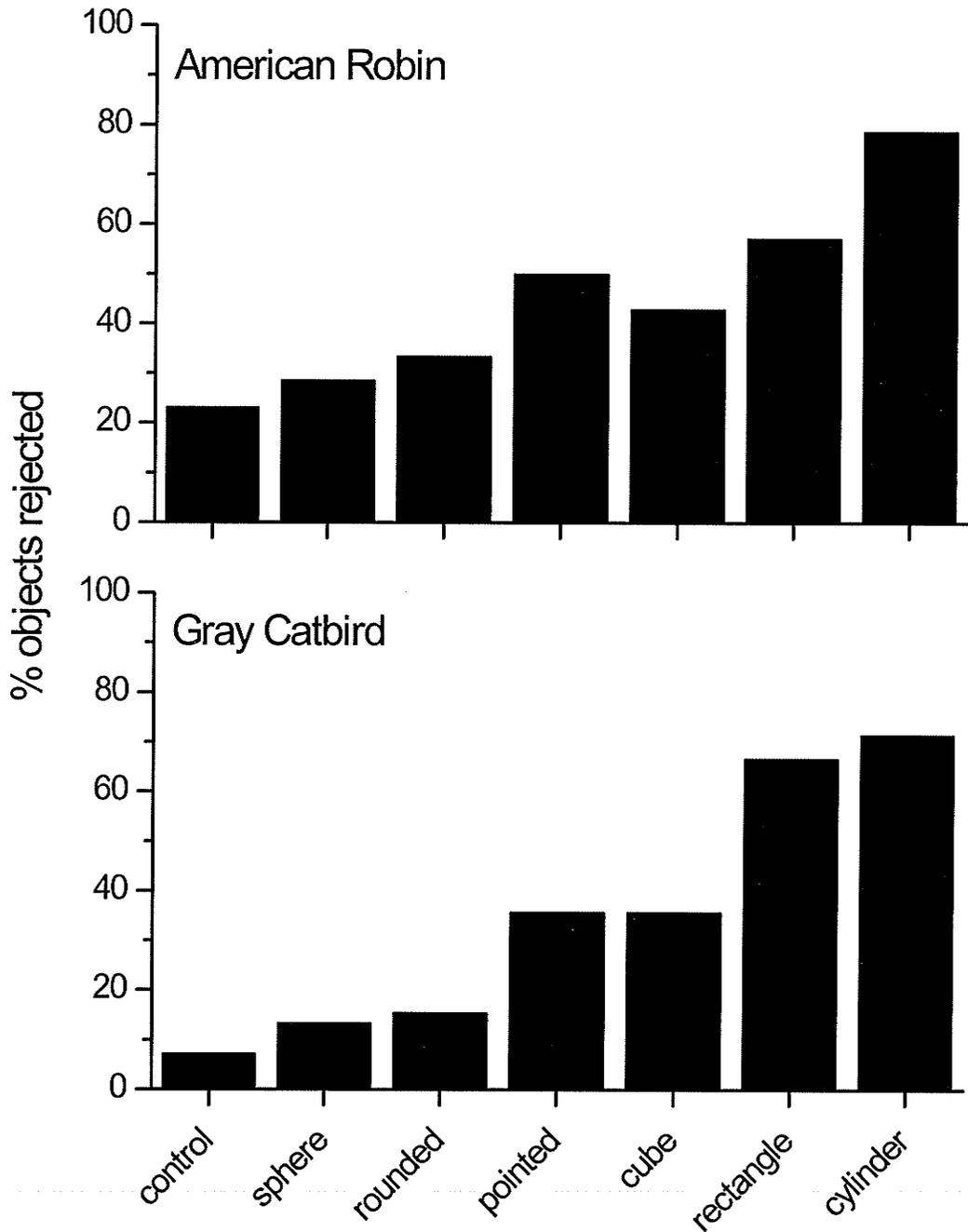
Species	Egg shape index (log)	SE	n
Brown-headed Cowbird	0.109	0.002	170
American Robin	0.147	0.002	96
Gray Catbird	0.129	0.002	99

I experimentally parasitized 113 robin nests and 117 catbird nests, but recorded complete responses at 98 robin nests and 99 catbird nests. The remaining nests were depredated during experiments. I do not believe these data were unduly biased toward rejections because of nests depredated during the 5-day acceptance period. My experimental protocol ensured that sample sizes were similar for all objects and the relatively long time it took for object rejection also would have limited any potential bias. The mean time until object rejection was 2.07 days (± 0.18 SE, $n = 44$) for robins and 2.60 days (± 0.25 SE, $n = 35$) for catbirds. Including those nests depredated after an object was accepted for more than two days (5 robin nests and 10 catbird nests) as acceptances did not change the significance or interpretation of any results.

Robins rejected 44.9 % ($n = 98$) of objects added to their nests and catbirds rejected 35.3 % ($n = 99$) of objects. Ejection was the most common form of rejection by both species, 95.4 % ($n = 44$) of all rejections by robins and 97.1 % ($n = 35$) of all rejections by catbirds. Three experimentally parasitized nests were deserted, two by robins and one by catbirds.

Nest stage did not significantly influence rejection frequency by robins (57.7 %, $n = 26$, rejected during laying versus 50.0 %, $n = 54$, rejected during incubation; Fisher exact test, two-tailed, $P = 0.216$) or catbirds (29.8 %, $n = 57$, rejected during laying versus 42.9 %, $n = 42$, rejected during incubation; Fisher exact test, two-tailed, $P = 0.206$). By contrast, object shape significantly influenced the frequency of rejection by robins ($G = 12.74$, $df = 6$, $P = 0.047$; Figure 2.2) and catbirds (Fisher exact test, two-tailed, $P < 0.001$; Figure 2.2). Robins and catbirds showed similar levels of rejection of each object, although most rejection frequencies were 10 – 15 % higher for robins

Figure 2.2. Response of American Robins and Gray Catbirds to experimental objects added to their nests as measured by proportion of eggs ejected. For robins, $n = 14$ for most objects, except for control eggs ($n = 13$) and rounded eggs ($n = 15$). For catbirds, $n = 14$ for most objects, except for spheres ($n = 15$), rectangles ($n = 15$) and rounded eggs ($n = 13$).



(Figure 2.2). Both species rejected a small proportion of control eggs and a slightly higher but similar proportion of rounded, cowbird-shaped eggs and spherical eggs. A relatively high proportion of pointed eggs was rejected and rejection frequencies increased as shapes progressed away from a traditional egg shape. Overall, significantly more odd-shaped objects (cubes, rectangles and cylinders) were rejected than egg-shaped objects (rounded eggs, pointed eggs and spheres) by robins (Fisher exact test, one-tailed, $P = 0.033$) and catbirds (Fisher exact test, one-tailed, $P < 0.001$; Table 2.5).

Nest stage did not influence object survival in robins (Log-rank test, $\chi^2 = 1.87$, $df = 1$, $P = 0.172$; Wilcoxon-rank test, $\chi^2 = 1.93$, $df = 1$, $P = 0.165$; Figure 2.3A) or catbirds (Log-rank test, $\chi^2 = 2.08$, $df = 1$, $P = 0.150$; Wilcoxon-rank test, $\chi^2 = 2.21$, $df = 1$, $P = 0.137$; Figure 2.3B). By contrast, shape significantly influenced object survival in robin nests (Log-rank test, $\chi^2 = 15.49$, $df = 6$, $P = 0.017$; Wilcoxon-rank test, $\chi^2 = 16.36$, $df = 6$, $P = 0.016$; Figure 2.4) and catbird nests (Log-rank test, $\chi^2 = 32.21$, $df = 6$, $P < 0.0001$; Wilcoxon-rank test, $\chi^2 = 34.64$, $df = 6$, $P < 0.0001$; Figure 2.5). Object survival curves followed trends similar to those for the frequency of object rejection by both robins and catbirds (Figures 2.4, 2.5). A large proportion of control eggs survived over the 5-day test period for both species. Rounded eggs and spheres showed slightly lower survival in robin nests, whereas survival of these objects in catbird nests was similar to control eggs. Object survival decreased for both species as object shape that increasingly differed from a traditional egg shape (Figures 2.4, 2.5). Overall, egg-shaped objects had significantly higher survival curves compared to odd-shaped objects for robins (Log-rank test, $\chi^2 = 4.80$, $df = 1$, $P = 0.029$; Wilcoxon-rank test, $\chi^2 = 5.36$, $df = 1$, $P = 0.021$; Figure 2.6A) and

Table 2.5. Frequency of rejection of egg-shaped and odd-shaped objects by American Robins and Gray Catbirds.

Species	Egg Category	Rejected	Accepted	% Rejected
American Robin	egg-shaped	16	27	37.2
	odd-shaped	25	17	59.5
Gray Catbird	egg-shaped	9	33	21.4
	odd-shaped	25	18	58.1

Figure 2.3. Survival curves by nest stage for objects added to American Robin (A) and Gray Catbird (B) nests.

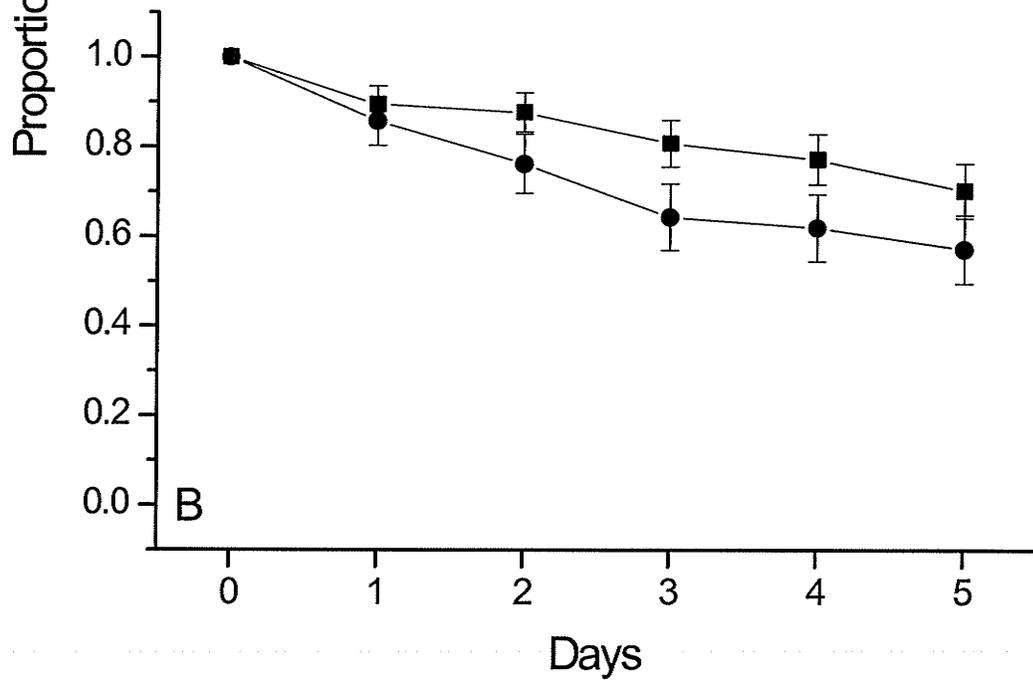
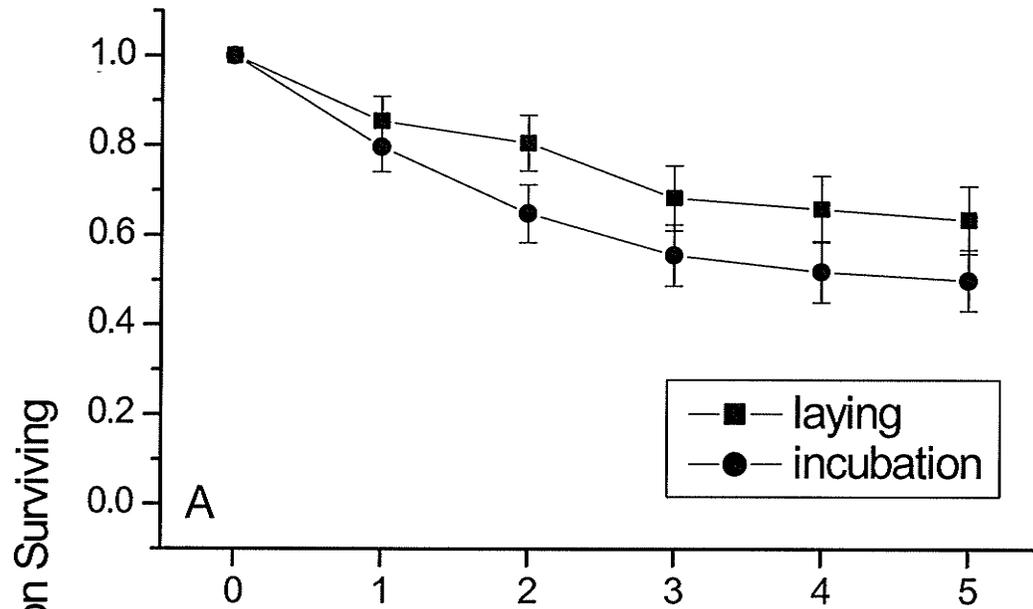


Figure 2.4. Survival curves for experimental objects added to American Robin nests.

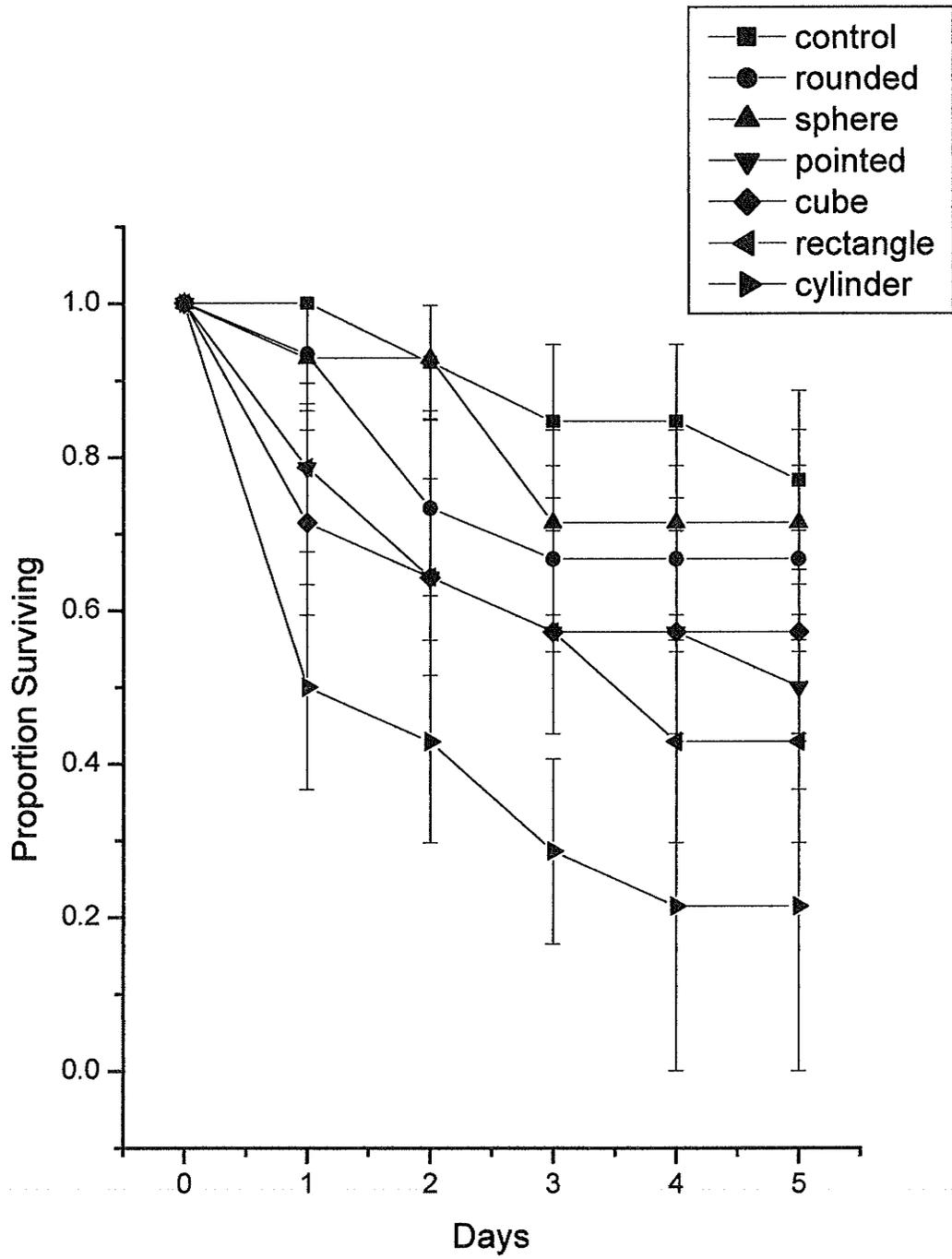


Figure 2.5. Survival curves for experimental objects added to Gray Catbird nests.

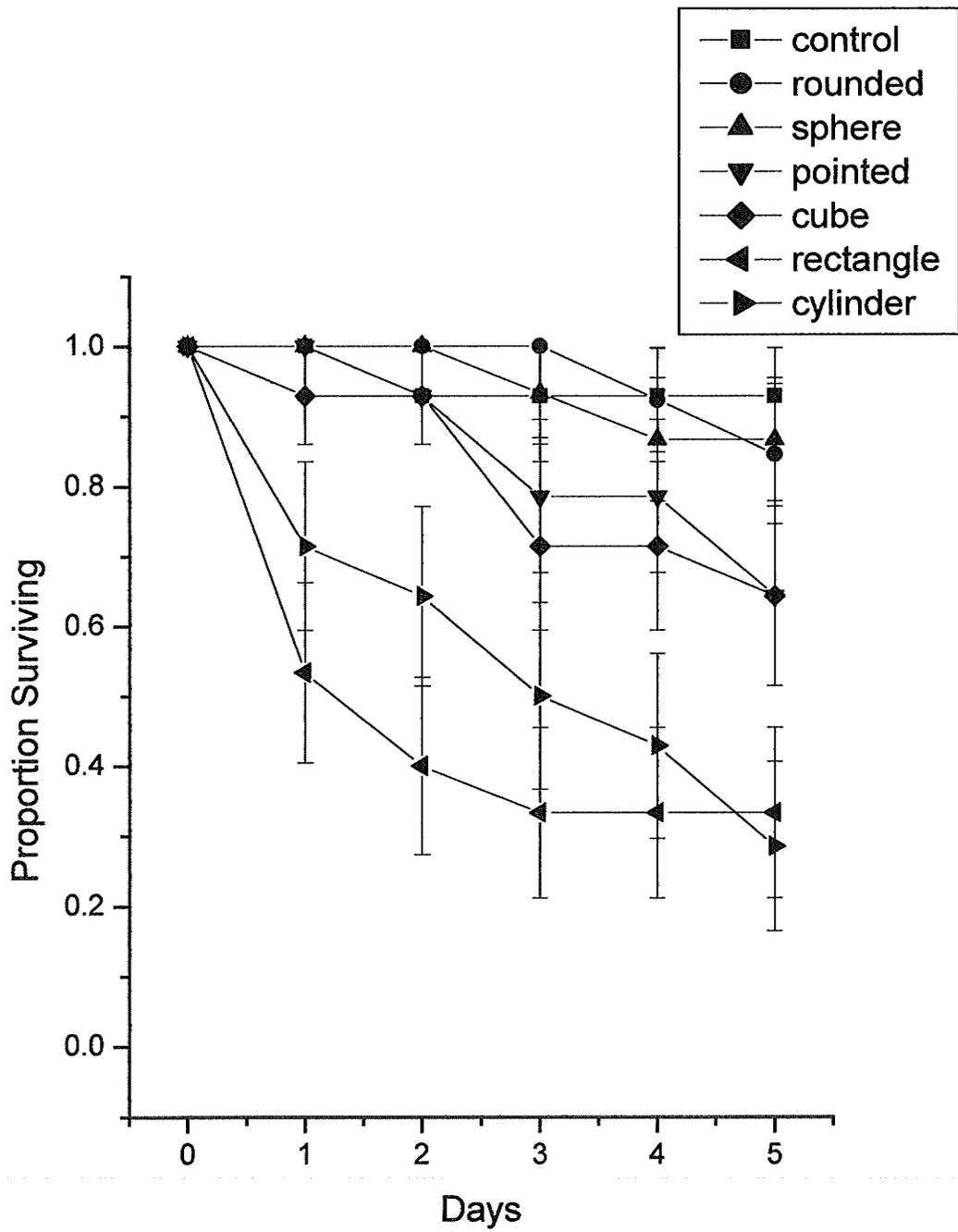
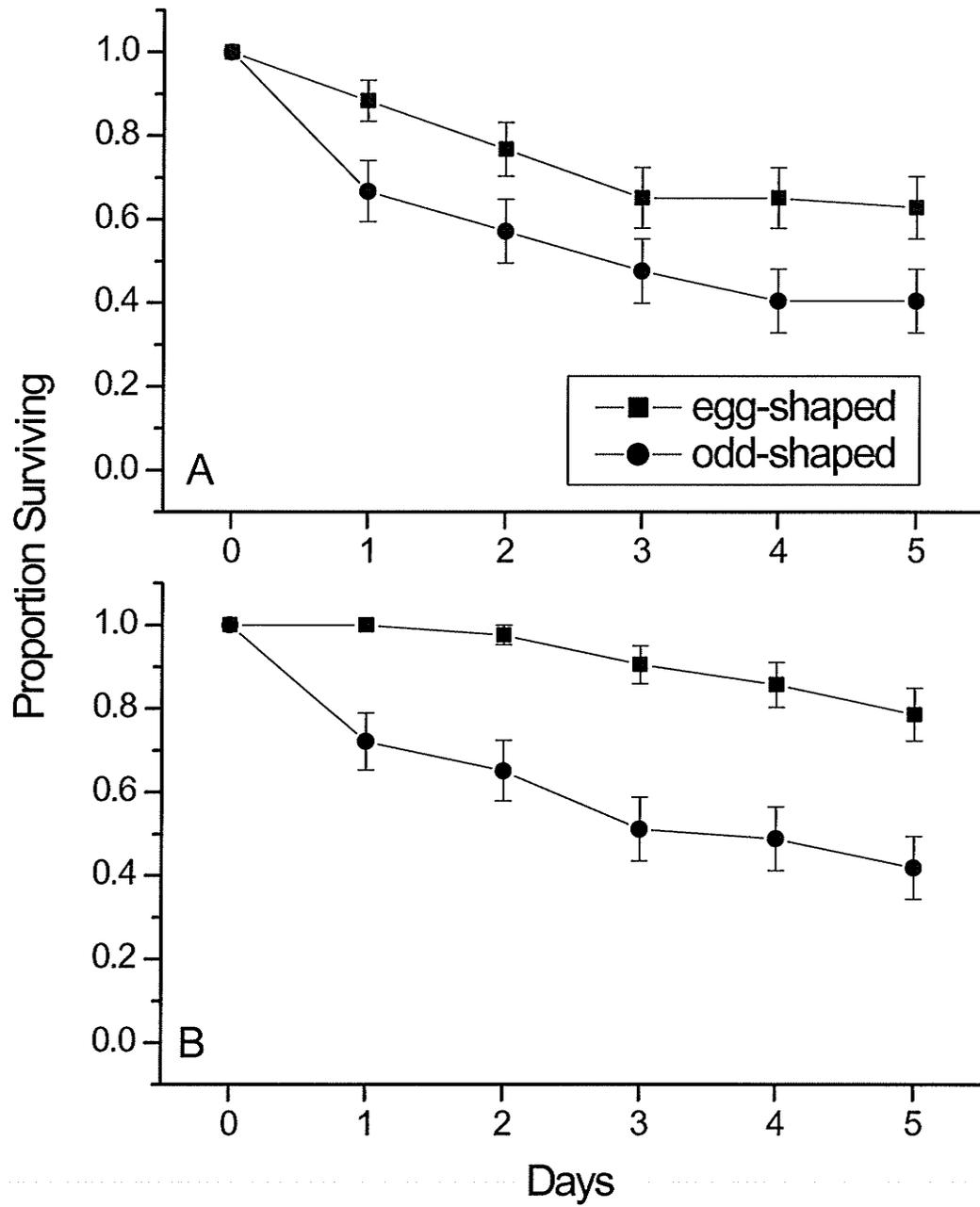


Figure 2.6. Survival curves for egg-shaped and odd-shaped objects added to American Robin (A) and Gray Catbird (B) nests.



catbirds (Log-rank test, $\chi^2 = 14.24$, $df = 1$, $P < 0.0001$; Wilcoxon-rank test, $\chi^2 = 16.20$, $df = 1$, $P < 0.0001$; Figure 2.6B).

DISCUSSION

Brown-headed Cowbird eggs were more spherical than the eggs of two rejecters, American Robins and Gray Catbirds. This supports Picman's (1989) previous work that the eggs of parasitic cowbirds were more spherical than those of 50 common Brown-headed Cowbird hosts, only two of which were ejecters. Thus, a potential shape cue for Brown-headed Cowbird egg recognition exists for at least the two rejecter species considered here.

Shape influenced egg recognition and rejection in both robins and catbirds. However, the rounder brood parasite's egg did not appear to induce egg rejection in either species. Rounded eggs, shaped like a parasite's egg, and spheres, an extreme form of a parasite's egg, were rejected at frequencies similar to that of control eggs. Of all the egg-shaped objects, pointed eggs, which presented a shape in the opposite direction from a parasite's egg shape, were rejected quickly and at relatively high frequencies. The stronger response to pointed eggs may have been related to their extreme length in comparison to control eggs (5.8 mm for robins and 4.9 mm for catbirds; see also Tables 2.2, 2.3). Nevertheless, subtle differences in egg shape did not elicit a strong rejection response by robins and catbirds. Thus, the shape of a Brown-headed Cowbird's egg does not appear to be used as a cue for egg recognition, which supports Rothstein's (1982b) prediction, and host discrimination does not appear to represent a potential conflicting selection pressure on the shape of cowbird eggs.

Robins and catbirds showed remarkably similar responses to the variously-shaped objects. Both species infrequently rejected traditional egg-shaped objects and these objects survived longer. Rejection frequencies increased and survivorship decreased as object shapes became increasingly different in shape from control eggs. Over the two main groups of experimental objects, fewer egg-shaped objects were rejected and these took longer to be rejected than odd-shaped objects. A similar result was recorded for Eurasian Magpies, a rejecter of cuckoo eggs, which rejected odd-shaped objects faster than a host-like control egg (Alvarez et al. 1976).

For most objects, robins rejected 10 to 15 % more objects than catbirds rejected. This greater response to artificial objects by robins may have been due to the ability of some individuals to reject objects that differed in only one parameter. I used a white ground colour on objects used to test robins because Rothstein (1982b) found that most robins rejected foreign eggs only when they differed in two parameters. Nevertheless, approximately 20 % of robins rejected foreign eggs that differed in only a single parameter (Rothstein 1982b). This level of rejection is similar to the proportion of control eggs (that differed only in ground colour) rejected in this study. Alternatively, some rejections may have been due to a buildup of frass on some of the objects after a few days in the nest (see Figure 2.1A) from the sometimes superabundant midges (Diptera: Chironomidae) at Delta Marsh. These "spots" may have provided the crucial second parameter required by robins to be able to discriminate between their own eggs and a foreign egg.

The abilities of robins and catbirds to detect differences in shape appear to be more refined than those of species that accept of Brown-headed Cowbird parasitism that

have been tested with somewhat similar shapes. Red-winged Blackbirds ejected odd-shaped objects that were more divergent in shape than those used in this study (see Table 2.1), but accepted nearly all cylindrical objects added to their nests (Ortega et al. 1993). Red-winged Blackbirds and Yellow-headed Blackbirds also ejected a large proportion of spherical and oblong objects, but these had holes in them and the birds likely responded to them as they would to broken eggs (Ortega and Cruz 1988, Ortega et al. 1993). In addition, another accepter species, the Prothonotary Warbler (*Protonotaria citrea*), accepted most cubes during egg laying (Hoover 2003). By contrast to these accepters, robins and catbirds rejected a higher proportion of odd-shaped objects (i.e. cylinders and cubes). Rejection of highly divergent, odd-shaped objects appears to be a manifestation of nest-sanitation behaviour where accepter and rejecter individuals remove objects that look like debris from their nests (e.g. Moskát et al. 2003). Many species of birds remove fecal sacs, egg shells, broken eggs, and other debris from their nests because this material may attract predators or interfere with incubation (Tinbergen et al. 1962, Kemal and Rothstein 1988, Petit et al. 1989). Based on my results, rejecter species apparently have a lower threshold than accepter species for the shape of objects that they may consider as nest debris. However, such conclusions are tentative because the rejecters and accepters considered are not closely related. For a strong comparison of shape-recognition abilities and nest-sanitation behaviour of accepters and rejecters, experimental parasitism of closely related accepters and rejecters is needed.

Although the results of my study do not implicate host discrimination as a potential conflicting selection pressure on the shape of Brown-headed Cowbird eggs, other research suggests that egg recognition and rejection present a potential selection

pressure on egg shape for other species of brood parasites. Unlike robins and catbirds, Eurasian Magpies, a host of the Great Spotted Cuckoo, recognized and ejected spheres significantly faster than control shapes (Alvarez et al. 1976). *Clamator* cuckoos, such as the Great Spotted Cuckoo, lay more spherical eggs than their hosts (Brooker and Brooker 1991). The ability of magpies to respond to spherical objects suggests they may also respond to the more spherical shape of Great Spotted Cuckoo eggs. In addition, there is circumstantial evidence for possible egg shape mimicry in other cuckoos. Brooker and Brooker (1991) found that cuckoos of the genera *Cuculus*, *Cacomatis* and *Chrysococcyx* (*Cuculus* group) lay eggs that are less spherical than most of their hosts and concluded the eggs of these cuckoos were not as strong as those of other brood parasites because of this less spherical shape. However, Picman and Pribil (1997) found that cuckoos of the *Cuculus* group increased the strength of their eggs with a higher eggshell density that other parasitic and non-parasitic cuckoos lacked. This and the lack of a spherical shape, suggest that egg shape in the *Cuculus* group may have been constrained by some other selection pressure, such as host discrimination, that may have resulted in egg shape mimicry.

Finally, there is evidence for egg shape mimicry in the Screaming Cowbird (*M. rufoaxillaris*), a host specialist that parasitizes mainly the Bay-winged Cowbird (*M. badius*). In some areas of Argentina, the eggs of the Screaming Cowbird match those of the Bay-winged Cowbird in size and shape (Jaramillo 1993). Where the match is poor in other parts of Argentina, Screaming Cowbird eggs are rejected more often than host eggs from Bay-winged Cowbird nests. Because Bay-winged Cowbirds are accepters, Jaramillo (1993) concluded that egg mimicry is likely due to egg rejection by other

competing female Screaming Cowbirds. Although there is little support for parasite competition selecting for egg mimicry in cuckoos (Underwood and Sealy 2002), this would be an ideal system for parasite competition to select for egg mimicry because of the high frequencies of multiple parasitism and the egg puncture/ejection behaviour expressed by Screaming Cowbirds (Fraga 1998). These intriguing possibilities for egg shape as a factor in egg recognition and mimicry will require future studies before the importance of egg shape can be fully understood for all brood parasites.

Summary

The shape of Brown-headed Cowbird eggs was more spherical than that of American Robins and Gray Catbirds. This provides a potential parameter for use in egg recognition by rejecter species. However, subtle differences in egg shape, including a more spherical shape, did not appear to influence egg recognition and rejection by robins and catbirds. This supports Rothstein's (1982b) prediction that egg shape is not used as a cue for egg recognition. In general, egg recognition by robins and catbirds was influenced by object shape and more odd-shaped objects were rejected than egg-shaped objects. Rejection of these odd-shaped objects most likely represents a manifestation of nest-sanitation behaviour. By comparison to a few accepters of cowbird eggs (Ortega and Cruz 1988, Ortega et al. 1993, Hoover 2003), robins and catbirds appear to be more intolerant of odd-shaped objects than accepters. Further experiments are needed on more closely related accepters and rejecters to confirm this trend. Finally, although egg shape may not be an important component of egg recognition for Brown-headed Cowbird hosts, some evidence suggests a shape cue may be used by hosts of other cowbirds and Old World cuckoos.

CHAPTER 3. THE POTENTIAL INFLUENCE OF ULTRAVIOLET LIGHT REFLECTANCE IN EGG RECOGNITION BY HOSTS OF THE BROWN- HEADED COWBIRD

INTRODUCTION

Obligate brood parasites impose large reproductive costs on many of their hosts (Wyllie 1981, Payne 1997, Ortega 1998, Lorenzana and Sealy 2001, General Introduction). These costs represent strong selection pressures favouring the evolution of host defences against parasitism. Host defences involve either defending the nest to thwart parasitism (Sealy et al. 1998) or rejecting parasitism after the nest has been parasitized (Rothstein 1975a, Davies and Brooke 1988). Rejection behaviour consists of ejecting the parasitic egg (Rothstein 1975a), burying the parasitic egg under nest material (Sealy 1995) and deserting a parasitized nest (Hill and Sealy 1994, Hosoi and Rothstein 2000). Some brood parasites, such as Common Cuckoos (*Cuculus canorus*), have evolved host egg mimicry as a counter defence to egg rejection (Brooke and Davies 1988, Moksnes and Røskaft 1995, Underwood and Sealy 2002), which in turn favours additional host defences against mimetic eggs (Davies and Brooke 1998). Despite the well-developed rejection behaviour of some hosts and the coevolutionary interaction between some brood parasites and their hosts, many host species accept the reproductive cost of parasitism.

To explain why so many hosts accept parasitic eggs, two major hypotheses have been proposed: the evolutionary equilibrium hypothesis and the evolutionary lag hypothesis (see Chapter 4 for a full discussion). The evolutionary equilibrium hypothesis

proposes that egg rejection is not an optimal response to parasitism because the costs incurred during rejection, such as damage to host eggs or the loss of time and energy when nests are deserted, outweigh the costs of accepting parasitism (Rohwer and Spaw 1988, Lotem and Nakamura 1998). By contrast, the evolutionary lag hypothesis proposes that egg rejection is an adaptive response to parasitism that has not evolved in most species due to a short duration of sympatry with parasites or a lack of genetic variability (Rothstein 1975a, 1990; Davies and Brooke 1989a). Recently, Cherry and Bennett (2001) proposed an alternative hypothesis suggesting that acceptance of non-mimetic eggs by hosts may be due to host egg matching or mimicry in the ultraviolet (UV) portion of the spectrum, which is beyond the limits of human visual perception.

Many birds can see in the near-ultraviolet range, 300-400 nm (Kreithen and Eisner 1978, Goldsmith 1980, Chen et al. 1984), with passerines having peak UV sensitivity at about 365 nm (Cuthill et al. 2000). By contrast, most mammals, including humans, cannot detect UV light (Jacobs 1992, 1993; Tovée 1995). The discovery of UV vision in birds has uncovered a large potential for new signals previously unknown to researchers. UV vision in birds has been proposed for use in orientation, foraging and sexual selection (Bennett and Cuthill 1994, Cuthill et al. 2000). Several recent studies have shown that birds make behavioural decisions based on UV signals. Many fruits reflect UV light but green foliage does not, suggesting that fruits will stand out from their background (Burkhardt 1982, Willson and Whelan 1989). Altshuler (2001) found that UV-reflecting fruits were associated with dispersal by birds and rodents and that fruit removal was reduced when UV light was removed. However, other studies have found no influence of UV reflectance on fruit preferences in birds (Willson and Whelan 1989,

Honkavaara et al. 2002). In addition to the importance of UV signals to frugivores, Eurasian Kestrels (*Falco tinnunculus*) preferentially foraged in areas with vole urine and feces that naturally reflect UV light (Viitala et al. 1995). Mate choice is influenced significantly by the UV light-reflecting plumage of several species, such as Zebra Finches (*Taeniopygia guttata*) and Bluethroats (*Luscinia svecica*; Bennett et al. 1996, Andersson and Amundsen 1997). Interestingly, a few birds previously believed to be sexually monomorphic in plumage, such as Blue Tits (*Parus caeruleus*) and European Starlings (*Sturnus vulgaris*), have been found to be dimorphic when the UV reflectance of their plumage was measured (Andersson et al. 1998, Hunt et al. 1998, Cuthill et al. 1999). The importance of UV signals in avian mate choice and foraging has received much attention, whereas the importance of UV signals in relation to brood parasitism is just beginning to be investigated.

Cherry and Bennett (2001) tested their UV matching hypothesis by examining host egg matching by Red-chested Cuckoos (*C. solitarius*) as assessed by UV-visible spectrophotometry and human observers. Although their sample of parasitized nests was small, human observers documented relatively poor host egg matching for most parasitized clutches. However, spectrophotometry revealed evidence for host egg matching in the UV range providing evidence for their hypothesis. Cherry and Bennett (2001) suggested that the lack of egg rejection by Red-chested Cuckoo hosts may be due to egg matching in the UV range and that UV signals may be important for cuckoo egg recognition.

Could the UV matching hypothesis (Cherry and Bennett 2001) explain the dichotomy of responses to parasitism by hosts of the Brown-headed Cowbird (*Molothrus*

ater)? Brown-headed Cowbirds parasitize the nests of more than 200 species of birds in North America (Friedmann and Kiff 1985), and there is little apparent evidence for host egg matching in the visible portion of the spectrum (Underwood and Sealy 2002). Even though cowbird eggs appear non-mimetic in comparison to most host eggs (but see Peer et al. 2000), the majority of hosts accept the cost of parasitism (Rothstein 1992, Davies 1999, Appendix 1). Currently, the results of most studies support the evolutionary lag hypothesis as an explanation for host acceptance. Small cowbird hosts can eject cowbird eggs at a cost lower than that of accepting and raising a cowbird (Røskaft et al. 1993, Sealy 1996, Sealy et al. 2000, Lorenzana and Sealy 2001, Chapter 4). In addition, hosts sympatric with cowbirds for a shorter time appear to lack defences against parasitism (Sealy 1996, Sealy et al. 2000, Hosoi and Rothstein 2000). However, the potential importance of the UV reflectance of eggs has not been considered for cowbirds and their hosts.

Several North American passerines have been tested for the ability to see UV light. Brown-headed Cowbirds have been determined to be capable of detecting UV light (Parrish et al. 1984) and so have a number of its hosts (Table 3.1). UV vision does not appear to separate accepter species from rejecter species. Of those species tested, an equal number of accepter and rejecter species can detect UV light. However, differences in UV reflectance between the eggs of cowbirds and their hosts could play a role in foreign egg recognition. A cowbird egg that matches the host clutch in UV reflectance may prevent some hosts from detecting the parasitic egg. By contrast, a cowbird egg that is a mismatch in UV reflectance in comparison to the host clutch may stand out among

Table 3.1. Hosts of the Brown-headed Cowbird experimentally determined to be capable of detecting ultraviolet light.

Host Species ^a	Reference
Rejecters	Rothstein (1975a)
Blue Jay	Parrish et al. (1984), Chen and Goldsmith (1986)
Gray Catbird	Chen et al. (1984), Chen and Goldsmith (1986)
Brown Thrasher	Chen et al. (1984), Chen and Goldsmith (1986)
American Robin	Chen et al. (1984), Chen and Goldsmith (1986)
Accepters	Rothstein (1975a)
Barn Swallow	Chen et al. (1984), Chen and Goldsmith (1986)
Wood Thrush	Chen et al. (1984), Chen and Goldsmith (1986)
European Starling	Parrish et al. (1984)
Red-winged Blackbird	Chen et al. (1984), Chen and Goldsmith (1986)
Common Grackle	Parrish et al. (1984)
Song Sparrow	Chen et al. (1984), Chen and Goldsmith (1986)
Northern Cardinal	Chen et al. (1984), Chen and Goldsmith (1986)
House Finch	Chen et al. (1984), Chen and Goldsmith (1986)

^a Scientific names of species not mentioned in the text: Blue Jay (*Cyanocitta cristata*), Barn Swallow (*Hirundo rustica*), Wood Thrush (*Hylocichla mustelina*), Gray Catbird (*Dumetella carolinensis*), Brown Thrasher (*Toxostoma rufum*), Common Grackle (*Quiscalus quiscula*), Northern Cardinal (*Cardinalis cardinalis*), and House Finch (*Carpodacus mexicanus*).

the host eggs, similar to fruit against foliage, providing an additional parameter for use in egg recognition.

The objective of this study was to determine whether there are differences in the UV reflectance of eggs of rejecter and accepter species in comparison to cowbird eggs that may influence egg recognition. I tested the prediction that the eggs of rejecter species have a different UV reflectance than cowbird eggs, whereas the eggs of accepter species reflect the same amount of UV light as cowbird eggs. In addition, I examined host egg matching by cowbird eggs in the UV range to test Cherry and Bennett's (2001) hypothesis.

METHODS

I investigated the UV reflectance of Brown-headed Cowbird eggs and those of their hosts using eggs laid in nests in the field instead of eggs housed in museum collections due to the potential for fading of egg coloration over time (i.e. most eggs in collections are > 50 years old) and potential differences in reflectance of blown eggs. Fieldwork was conducted at Delta Marsh, Manitoba (50° 11' N, 98° 23' W), on the properties of the Delta Marsh Field Station (University of Manitoba), Delta Waterfowl and Wetlands Research Station, Portage Country Club, private cottage owners, and on the Bell Estate. Songbird breeding habitat at this site consists of an extensive marsh dominated by cattails (*Typha* spp.) and reeds (*Phragmites* spp.) and a narrow dune-ridge forest composed of deciduous trees and shrubs (see Mackenzie 1982, Mackenzie et al. 1982 for a detailed description of the study site and Sealy 1980 for a map of the area).

From May to July 2001, I found nests of the 11 potential host species (five rejecters and six accepters; Table 3.2). I relied on natural parasitism on the accepters to provide a sample of Brown-headed Cowbird eggs. Fifty nests were parasitized by Brown-headed Cowbirds. All nests found during the building or laying stages were monitored until they contained complete clutches. When each nest reached a complete clutch or when it contained a complete clutch when found, all eggs were temporarily removed to measure their reflectance. Artificial eggs were placed into nests after removing the host's eggs to ensure the nest owners did not desert. For rejecter species, artificial eggs made of plaster or wood were painted with non-toxic, acrylic paints (Folk Art Acrylic Paint by Plaid®) to match the characteristics of host eggs of each species to reduce the probability that hosts would reject them. Eggs used to replace the eggs of accepter species were not painted to resemble the eggs of each species but represented a few different egg types. None of the artificial eggs switched with host eggs was rejected during the short time they remained in the nest, although occasionally one of these was pecked. Host eggs were returned to the nest after measurements of reflectance. The incubation stage of each host clutch when measurements were made was determined by recording laying between daily nest checks or by candling the eggs with a foam tube candler (Lokemoen and Koford 1996). I separated the incubation stages of all nests into an early period, the first through the fifth day of incubation, and a late stage, from day six until hatching. The influence of incubation stage was considered because the ground colour of the eggshells of some species, e.g. American Robins (*Turdus migratorius*), appears to change during incubation (personal observation).

Table 3.2. Rejecter and accepter species of Brown-headed Cowbird eggs for which egg reflectance measurements were made at Delta Marsh.

Species ^a	Reference
Rejecters	
Eastern Kingbird (n = 28)	Rothstein (1975a), Sealy and Bazin (1995)
Warbling Vireo (n = 21)	Sealy (1996), Sealy et al. (2000)
American Robin (n = 31)	Rothstein (1975a)
Gray Catbird (n = 31)	Rothstein (1975a)
Baltimore Oriole (n = 30)	Sealy and Neudorf (1995)
Accepters	
Least Flycatcher (n = 27)	Briskie and Sealy (1987)
Red-eyed Vireo (n = 7)	Rothstein (1975a), Underwood unpublished data
Yellow Warbler (n = 30)	Rothstein (1975a), Sealy (1995)
Song Sparrow (n = 32)	Rothstein (1975a)
Red-winged Blackbird (n = 37)	Rothstein (1975a), Ortega and Cruz (1988)
Orchard Oriole (n = 19)	Sealy and Underwood (submitted)

^a Scientific names not mentioned in the text: Eastern Kingbird (*Tyrannus tyrannus*), Warbling Vireo (*V. gilvus*), Baltimore Oriole (*I. galbula*). Sample size is the number of host clutches on which reflectance measurements were taken.

I measured the spectral reflectance, 300-700 nm, of eggs using a UV and visible light spectrometer (USB2000 UV-VIS, Ocean Optics, Inc., Dunedin, FL, USA) with a Deuterium-Tungsten light source (DT-1000-MINI, Analytical Instrument Systems, Inc., Flemington, NJ, USA). A 400 μm fiber optic probe (R400-7-UV/VIS, Ocean Optics, Inc., Dunedin, FL, USA) was held at a 45° angle to the surface of an egg for each individual measurement. An anodized aluminum holder was used to secure the probe at a 45° angle to the egg (Figure 3.1). Eleven reflectance measurements were taken from each egg; eight from random locations on the side of the egg and three from the blunt end. A spectralon reflectance standard (WS-1, Ocean Optics, Inc., Dunedin, FL, USA), which reflects > 99 % of UV and visible light, was measured prior to measuring each egg, as well as a dark standard, which measures the baseline “noise” in the spectrophotometer. Light and dark measurements were used to standardize reflectance measurements for calculating the proportion of light reflected. Percent reflectance was calculated automatically for each measurement with data from the light and dark standards and the egg using OOIBase32™ software (Ocean Optics, Inc., Dunedin, FL, USA). All egg reflectance measurements were taken under a black cloth to eliminate potential interference from ambient light.

Analysis

The total UV reflectance was used as the sampling unit to examine the UV reflectance of eggs. The total UV reflectance was represented by the area under the reflectance curve in the UV region of the spectrum that birds are capable of detecting, 300-400 nm. The spectrophotometer produced reflectance measurements at every 0.3 nm. The area under the UV portion of the curve was determined by calculating the sum

Figure 3.1. Equipment setup for egg reflectance measurements. Fiber optic probe held at 45° angle to an egg by probe holder.



of the areas of all rectangles under the curve that were generated by reflectance measurements each 0.3 nm. For each egg, I determined the total UV reflectance, hereafter UV reflectance, for the side and the cap by calculating the mean UV reflectance values for the eight side measurements and the three cap measurements, respectively.

To compare the UV reflectance of eggs from host species to that of the reflectance of Brown-headed Cowbird eggs, I used the mean UV reflectance of all host eggs in a given clutch and that of the only cowbird egg in singly parasitized nests or one randomly chosen cowbird egg in multiply parasitized nests. Data were log-transformed to meet the assumptions of normality. I used a two-factor analysis of variance (ANOVA) with species and incubation stage as the factors to compare the UV reflectance of eggs. If species had a significant effect on UV reflectance, I used orthogonal contrasts for multiple comparisons of each host species to the cowbird. Probability values were Bonferroni-adjusted for making multiple comparisons. To compare the UV reflectance of the eggs of taxonomic pairs of rejecters and accepters (Table 3.3), I used a Wilcoxon paired-sample test on untransformed data to compare the mean UV reflectance of each host species between three pairs of rejecters and accepters.

I examined the potential for host egg matching in the UV range by cowbirds in two ways: by comparing the UV reflectance of cowbird eggs laid among the nests of five host species and by examining the correlation of UV reflectance of cowbird eggs with those of the host clutch in which they were laid. For each comparison, I used data from only one cowbird egg per host clutch. When nests were multiply parasitized, I randomly chose a cowbird egg from each nest. For host clutches, I used the mean UV reflectance for all eggs in the clutch. All data were log-transformed to meet the assumptions of

Table 3.3. Comparison of the UV reflectance of the cap and side of eggs from three closely related pairs of acceptor and rejecter species.

Rejecters	UV cap	UV side	Accepters	UV cap	UV side
Eastern Kingbird	2093.63	2922.42	Least Flycatcher	1474.95	1737.35
Warbling Vireo	3264.56	3760.65	Red-eyed Vireo	3263.52	3898.19
Baltimore Oriole	1784.94	2398.80	Orchard Oriole	1282.14	1991.27

normality. I used a two-factor ANOVA with host species and incubation stage as the factors to compare UV reflectance among cowbird eggs laid in different host nests. If a host species had a significant effect on UV reflectance, I used orthogonal contrasts to make multiple comparisons. Probability values were Bonferroni-adjusted for making multiple comparisons. In addition, I used correlation to test for a relationship of UV reflectance of cowbird eggs with that of the host clutch in which they were laid.

RESULTS

Comparison of host eggs to cowbird eggs

I measured the reflectance of 293 clutches of 11 host species at Delta Marsh (Table 3.2). Of the five rejecter species, 141 clutches were measured and, of the six acceptor species, 152 clutches were measured. Brown-headed Cowbird eggs were found in 50 nests of five host species: Red-eyed Vireo (*Vireo olivaceus*; $n = 5$), Yellow Warbler (*Dendroica petechia*; $n = 7$), Song Sparrow (*Melospiza melodia*; $n = 25$), Red-winged Blackbird (*Agelaius phoeniceus*; $n = 9$), and Orchard Oriole (*Icterus spurius*; $n = 4$).

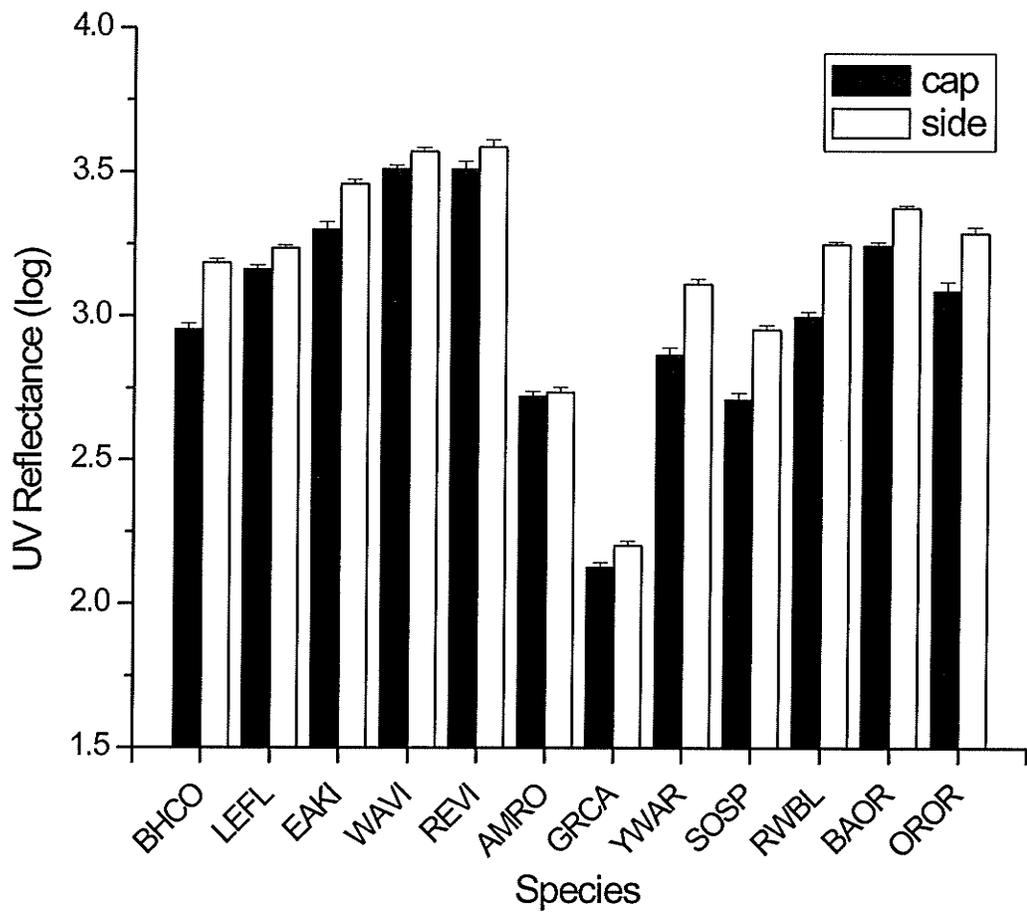
For the cap of the egg, UV reflectance differed significantly by species, but not by incubation stage (Table 3.4, Figure 3.2). UV reflectance varied considerably between hosts in relation to the cowbird egg. For all species, except Yellow Warblers and Red-winged Blackbirds, cap UV reflectance differed significantly between host eggs and cowbird eggs (Table 3.4, Figure 3.2). The eggs of six host species had significantly higher UV reflectance than cowbird eggs, including three rejecters and three accepters,

Table 3.4. Analysis of variance examining the influence of species and incubation stage on UV reflectance of the cap of Brown-headed Cowbird eggs and the eggs of 11 cowbird hosts.

Factor/Contrast^a	F	df	P
species	85.66	11, 314	<0.0001
incubation stage	0.40	1, 314	0.539
species x incubation stage	1.62	11, 314	0.091
Least Flycatcher	46.88	1	<0.001
Eastern Kingbird	130.44	1	<0.001
Warbling Vireo	288.01	1	<0.001
Red-eyed Vireo	108.68	1	<0.001
American Robin	36.18	1	<0.001
Gray Catbird	312.47	1	<0.001
Yellow Warbler	3.09	1	0.878
Song Sparrow	37.59	1	<0.001
Red-winged Blackbird	8.00	1	0.055
Orchard Oriole	28.15	1	<0.001
Baltimore Oriole	90.53	1	<0.001

^a Contrast of each host species with the Brown-headed Cowbird. Probability values of all contrasts have been adjusted using Bonferroni correction.

Figure 3.2. Mean UV reflectance (\pm SE) of the cap and side of Brown-headed Cowbird (BHCO) eggs and the eggs of 11 host species. Host species included: Least Flycatcher (LEFL), Eastern Kingbird (EAKI), Warbling Vireo (WAVI), Red-eyed Vireo (REVI), American Robin (AMRO), Gray Catbird (GRCA), Yellow Warbler (YWAR), Song Sparrow (SOSP), Red-winged Blackbird (RWBL), Baltimore Oriole (BAOR), and Orchard Oriole (OROR).



whereas the eggs of three species, two rejecters and one acceptor, had significantly lower UV reflectance than cowbird eggs (Table 3.4, Figure 3.2).

Trends in UV reflectance for the side of the egg were similar to those for the cap. Species had a significant effect on UV reflectance, but incubation stage did not (Table 3.5, Figure 3.2). However, there was a significant interaction between species and nest stage (Table 3.5), which suggests that there were non-significant trends in incubation stage among different species. UV reflectance of the side of host eggs differed significantly from cowbird eggs for all species, except Least Flycatchers (*Empidonax minimus*) and Yellow Warblers (Table 3.5, Figure 3.2). The eggs of six host species had significantly higher reflectance than cowbird eggs, including three rejecters and three acceptors, whereas the eggs of three species, two rejecters and one acceptor, had significantly lower UV reflectance than cowbird eggs (Table 3.5, Figure 3.2). Comparing the UV reflectance of the three taxonomic pairs of rejecters and acceptors, there was no significant difference between rejecters and acceptors in the cap (Wilcoxon paired-sample test, $Z = -1.604$, $P = 0.109$; Table 3.3) or in the side of the egg (Wilcoxon paired-sample test, $Z = -1.609$, $P = 0.285$; Table 3.3).

Cowbird eggs laid among different host species

The UV reflectance of the cap and the side of cowbird eggs did not differ significantly by host species or by the incubation stage of the egg (Table 3.6, Figure 3.3). In addition, UV reflectance of the cap of cowbird eggs was not significantly correlated with that of the cap of the host clutch in which it was laid ($r = 0.037$, $n = 49$, $P = 0.798$; Figure 3.4A). Similarly, UV reflectance of the side of cowbird eggs was not

Table 3.5. Analysis of variance examining the influence of species and incubation stage on UV reflectance of the side of Brown-headed Cowbird eggs and the eggs of 11 cowbird hosts.

Factor/Contrast ^a	F	df	P
Species	143.20	11, 314	<0.0001
incubation stage	1.37	1, 314	0.265
species x incubation stage	1.88	11, 314	0.041
Least Flycatcher	6.34	1	0.135
Eastern Kingbird	128.88	1	<0.001
Warbling Vireo	260.84	1	<0.001
Red-eyed Vireo	105.33	1	<0.001
American Robin	322.10	1	<0.001
Gray Catbird	958.87	1	<0.001
Yellow Warbler	7.15	1	0.087
Song Sparrow	52.28	1	<0.001
Red-winged Blackbird	15.30	1	<0.001
Orchard Oriole	28.11	1	<0.001
Baltimore Oriole	73.07	1	<0.001

^a Contrast of each host species with the Brown-headed Cowbird. Probability values of all contrasts have been adjusted using Bonferroni correction.

Table 3.6. Analysis of variance examining the influence of host species and incubation stage on the UV reflectance of Brown-headed Cowbird eggs.

Variable/Factor	F	df	P
Cap			
host species	0.39	4, 40	0.806
incubation stage	2.01	1, 40	0.251
host species x incubation stage	1.04	3, 40	0.386
Side			
host species	0.54	4, 40	0.720
incubation stage	1.79	1, 40	0.273
host species x incubation stage	1.14	3, 40	0.345

Figure 3.3. Mean UV reflectance (\pm SE) of Brown-headed Cowbird (BHCO) eggs laid in the nests of five different host species at Delta Marsh. Host species included: Red-eyed Vireo (REVI), Yellow Warbler (YWAR), Song Sparrow (SOSP), Red-winged Blackbird (RWBL), and Orchard Oriole (OROR).

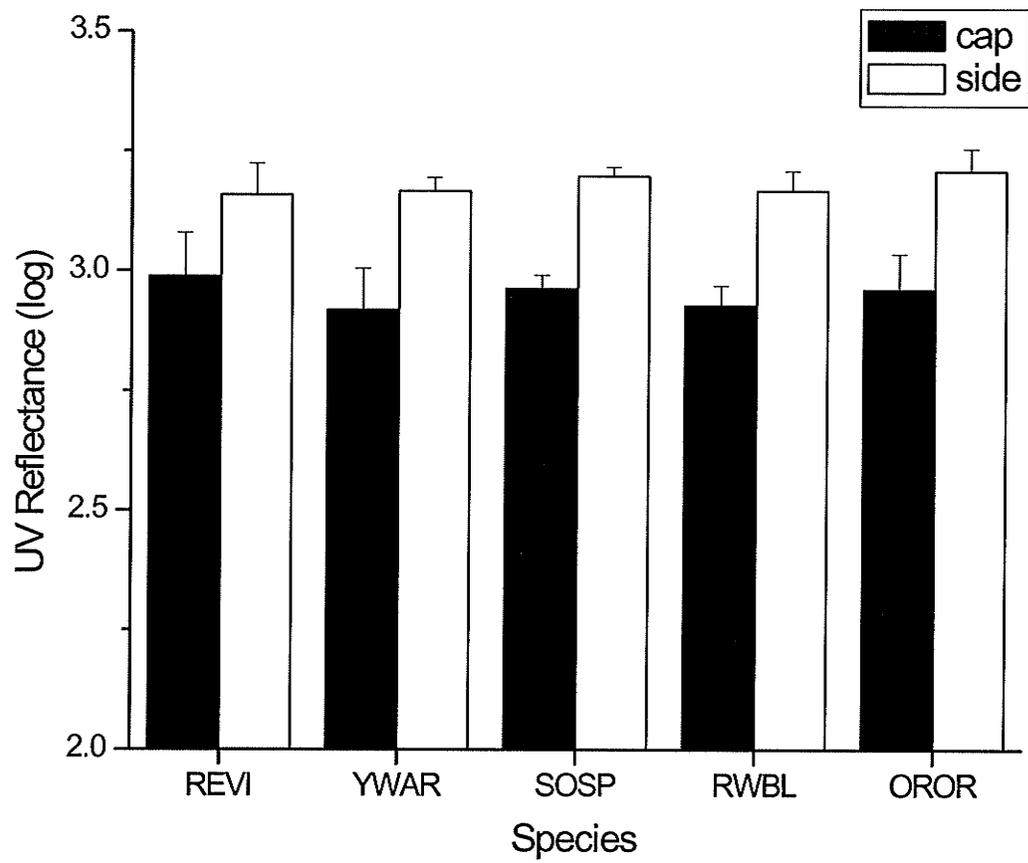
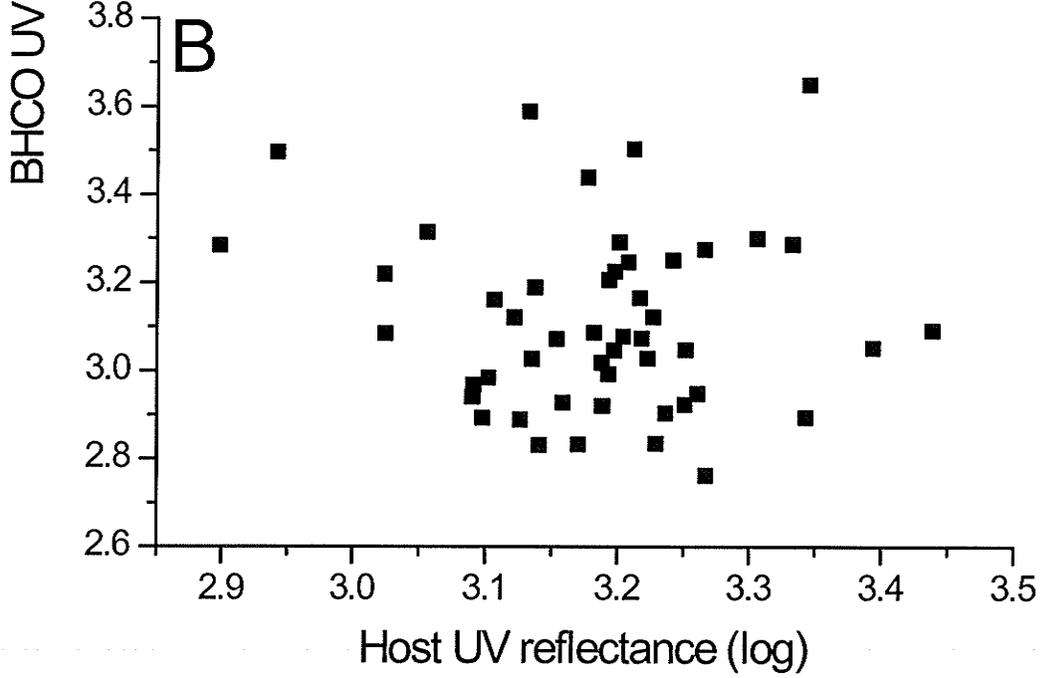
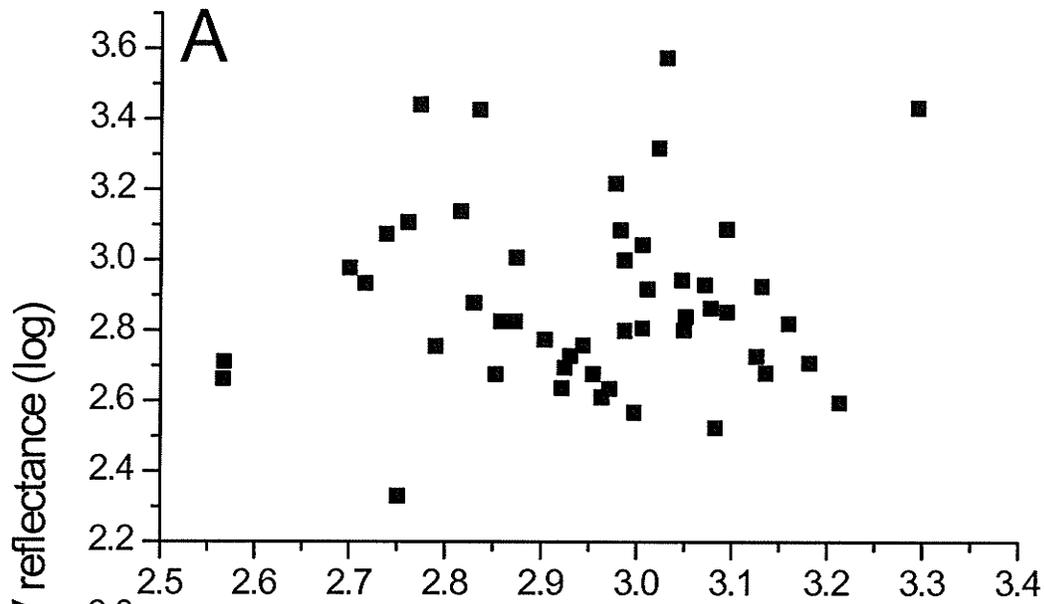


Figure 3.4. Relationship between UV reflectance of Brown-headed Cowbird (BHCO) eggs and the UV reflectance of the host clutch in which they were laid: A, cap; B, side.



significantly correlated with that of the side of the host clutch in which it was laid ($r = -0.082$, $n = 49$, $P = 0.574$; Figure 3.4B).

DISCUSSION

The eggs of most host species had a UV reflectance that was significantly different from cowbird eggs. Only one acceptor, the Yellow Warbler, matched the UV reflectance of cowbird eggs in both cap and side measurements. In addition, one acceptor matched only the cap area and another acceptor matched only the side of the egg. Despite the eggs of the cowbird matching those of a few acceptor species, there was a mix of accepters and rejecters showing significantly different UV reflectances compared to cowbird eggs. There was no real pattern to these differences; both accepters and ejecters had higher and lower UV reflectances than cowbird eggs. At the species level, there was also no difference in the UV reflectance of the eggs of closely related pairs of accepters and rejecters. The eggs of all three pairs showed higher UV reflectance than cowbird eggs, although the side measurement of one acceptor was not significantly different from the cowbird egg. Thus, differences in the UV reflectance of host eggs compared to cowbird eggs does not appear to separate accepter and rejecter species.

The variability of the UV reflectance of cowbird eggs also showed no evidence for host egg matching. There was no significant difference in the UV reflectance of cowbird eggs laid among the five different host species. Furthermore, the UV reflectance of cowbird eggs was not significantly correlated with that of the host clutch in which they were laid. Therefore, based on the UV reflectance of cowbird eggs and those of 11 hosts,

there is no support for Cherry and Bennett's (2001) UV matching hypothesis as an explanation for why so many cowbird hosts accept apparently non-mimetic eggs.

The lack of host egg matching in UV wavelengths by Brown-headed Cowbirds is not surprising. Individual female cowbirds lay their eggs among the nests of different host species (Fleischer 1985, Woolfenden et al. 2003) and there is no genetic evidence for host-specific races (Gibbs et al. 1997). Both host specificity and a genetic basis for host-specific races are necessary for the maintenance of egg mimicry among Common Cuckoos (Underwood and Sealy 2002). Thus, there is no mechanism by which host egg matching or mimicry could be maintained in Brown-headed Cowbirds in either the UV or visible spectrum unless cowbirds became host specific.

Even though UV reflectance of eggs does not explain acceptance of cowbird eggs, UV reflectance still may provide an important parameter for egg recognition. The eggs of most species examined differed from cowbird eggs in UV reflectance of the cap or side providing a potential cue or signal for use in egg recognition. Interestingly, the Yellow Warbler was the only species with a UV reflectance similar to that of cowbirds in both the cap and side of the egg. Yellow Warblers are sometimes considered a rejecter species because they often bury naturally laid cowbird eggs (Sealy 1995), but the stimulus for rejection is unknown because Yellow Warblers rarely reject cowbird eggs added experimentally to their nests and do not recognize their own eggs (Sealy and Lorenzana 1998). UV matching of cowbird and Yellow Warbler eggs might contribute to the lack of egg recognition in Yellow Warblers. However, it is doubtful that UV reflectance has an overriding influence on host discrimination or egg recognition, as Cherry and Bennett (2001) suggested for Red-crested Cuckoos and their hosts.

All seven hosts of the Red-chested Cuckoo examined for UV matching show no evidence of rejection behaviour and the most common host, the Cape Robin (*Cossypha caffra*), apparently accepts experimental mimetic and non-mimetic eggs, at least as seen by the human eye (Cherry and Bennett 2001). The UV reflectance of eggs is only one of many potential parameters, such as egg size, shape, ground colour, and maculation, which may be important for egg recognition and rejection. Most of these parameters, which can be assessed by human vision, have been previously shown to influence egg-recognition and rejection behaviour by both cowbird hosts (Rothstein 1982b, Mason and Rothstein 1986, Burhans and Freeman 1997; Chapters 1, 2) and cuckoo hosts (Alvarez et al. 1976, Davies and Brooke 1988, Marchetti 2000, Lahti and Lahti 2002). No evidence suggests that a UV parameter would outweigh other potential parameters that differ between parasite and host eggs.

Recent studies of the relative importance of UV signals in mate choice have suggested that UV signals may not be any more unique than those originating from other wavelengths, such as red, blue or green (Banks 2001). Previous studies on UV and mate choice have simply altered the UV reflectance of males as viewed by females using filters to remove potential UV signals or allow them to be seen (e.g. Bennett et al. 1996). Hunt et al. (2001) examined the relative importance of UV wavelengths for mate choice in Zebra Finches by manipulating not only UV wavelengths but three other wavelengths (short, medium and long) corresponding to the visible portion (i.e. blue, green and red, respectively) of the spectrum. Long wavelengths had the strongest influence on mate choice by female Zebra Finches, whereas UV wavelengths had the least influence on female preference (Hunt et al. 2001). In a similar experiment on foraging, long

wavelengths also were found to be more important to Zebra Finches than were UV wavelengths (Maddocks et al. 2001). These experiments suggest that UV signals are not more important for mate choice and foraging than signals present in other wavelengths (Banks 2001, Hunt et al. 2001). Therefore, it is doubtful also that UV signals would be more important than other potential signals for egg recognition.

Summary

My results do not support the UV matching hypothesis (Cherry and Bennett 2001) as an explanation for the acceptance of Brown-headed Cowbird eggs. The mismatch of most host species' eggs with cowbird eggs in the UV range provides a potential parameter for egg recognition previously unknown for cowbird hosts. However, similar to the conclusions of recent studies on mate choice (Hunt et al. 2001), I suggest that this parameter is not likely to be an overriding parameter for foreign egg recognition, but may play a role alongside those parameters already documented as being important for egg recognition. However, before the relative importance of UV signals in egg recognition by cuckoo and cowbird hosts can be completely understood, experimental tests using foreign eggs with manipulated UV signals must be conducted.

CHAPTER 4. GRASP-EJECTION OF COWBIRD EGGS BY WARBLING VIREOS AND BALTIMORE ORIOLES

INTRODUCTION

Despite well-developed egg-recognition and ejection behaviour of some hosts of brood parasites (Rothstein 1975a, Davies and Brooke 1988, Chapter 1), many hosts accept the costs of caring for a parasite's offspring (Rothstein 1982a, Brooker and Brooker 1989, Appendix 1). This dichotomy of response to parasitism is especially pronounced in hosts of the generalist cowbirds (*Molothrus* spp.; Rothstein 1992, Davies 1999), two species of which are known to have parasitized over 200 species of birds each (Friedmann and Kiff 1985, Lowther 1993, Lowther and Post 1999). For example, most species accept Brown-headed Cowbird (*M. ater*) eggs and young in their nests (Rothstein 1975a, Underwood and Sealy 2002, Appendix 1), which begs the question: why do host species accept the cost of parasitism? Two main hypotheses have been proposed to explain the acceptance of brood parasitism by hosts: the evolutionary lag hypothesis and the evolutionary equilibrium hypothesis.

The evolutionary lag hypothesis proposes that rejection behaviour is an adaptive response to parasitism that has not yet evolved because hosts lack the proper genetic variation or have not been exposed to parasitism long enough (Rothstein 1975a, 1975c, 1982a, 1990; Davies and Brooke 1989b). By contrast, the evolutionary equilibrium hypothesis predicts that acceptance of a brood parasite's egg by a host is adaptive because the cost of acceptance is lower than the cost of rejection (Rohwer and Spaw 1988, Lotem and Nakamura 1998). The costs of acceptance result from host egg removal

by brood parasites (Sealy 1992, Davies 2000), incubation interference (Sealy et al. 2002) and nestling competition (Soler et al. 1995a, 1996; Dearborn 1998, Dearborn et al. 1998; Lichtenstein and Sealy 1998) or the eviction/killing of host eggs and nestlings by young brood parasites (Friedmann 1955, Morton and Farabaugh 1979, Wyllie 1981). All of these costs ultimately lower the production of fledglings from parasitized nests (Payne 1997, Lorenzana and Sealy 1999) and possibly compromise fledgling survival (Payne and Payne 1998), adult survival and/or future adult reproductive success (May and Robinson 1985, Dearborn et al. 1998). By contrast, the costs of rejection may accrue through host egg damage during ejection attempts (Spaw and Rohwer 1987), the mistaken ejection of a host egg instead of a parasite's egg (i.e. recognition errors, Marchetti 1992), or the loss of time and energy when deserting or burying a parasite's egg (Lotem and Nakamura 1998). Because egg ejection is the most well studied defence against parasitism (Rothstein and Robinson 1998) and it appears to be the most effective defence (Rothstein 1975a, 1976), the majority of studies have focused on this response when examining the evolutionary lag and equilibrium hypotheses.

A major assumption of the evolutionary equilibrium hypothesis is that bill-size constraints prevent small hosts from grasp-ejecting cowbird eggs, which limits them to puncture-ejection (Spaw and Rohwer 1987, Rohwer and Spaw 1988). The unusually strong shells of cowbird eggs (Spaw and Rohwer 1987, Rahn et al. 1988, Picman 1989) and the eggs of some cuckoos (*Cuculus* spp. and *Clamator* spp.; Brooker and Brooker 1991, Picman and Pribil 1997) have been proposed to counter puncture-ejection by hosts (Swynnerton 1918, Spaw and Rohwer 1987). Small hosts, assumed to be incapable of grasp-ejection, are believed to be unable to puncture these unusually strong shells, or are

capable of puncture-ejection but incur a higher cost due to egg damage (Spaw and Rohwer 1987). Thus, acceptance of a brood parasite's egg may be favoured if these small hosts incur high costs of rejection because they are limited to puncture-ejection, desertion or egg burial.

For cuckoo hosts, some evidence suggests that an evolutionary equilibrium is occurring because the cost of ejecting a mimetic egg may be high. Hosts with small bills reject more often by desertion than ejection compared to large-billed hosts (Davies and Brooke 1989a). Cuckoo hosts also may have a high probability of making recognition errors (Davies and Brooke 1988, Marchetti 1992; but see Røskaft et al. 2002) and damage their own eggs during an ejection attempt, especially small hosts (Davies and Brooke 1988, 1989a, Soler et al. 2002; but see Martin-Vivaldi et al. 2002). The high cost of ejection may favour acceptance of parasitism, especially when the frequency of parasitism or probability of being parasitized is low. Using a signal detection model, Davies et al. (1996) predicted that Reed Warblers (*Acrocephalus scirpaceus*) would accept mimetic cuckoo eggs unless parasitism frequencies reached a threshold of 19-41 % of nests. Because the cost of ejection is high, ejection would be profitable only when the probability of parasitism is also high. Davies et al. (1996) found that Reed Warblers indeed were at an evolutionary equilibrium because most accepted mimetic cuckoo eggs (models and real eggs) when parasitism frequencies were below the threshold level of parasitism.

There is less support for an evolutionary equilibrium explaining a lack of ejection in cowbird hosts. Rohwer and Spaw (1988) measured the grasp index (the product of the diagonal bill length and commissural bill width) of several species of ejecters and

accepters of Brown-headed Cowbird eggs. Grasp-ejecters had larger grasp indices, whereas puncture-ejecters and accepters had smaller indices (Rohwer and Spaw 1988). Puncture-ejection also has been found to cost more than grasp-ejection (Rohwer et al. 1989, Lorenzana and Sealy 2001; Table 4.1). These results fit the pattern predicted by the evolutionary equilibrium hypothesis. However, further work on Bullock's Orioles (*Icterus bullockii*), one of the largest puncture-ejecters, and Gray Catbirds (*Dumetella carolinensis*), one of the smallest grasp-ejecters, has demonstrated that for these species the costs of both puncture-ejection and grasp-ejection do not exceed the cost of raising a cowbird (Røskaft et al. 1993, Lorenzana and Sealy 2001). In addition, the 15-gram Warbling Vireo (*Vireo gilvus*) has recently been identified as the smallest puncture-ejecter of cowbird eggs with a cost lower than that incurred by the larger Baltimore Oriole (*I. galbula*) and Bullock's Oriole (Sealy 1996). Nevertheless, most acceptor hosts of Brown-headed Cowbirds are small (Rohwer and Spaw 1988) and may be constrained by small bills that prevent efficient ejection of cowbird eggs.

As an alternative explanation to a small bill forcing orioles to puncture-eject cowbird eggs, Rothstein (1977) suggested that orioles (*Icterus* spp.) are unable to grasp and then eject cowbird eggs because of their deep, pendant-shaped nests. Baltimore Oriole nests are typically long, up to 16 cm, but vary considerably in size and shape and may be as shallow as 4 cm (Nickell 1958, Schaefer 1974; Figure 4.1). If the cowbird egg is not securely impaled on the oriole's bill, the oriole risks dropping the egg onto its own clutch while attempting to remove it from a deep nest. Rohwer et al. (1989) indirectly tested Rothstein's hypothesis with Bullock's Orioles by comparing the mean nest depth of nests in which orioles damaged their own eggs while ejecting a real cowbird egg to

Table 4.1. Cost of ejection in hosts of the Brown-headed Cowbird. Cost is the number of host eggs damaged or missing per cowbird egg ejected.

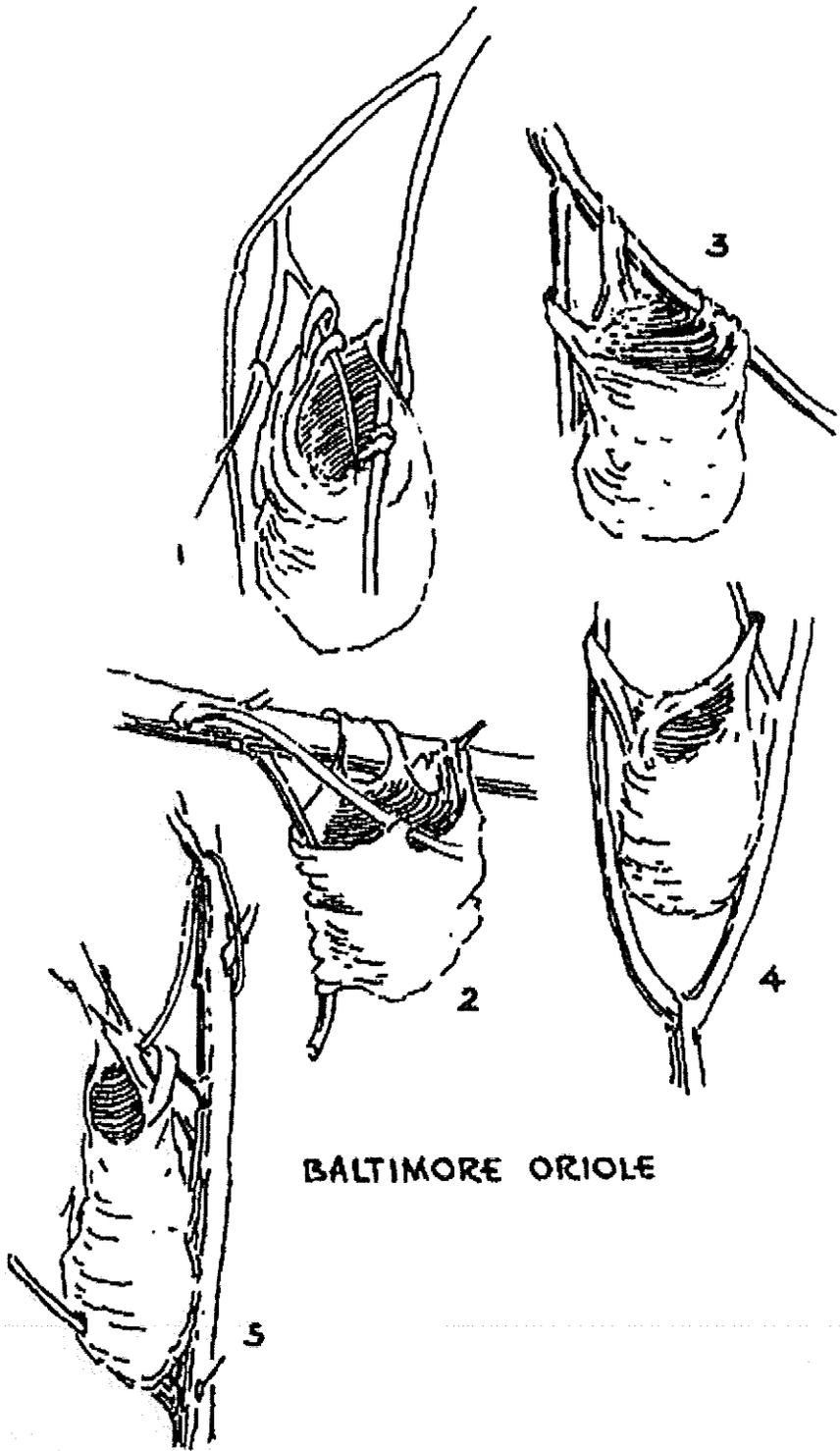
Species ^a	Cost (n)	Ejection method ^b	Egg Type	Reference
Western Kingbird	0.00 (2)	Grasp	Artificial	Rothstein 1976
Western Kingbird	0.00 (7)	Grasp	Real	Rohwer et al. 1989
Eastern Kingbird	0.07 (88)	Grasp	Real	Sealy and Bazin 1995
Scissor-tailed Flycatchers	0.05 (20)	Grasp	Artificial	Peer and Sealy 2000b
Warbling Vireo	0.10 (29)	Puncture	Real	Sealy 1996, Sealy et al. 2000
Warbling Vireo	0.00 (20)	Grasp	Artificial	This Study
Blue Jay	0.09 (23)	Grasp	Artificial	Rothstein 1976
American Robin	0.03 (38)	Grasp	Artificial	Rothstein 1976
American Robin	0.00 (2)	Grasp	Real	Rohwer et al. 1989
American Robin	0.08 (59)	Grasp	Artificial	Sealy unpublished data
Gray Catbird	0.02 (90)	Grasp	Artificial	Lorenzana and Sealy 2001
Gray Catbird	0.02 (86)	Grasp	Artificial	Rothstein 2001
Northern Mockingbird	0.05 (18)	Grasp	Artificial	Peer et al. 2002
Sage Thrasher	0.20 (10)	Grasp	Artificial	Rich and Rothstein 1985
Brown Thrasher	0.04 (25)	Grasp	Artificial	Rothstein 1976
Baltimore Oriole	0.38 (16)	Puncture	Real	Sealy and Neudorf 1995
Baltimore Oriole	0.23 (13)	Grasp?	Artificial	This Study

Bullock's Oriole 0.45 (33) Puncture Real Rohwer et al. 1989

^a Scientific names of species not mentioned in text: Western Kingbird (*Tyrannus verticalis*), Eastern Kingbird (*T. tyrannus*), Scissor-tailed Flycatcher (*T. forficatus*), Blue Jay (*Cyanocitta cristata*), Northern Mockingbird (*Mimus polyglottos*), Sage Thrasher (*Oreoscoptes montanus*), and Brown Thrasher (*Toxostoma rufum*).

^b For most studies and species, the method of ejection is assumed based on host size and ability to eject solid, artificial eggs.

Figure 4.1. Variation in Baltimore Oriole nests illustrating their considerable structural variability in shape and size, especially in relation to nest depth and the diameter of the nest opening (figure from Nickell 1958).



BALTIMORE ORIOLE

nests where no damage occurred during ejection. They predicted that nests with egg damage would be deeper than those without damage if nest depth makes it more difficult to eject cowbird eggs. In contrast to Rothstein's hypothesis, there was no significant difference in nest depth between nests with and without host egg damage (Rohwer et al. 1989).

Based on a small number of videotaped ejections by Warbling Vireos (Chapter 1), I suspected that small puncture-ejecters of cowbird eggs might also be capable of grasp-ejection. The objective of this study was to test the assumption of bill-size constraints of the evolutionary equilibrium hypothesis by determining whether Warbling Vireos of the eastern subspecies (*V. g. gilvus*) and Baltimore Orioles, the smallest known puncture-ejecters (Rothstein 1977, Sealy and Neudorf 1995, Sealy 1996), are capable of grasp-ejecting cowbird eggs. Warbling Vireos and Baltimore Orioles are excellent species in which to examine bill-size constraints. Both are small cowbird hosts and Warbling Vireos exhibit geographic variation in size and vary in their response to parasitism (the eastern subspecies ejects cowbird eggs and the western subspecies, *V. g. swainsoni*, accepts them; Sealy 1996, Sealy et al. 2000). In addition, I tested Rothstein's (1977) hypothesis that the depth of Baltimore Oriole nests may prevent orioles from grasp-ejecting cowbird eggs.

METHODS

General

The study area was located at Delta Marsh, Manitoba (50° 11' N, 98° 23' W), which is characterized by a narrow dune-ridge forest that separates Lake Manitoba from

an extensive marsh (see MacKenzie 1982, Mackenzie et al. 1982 for a detailed description of the study site and Sealy 1980 for a map of the area). Fieldwork was conducted on the properties of the Delta Marsh Field Station (University of Manitoba), Delta Waterfowl and Wetlands Research Station, Portage Country Club, private cottage owners and the Bell estate. Warbling Vireo and Baltimore Oriole nests were located from May to early July in the dune-ridge forest. Because both species nest high in the canopy, e.g. Warbling Vireo nests average 8.6 m high ($n = 156$; unpublished data), I used a TV antenna tower guyed with ropes to climb to most nests (Figure 1.1).

Grasp-ejection tests

I experimentally parasitized Warbling Vireo nests in 1999 and Baltimore Oriole nests in 1999 and 2000. Nests were parasitized with model cowbird eggs made of plaster and painted to match natural cowbird eggs, according to Rothstein's (1970) methods. In contrast to some previous studies on these species where real cowbird eggs were used (Sealy and Neudorf 1995, Sealy 1996), vireos and orioles were not expected to be able to puncture-eject the solid plaster eggs used in this study. Thus, the only way to remove them was by grasp-ejection. All vireo nests and most oriole nests (93 %) were parasitized during the incubation stage. I parasitized nests throughout the incubation period because the exact day of incubation was unknown. These two species do not show a differential response to parasitism by nest stage (Rothstein 1977, Sealy 1996, Chapter 1). Four Warbling Vireo nests and four Baltimore Oriole nests, which were unobscured by leaves and accessible (i.e. most nests were too high and/or obscured), were videotaped for one hour following egg addition to confirm the method of ejection.

A single plaster cowbird egg was added to each nest without the removal of a host egg. Response to experimental parasitism is not influenced by host egg removal or lack thereof (Rothstein 1975a, Davies and Brooke 1988) and cowbirds do not always remove host eggs from parasitized nests (Sealy 1992). Nests were inspected after 24 hours to determine whether the model egg was ejected and to detect damaged or missing host eggs to calculate the cost of ejection. Host eggs were considered damaged when there was a large crack present or when punctured. Model eggs still present in the nest at the 24 hour inspection were removed and inspected for evidence of an ejection attempt, i.e. peck marks (sensu Rothstein 1977). Any model egg without evidence of an ejection attempt was assumed to be accepted. For model eggs with evidence of an ejection attempt, I assumed that nest owners were not capable of grasp-ejection because nearly all real cowbird eggs are ejected within this time period (Sealy and Neudorf 1995, Sealy 1996, Chapter 1). All nests tested in these experiments had been previously tested with a real egg of one of several treatments (Table 1.3) used in experiments to identify the parameters of egg recognition (Chapter 1). I did not consider this a bias because the method of ejection was being tested and not an individual's ability to recognize a foreign egg.

Model eggs averaged 20.8×17.1 mm ($\pm 0.10 \times 0.09$ SE; $n = 22$) for Warbling Vireo experiments and 21.1×17.2 mm ($\pm 0.08 \times 0.09$ SE; $n = 23$) for Baltimore Oriole experiments. The mass of a subset of these model eggs averaged 3.4 g (± 0.09 SE; $n = 20$). Experimental eggs were very similar in size and mass to real cowbird eggs (21.1×16.4 mm $\pm 0.10 \times 0.07$ SE; mass = 3.2 g ± 0.03 SE, $n = 113$; Sealy unpublished data)

from Delta Marsh and well within the range of variation of these real eggs (range = 18.1 – 23.3 x 14.3 – 18.8 mm, 2.1 – 3.9 g; Sealy unpublished data).

Grasp-index measurements

I calculated the grasp index (diagonal bill length x commissural breadth; Rohwer and Spaw 1988) of Warbling Vireos of the eastern and western subspecies (*gilvus* and *swainsoni*) and of Baltimore Orioles. I compared grasp-index measurements of the eastern and western subspecies of Warbling Vireos to determine whether a difference in the size of bills may explain the lack of ejection behaviour in the western subspecies. Grasp-index measurements were also used to compare Warbling Vireo and Baltimore Oriole bill sizes with those of other known grasp-ejecters and puncture-ejecters. Because male Warbling Vireos and Baltimore Orioles are known to eject cowbird eggs (Sealy and Neudorf 1995, this study), I measured grasp indices of both sexes. In addition, Rohwer and Spaw (1988) measured the grasp index of females only, therefore, I also measured the grasp indices of male and female American Robins (*Turdus migratorius*), Gray Catbirds, Cedar Waxings (*Bombycilla cedrorum*), and Bullock's Orioles for comparison.

Bills were measured on study skins in the collections of the Canadian Museum of Nature, Delaware Museum of Natural History, Manitoba Museum, and University of Manitoba Zoology Museum. Because of the difficulties of identifying Warbling Vireos to subspecies based only on visual characters, I measured birds collected only during the breeding season and used geographic location to confirm subspecific identification based on descriptions of breeding distributions (American Ornithologists' Union 1957, Gardali and Ballard 2000). Because of the lack of uniformity in treatment of Warbling Vireo subspecies in western North America (American Ornithologists' Union 1957, 1998;

Blake 1968; Phillips 1991; Gardali and Ballard 2000), I considered both a widespread western Warbling Vireo subspecies group (*swainsoni* group; American Ornithologists' Union 1998, Gardali and Ballard 2000) and the more restrictive true *swainsoni* subspecies (American Ornithologists' Union 1957, Gardali and Ballard 2000). Warbling Vireos measured from the *swainsoni* group were collected in Arizona, British Columbia, California, Idaho, Oregon, South Dakota and Wyoming, whereas only those from British Columbia were used in comparisons of the true *swainsoni* subspecies. Measurements of the eastern subspecies (*gilvus*) were from specimens collected in Indiana, Manitoba, Michigan, Ontario, and Quebec. Baltimore Oriole measurements were from specimens collected in Manitoba, Ontario and Quebec, whereas Bullock's Oriole measurements were from specimens collected throughout the western United States and western Canada. Measurements of the remaining species were from specimens collected throughout Canada.

Baltimore Oriole nest dimensions

In 2001, I tested Baltimore Oriole nests with plaster cowbird eggs to compare the dimensions of nests from which plaster eggs were ejected to those where plaster eggs were accepted. In addition to the possibility of nest depth constraining grasp-ejection, I also considered the diameter of the nest opening as a possible constraint. Prior to adding a plaster cowbird egg, I measured the depth and diameter of the opening of all Baltimore Oriole nests using a straight ruler. Similar to Rohwer et al.'s (1989) definition of nest depth, I considered depth as the vertical distance from the bottom of the nest cup to the lowest point of the rim of the nest opening. Because the openings of oriole nests were not symmetrical, the nest opening was defined as the mean of two measurements of the

diameter of the opening, i.e. a north-south oriented diameter and an east-west oriented diameter. I monitored these nests using the same protocol as described for grasp-ejection tests with Warbling Vireos and previous tests with Baltimore Orioles. This included the videotaping of four additional Baltimore Oriole nests to confirm the method of ejection. Plaster cowbird eggs for this experiment averaged 20.8×16.7 mm ($\pm 0.09 \times 0.07$ SE; $n = 30$) with a mass that averaged 3.5 g (± 0.10 SE; $n = 30$).

Statistical analysis

I analyzed the response to plaster eggs (number of acceptances and ejections) using a Binomial Test to determine whether the proportion of accepted to ejected cowbird eggs differed from equality, i.e. whether vireos and orioles accepted or ejected the majority of eggs. To compare the cost of ejection, I used Mann-Whitney U tests because the data were not normally distributed. For all other data, I determined that the assumptions of normality were met by graphical measures and Shapiro-Wilk tests. To compare the grasp indices of Warbling Vireos, I used a two-factor analysis of variance (ANOVA) with subspecies and sex as the factors. For Baltimore Oriole nest dimensions, I used Independent Samples t-tests to compare nest depth and nest opening diameter between nests from which plaster eggs were ejected and those where plaster eggs were accepted. All statistical tests were two-tailed with a significance level of $\alpha = 0.05$.

RESULTS

Grasp-ejection tests

Warbling Vireos ejected a significant proportion of model cowbird eggs added to their nests (91 % ejected, $n = 22$; $P < 0.001$, Binomial Test). Grasp-ejection was

confirmed as the method of ejection on videotape (Figure 4.2; see also Figure 1.5). No vireo eggs were damaged in any of the 20 nests from which a model egg was ejected. Four of the ejected model cowbird eggs were found on the ground within 5 m of the vireo nests. Two of these eggs had no discernable peck marks on them, whereas the other two eggs each had a few slight peck marks or chipped paint. The two model eggs I removed from nests after 24 hrs had small peck marks on them indicating attempts had been made to puncture-eject them and both had previously ejected real cowbird eggs. Clearly, Warbling Vireos did not seriously damage the plaster eggs and did not puncture-eject these solid eggs (Figure 4.3A). At one nest where a model egg was accepted, two host eggs were missing, which were likely damaged during ejection attempts and removed from the nest. Including ejection attempts at these two nests, the cost of attempted ejection was $0.09 (\pm 0.09 \text{ SE}; n = 22)$ host eggs damaged or missing per cowbird ejection attempt.

In contrast to Warbling Vireos, Baltimore Orioles did not eject or accept a significant proportion of model cowbird eggs (44.8 % ejected, $n = 29$, $P = 0.711$, Binomial Test). The method of ejection was not confirmed at the four nests that were videotaped after the addition of plaster eggs. In the two videos where Baltimore Orioles ejected the plaster egg, the view was obscured because of the direction orioles exited the nests, preventing visual assessment of ejection method. At all nests where plaster eggs were accepted, there was evidence of an ejection attempt, i.e. pecked eggs and sometimes missing host eggs. Baltimore Orioles damaged or lost an average of $0.23 (\pm 0.12 \text{ SE}; n = 13)$ eggs per ejection and $0.24 (\pm 0.09 \text{ SE}; n = 29)$ eggs per ejection attempt. There was no significant difference ($U = 101.0$, $P = 1.0$, Mann-Whitney U Test) in the cost of

Figure 4.2. Male Warbling Vireo (sex identified by song just prior to ejection) at nest
1999-75 grasp-ejecting a plaster model cowbird egg.

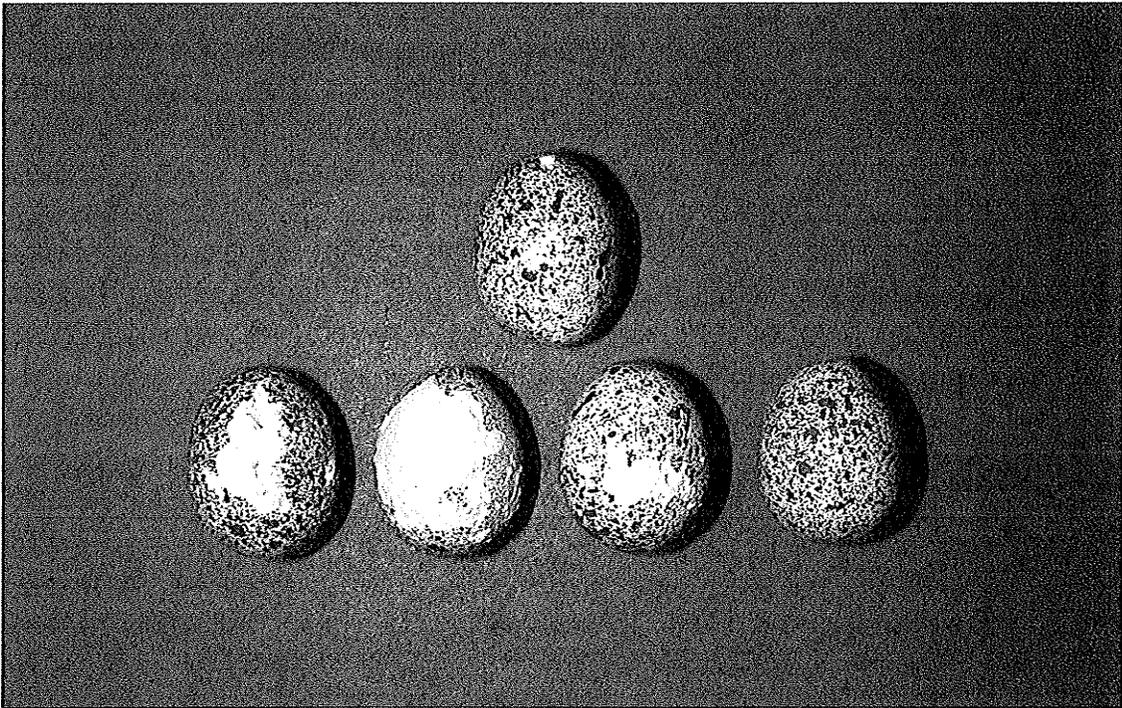


Figure 4.3. Plaster model cowbird eggs from experiments with Warbling Vireos (A) and Baltimore Orioles (B). For each photograph, the top row contains ejected eggs that were recovered near the nests and the bottom row contains eggs that were accepted and subsequently removed from nests.

A



B



attempted ejection between nests where a plaster egg was successfully ejected (cost = 0.23 eggs/ejection \pm 0.12 SE; n = 13) and nests where a failed ejection attempt occurred (cost = 0.25 eggs/attempt \pm 0.14 SE; n = 16).

Grasp-index measurements

Including the *swainsoni* group in the analysis, the grasp index of Warbling Vireos differed significantly by subspecies, with *gilvus* larger than *swainsoni* group (ANOVA $F_{1, 141} = 91.430$, $P < 0.001$) but not by sex (ANOVA $F_{1, 141} = 0.836$, $P = 0.362$; Table 4.2). There was a strong trend for the interaction of subspecies and sex (ANOVA $F_{1, 141} = 3.588$, $P = 0.060$), indicating *swainsoni* group males tended to have a larger grasp index than females (Table 4.2). Using the more restrictive subspecies designation of the *swainsoni* subspecies only, the same trends in the grasp index of Warbling Vireos were found for subspecies (ANOVA $F_{1, 130} = 86.988$, $P < 0.001$), sex (ANOVA $F_{1, 130} = 0.829$, $P = 0.364$), and the interaction of subspecies and sex (ANOVA $F_{1, 130} = 3.407$, $P = 0.067$). Compared to previously known ejecter species, the grasp index of *V. g. gilvus* is much smaller than that of the other grasp-ejecters or puncture-ejecters (Table 4.2).

Baltimore Oriole nest dimensions

In 2001, I tested 30 Baltimore Oriole nests with plaster cowbird eggs, where nest dimensions were measured. None of these nests was depredated before a 24-hour result was obtained. Baltimore Orioles ejected 30 % of plaster eggs, similar to the results obtained in 1999 and 2000. At all nests where eggs were accepted, the model eggs were pecked indicating an attempt was made to eject each egg. There was no significant difference in nest depth ($t = 0.110$, $df = 28$, $P = 0.913$, Independent Samples t Test) or nest width ($t = 0.340$, $df = 28$, $P = 0.741$, Independent Samples t Test, equal variances not

Table 4.2. Grasp-index measurements (mean \pm SE) for Warbling Vireos, Baltimore Orioles and a few other grasp-ejecters and puncture-ejecters.

Species	Tomial	Commisural	Grasp Index	n
	Length	Width		
<i>V. g. gilvus</i> ^a	17.21 \pm 0.08	8.92 \pm 0.07	153.50 \pm 1.44	65
♂♂	17.27 \pm 0.09	8.85 \pm 0.08	152.95 \pm 1.89	46
♀♀	17.08 \pm 0.13	9.07 \pm 0.11	154.83 \pm 1.92	19
<i>V. g. swainsoni</i> ^b	16.19 \pm 0.07	8.39 \pm 0.06	135.88 \pm 1.24	69
♂♂	16.39 \pm 0.07	8.42 \pm 0.07	137.96 \pm 1.40	43
♀♀	15.87 \pm 0.11	8.34 \pm 0.11	132.44 \pm 2.21	26
<i>V. g. swainsoni</i> group ^c	16.21 \pm 0.06	8.40 \pm 0.05	136.34 \pm 1.14	79
♂♂	16.39 \pm 0.06	8.44 \pm 0.06	138.28 \pm 1.25	50
♀♀	15.92 \pm 0.10	8.35 \pm 0.10	133.00 \pm 2.13	29
American Robin	27.55 \pm 0.10	13.19 \pm 0.07	363.66 \pm 2.59	97
♂♂	27.52 \pm 0.13	13.03 \pm 0.09	358.59 \pm 3.05	43
♀♀	27.57 \pm 0.15	13.33 \pm 0.11	367.70 \pm 3.91	54
Gray Catbird	24.34 \pm 0.09	10.81 \pm 0.07	263.27 \pm 2.13	90
♂♂	24.52 \pm 0.10	10.99 \pm 0.08	269.60 \pm 2.25	52
♀♀	24.09 \pm 0.14	10.57 \pm 0.13	254.60 \pm 3.56	38
Cedar Waxwing	19.15 \pm 0.08	12.59 \pm 0.06	241.19 \pm 1.59	106
♂♂	19.37 \pm 0.10	12.66 \pm 0.07	245.18 \pm 2.05	58
♀♀	18.90 \pm 0.11	12.51 \pm 0.09	236.37 \pm 2.34	48

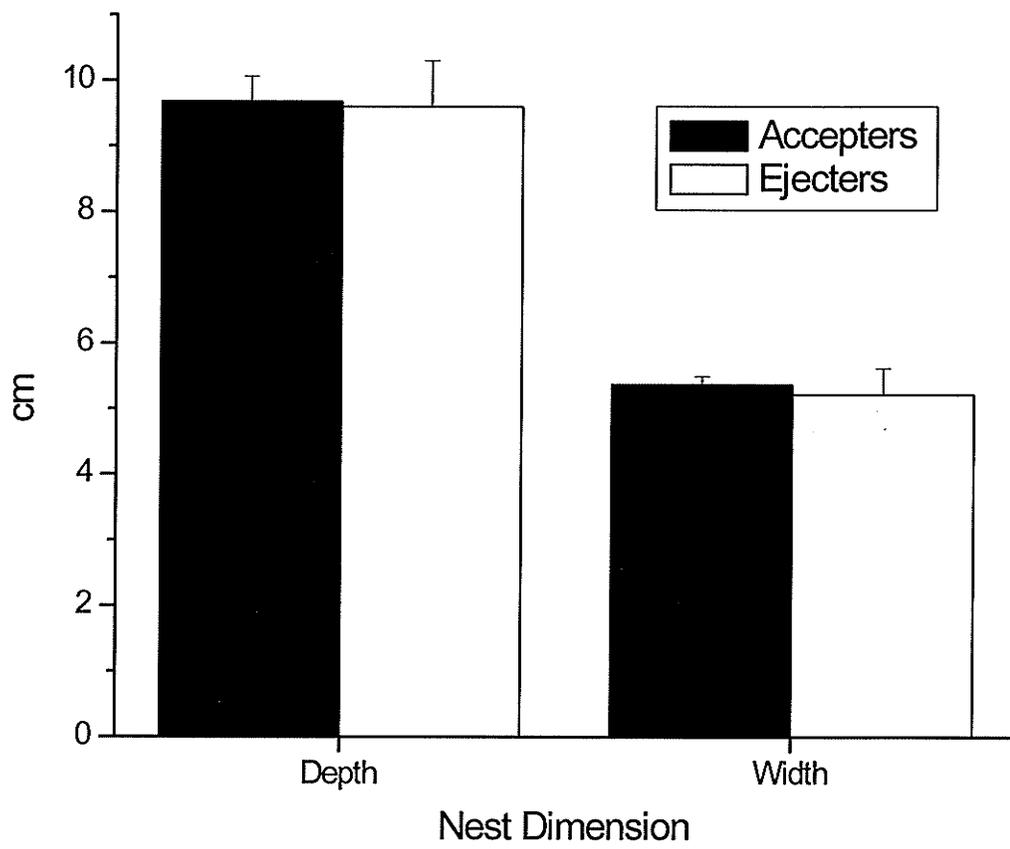
Bullock's Oriole	21.21 ± 0.11	10.50 ± 0.12	222.92 ± 3.22	51
♂♂	21.38 ± 0.13	10.54 ± 0.15	225.44 ± 3.80	36
♀♀	20.79 ± 0.18	10.36 ± 0.21	215.68 ± 5.73	16
Baltimore Oriole	20.58 ± 0.12	9.96 ± 0.04	204.97 ± 1.53	106
♂♂	20.84 ± 0.10	9.97 ± 0.06	207.85 ± 1.71	60
♀♀	20.24 ± 0.23	9.94 ± 0.06	201.22 ± 2.66	46

^a First row for each species includes measurements of both males and females.

^b Measurements are from *swainsoni* subspecies only, collected in British Columbia (see methods for details).

^c Measurements are from the western Warbling Vireo subspecies group, which breeds in western North America and Mexico (American Ornithologists' Union 1998, Gardali and Ballard 2000; see methods for details).

Figure 4.4. Nest dimensions (means \pm SE) for Baltimore Orioles that ejected ($n = 9$) or accepted ($n = 21$) plaster cowbird eggs.



assumed) between accepters and ejecters of plaster cowbird eggs (Figure 4.4). Although the power of the tests were very low, Power = 0.05 for depth and Power = 0.07 for width, the effect sizes also were very low, 0.04 for depth and 0.18 for width (Erdfelder et al. 1996). With effect sizes this small, it would take a sample of > 1,500 nests before a significant difference would be detected in either depth or width between nests of accepters and ejecters. Regardless of statistical significance, it is very doubtful that an increase in nest depth or a decrease in diameter of the nest opening of only 1 or 2 mm would have any biological significance and prevent an oriole from removing a cowbird egg by grasp-ejection. When nest dimensions of nests where egg damage occurred were compared to those where there was no egg damage, as Rohwer et al. (1989) did, there also was no significant difference in mean depth ($t = 0.234$, $df = 28$, $P = 0.817$) or width ($t = 0.275$, $df = 28$, $P = 0.785$; Table 4.3).

DISCUSSION

Warbling Vireos of the eastern subspecies ejected plaster model cowbird eggs with a negligible cost to their own eggs. Based on inspections of ejected and accepted model eggs, vireos inflicted only minor damage to these plaster eggs (Figure 4.3A) and must have ejected eggs by grasp-ejection, as the videotape confirmed (Figure 4.2). As further evidence of grasp-ejection, the cost of ejection was similar to that of other known grasp-ejecters (Table 4.1). The grasp index of *gilvus* was significantly larger than that of *swainsoni*, although there was some overlap between the subspecies. Nevertheless, the grasp index of *gilvus* is much smaller than that of any previously known grasp-ejecters or

Table 4.3. Baltimore Oriole nest dimensions (mean \pm SE) where individuals damaged their own eggs during an ejection attempt compared to those where no damage occurred.

Nest Dimension	Eggs Damaged (n)	No Damage (n)
Depth (cm)	9.48 \pm 0.43 (5)	9.69 \pm 0.39 (25)
Width (cm)	5.23 \pm 0.13 (5)	5.34 \pm 0.18 (25)

puncture-ejecters (Rohwer and Spaw 1988; Table 4.2). Therefore, being small does not appear to limit grasp-ejection, which is counter to the bill-size constraints assumption of the evolutionary equilibrium hypothesis.

The cost of ejection for Warbling Vireos was lower than that from two previous studies that used real cowbird eggs. Warbling Vireos damaged 0.1 host eggs per real cowbird egg ejected (Sealy 1996, Sealy et al. 2000). However, damage to eggs only occurred at two nests out of 29 tested. This low number of individuals that damaged their eggs is similar to the two in this study that did not grasp-eject. Due to size variation, these birds may be too small to grasp-eject and are capable only of puncture-ejection. The grasp index overlap between subspecies, the inability of a few individuals to grasp-eject, and the apparent lack of ejection behaviour in *swainsoni* (Sealy et al. 2000) suggest that Warbling Vireos may be at the small end of a size threshold for grasp-ejection of cowbird eggs. Even if the western subspecies is too small to eject cowbird eggs, the very high cost of parasitism (i.e. most Warbling Vireos in western populations lose all their young from parasitized nests; Ward and Smith 2000, Ortega and Ortega 2003) favours other more costly forms of rejection, such as nest desertion. The apparent lack of any form of rejection behaviour by *swainsoni*, despite the high cost of acceptance, provides support for the evolutionary lag hypothesis (Sealy et al. 2000, Ward and Smith 2000, Ortega and Ortega 2003).

In contrast to Warbling Vireos, an intermediate proportion of Baltimore Orioles was capable of ejecting plaster model cowbird eggs. Similar levels of ejection of plaster cowbird eggs have been previously recorded by Rothstein (1977) in Baltimore Orioles, based on a small sample (33 % ejection; $n = 3$) and from a larger sample of Bullock's

Orioles (20 % ejection; $n = 15$). However, orioles caused heavy damage to accepted and ejected plaster eggs and a few eggs had holes up to ca. 3 mm pecked into them (Figure 4.3B). Plaster is brittle if a strong enough force is applied to it, therefore, some orioles may have been strong enough to peck holes into the eggs or break the eggs into small pieces as sometimes occurs with real cowbird eggs (e.g. Sealy and Neudorf 1995, Sealy 1996). The single ejected plaster egg that was found near an oriole nest had a hole 2 mm in diameter and 2 mm deep pecked into it. Plaster eggs with holes or broken plaster eggs may have allowed a few orioles to remove eggs by puncture-ejection or to remove small portions of the eggs piecemeal. Similarly, some Great Reed Warblers (*A. arundinaceus*) were suspected of removing clay eggs by pecking small holes and using these to eject the model eggs (Lotem et al. 1995). Unfortunately, the method of ejection by orioles was not confirmed, but an anecdotal observation suggests grasp-ejection does occur. A real egg ejected by Baltimore Orioles as part of another study (Chapter 1) was found on the ground within a few meters of nest 1999-28. This egg was intact, without punctures or other damage, indicating it must have been grasp-ejected.

Moksnes et al. (1991) assumed birds that removed model eggs made of plastic without damaging their own eggs were grasp-ejectors, whereas those that damaged their eggs while ejecting a model egg were puncture-ejectors. This assumption was later confirmed for two puncture-ejectors by videotaping nests where real eggs were ejected (Moksnes et al. 1994). Applying these criteria to Baltimore Orioles that ejected plaster eggs (no vireos damaged their own eggs during ejection), damage to eggs occurred at three of 13 oriole nests during ejection. Thus, 77 % (10 of 13) of orioles that ejected plaster eggs were grasp-ejectors (or 34 % of all those tested).

If most eastern Warbling Vireos are capable of grasp-ejecting cowbird eggs, why are most individuals of the larger-billed and heavier (15 g versus 34 g; Dunning 1993) orioles incapable of grasp-ejection? Rothstein's (1977) nest depth hypothesis was not supported. There was no significant difference in either nest dimension between ejecters and accepters of plaster eggs. Individual orioles grasp-ejected plaster eggs from both relatively shallow (i.e. 4 cm deep) and deep (i.e. 13 cm deep) nests. There also was no evidence that nest dimensions caused more host eggs to be damaged during ejection attempts.

The ejection abilities of Cedar Waxwings (Rothstein 1975a) provide additional evidence that nest dimensions do not constrain grasp-ejection of cowbird eggs. Waxwings also were unable to grasp-eject most plaster cowbird eggs with only 23 % of plaster eggs ejected during laying versus 67 % of real eggs during this period (Rothstein 1976). Some plaster eggs were heavily damaged indicating attempts were made to puncture these eggs. Despite their difficulty grasp-ejecting cowbird eggs, Cedar Waxwing nests are shallow cups with an average depth of 3.9 cm (Witmer et al. 1997), which is similar to or shallower than the nests of other grasp-ejecters, such as American Robins and Gray Catbirds (Nickell 1965, Sallabanks and James 1999).

Rothstein (1977) also suggested that the straight and acute shape of oriole bills further physically constrained grasp-ejection ability. Indeed, most other grasp-ejecters have a slightly hooked or decurved bill, e.g. kingbirds (*Tyrannus* spp.) and thrashers (Mimidae). Perhaps the slightly hooked bill of Warbling Vireos, a characteristic of the Vireonidae (Sibley and Ahlquist 1982), enhances their ability to grasp-eject cowbird eggs. However, waxwings also have a hooked bill and difficulty with grasp-ejection

(Rothstein 1976), therefore, bill shape may not entirely account for a lack of grasp-ejection by orioles.

The results of my Warbling Vireo experiments confirmed that most vireos were capable of grasp-ejection. However, of the four ejections of real cowbird eggs observed by Sealy (1996), none was by grasp-ejection and all cowbird eggs appeared to be puncture-ejected. In addition, in one videotaped ejection of a plaster cowbird egg, the vireo appeared to peck the egg many times before finally grasping and ejecting it. Other presumed grasp-ejecters also have been observed pecking plaster cowbird eggs before ejecting them (Rothstein 1975a). Furthermore, a recent study of the method of ejection of cuckoo eggs found that both puncture-ejecters and grasp-ejecters pecked model eggs before ejecting them, including the large European Blackbird (*Turdus merula*), which pecked the model eggs an average of 18 times before removing them by grasp-ejection (Soler et al. 2002). Warbling Vireos are not alone in displaying both methods of ejection even though most individuals are capable of grasp-ejection. Using both their own observations and those from the literature, Sealy and Neudorf (1995) summarized the method of cowbird egg ejection for several species in which ejections of real cowbird eggs were observed. Most species grasp-ejected only, but three out of four ejections of real cowbird eggs by American Robins were by puncture-ejection (Sealy and Neudorf 1995). The American Robin is a large species (Table 4.2) and has been assumed to be a grasp-ejecter, along with several other species, because it ejects most plaster eggs (Rothstein 1975a). Thus, based on observational data (Sealy and Neudorf 1995, Sealy 1996) and experiments (Rothstein 1976, 1977; this study), five ejecters (Warbling Vireos,

American Robins, Cedar Waxwings, Bullock's Orioles, and Baltimore Orioles) have been identified using both puncture-ejection and grasp-ejection.

Why do some individuals puncture-eject when grasp-ejection is the more efficient method and is physically possible? I propose that the grasp-ejection trait may not be fixed in some species because most species first evolved puncture-ejection to remove cowbird eggs. The unusually thick and strong shells of Brown-headed Cowbird eggs are believed to have evolved to resist puncture-ejection by hosts (Spaw and Rohwer 1987, Rahn et al. 1988, Picman 1989; but see Blankespoor et al. 1982, Rothstein 1990, Brooker and Brooker 1991 for alternative hypotheses). Selection for strong shells was interpreted to have come from small hosts, incapable of grasp-ejection due to size constraints, that are now accepters because of the high costs of puncturing a thick-shelled egg (Spaw and Rohwer 1987, Rohwer and Spaw 1988). The grasp-ejection ability of Warbling Vireos suggests that many of these small accepter species are physically capable of grasp-ejection and are not constrained by size. Therefore, there is little evidence to support that selection for thick-shelled cowbird eggs has come only from small hosts.

The low levels of grasp-ejection in Cedar Waxwings, Bullock's Orioles and Baltimore Orioles along with the prevalence of some puncture-ejection in Warbling Vireos and American Robins suggests that these ejecters may have evolved first as puncture-ejecters before cowbirds evolved thick shells. Rohwer et al. (1989) found that puncture-ejection of real eggs of a "normal" thickness, i.e. Cliff Swallow (*Hirundo pyrrhonota*) eggs, incurs a very low cost, which is similar to the cost of grasp-ejecting cowbird eggs. Thus, for a cowbird egg with a shell of normal thickness, there would be no selective advantage of either method of ejection. Both grasping and pecking

behaviours are important aspects of nest sanitation (sensu Rothstein 1975a), nest building, and foraging activities. Thus, neither grasp-ejection nor puncture-ejection is likely to have been a “simpler” mechanism to evolve. Once cowbirds evolved eggs with thick shells as a counterdefence to puncture-ejection by these hosts, grasp-ejection would be selected because it is less costly. If supported, this scenario would reveal a much more involved coevolutionary arms race between Brown-headed Cowbirds and their hosts than previously suggested.

Summary

Warbling Vireos can grasp-eject cowbird eggs and do so with a negligible cost to their own eggs, whereas most Baltimore Orioles are not capable of grasp-ejection. Grasp-index measurements indicate that Warbling Vireos are much smaller than all other known grasp-ejecters or puncture-ejecters. This is counter to the bill-size constraints assumption of the evolutionary equilibrium hypothesis. Small size is not a constraint against ejection and many more species should be capable of grasp-ejecting cowbird eggs, especially other vireos that are larger, heavily parasitized and equipped with a similar bill, e.g. Red-eyed Vireos (*V. olivaceus*; Cimprich et al. 2000). These results combined with the high costs of accepting cowbird parasitism by small hosts (Lorenzana and Sealy 1999) and the relatively high probability of parasitism for many hosts suggest that acceptance of parasitism by cowbird hosts is due to an evolutionary lag in the appearance of rejection behaviour. By contrast, an evolutionary equilibrium is a more likely explanation for the acceptance of mimetic eggs by some cuckoo hosts that experience high costs of ejection, recognition errors and a lower probability of parasitism (Davies et al. 1996, Davies 1999).

The intermediate level of grasp-ejection found in Baltimore Orioles may be somewhat constrained by the shape of their bill and, ultimately, may be the result of an adaptation that has yet to become fixed in this species. Further evidence for a mixture of grasp-ejection and puncture-ejection in several species suggests that puncture-ejection may not be limited to small hosts, may have evolved before grasp-ejection in some species, and may represent a stronger selection pressure for thick-shelled cowbird eggs than previously suggested. Future research should focus on determining whether other ejecter species exhibit both types of ejection behaviour and whether the western subspecies of Warbling Vireos are too small to eject cowbird eggs or are incapable of egg recognition.

CHAPTER 5. EGG RECOGNITION IN THE ABSENCE OF A CURRENT SELECTION PRESSURE OF BROOD PARASITISM

INTRODUCTION

Some adaptations cannot be explained in the context of current selection pressures and utility (Jamieson 1986, Byers 1997, Rothstein 2001). These traits are considered 'relics' or 'ghosts' of past selection pressures that have been retained since selection pressures were relaxed thousands of years in the past (Coss 1993, 1999; Byers 1997, Rydell et al. 2000). For example, anti-snake behaviours in California ground squirrels (*Spermophilus beecheyi*) persist despite isolation of squirrels from predatory snakes for approximately 70,000 to 300,000 years (Coss 1993, 1999). Recently, relic behaviours related to past exposure to brood parasitism have been identified.

Currently, grackles (*Quiscalus* spp.) are rarely parasitized by cowbirds (*Molothrus* spp.) yet most species eject almost all cowbird eggs experimentally added to their nests (Peer 1998). In Great-tailed Grackles (*Q. mexicanus*), there was no evidence of cowbird or conspecific parasitism, which suggests a lack of a current selection pressure for egg recognition (Peer and Sealy 2000a). Peer (1998) concluded that ejection in grackles evolved in response to past parasitism by Giant Cowbirds (*M. oryzivora*) on Great-tailed Grackles and has been retained through speciation by Boat-tailed Grackles (*Q. major*). Similarly, Rothstein (2001) concluded that Loggerhead Shrikes (*Lanius ludovicianus*) have retained ejection behaviour from Old World congeners that eject cuckoo (Cuculinae) eggs and Gray Catbirds (*Dumetella carolinensis*) on Bermuda have retained ejection behaviour from their ancestral North American population. By contrast,

others have found that egg rejection frequencies were reduced in populations allopatric to brood parasites compared to those in sympatry, although rejection frequencies of some egg types in allopatry were still relatively high, i.e. 36 % to 66 % (Davies and Brooke 1989, Briskie et al. 1992). Cruz and Wiley (1989) found that egg ejection frequencies were reduced in an introduced population of Village Weavers (*Ploceus cucullatus*) allopatric to cuckoos (*Chrysococcyx* spp.) for over 100 years. After exposure to Shiny Cowbird (*M. bonariensis*) parasitism, ejection frequency in this population increased considerably in 16 years possibly due to rapid genetic microevolutionary change (Robert and Sorci 1999). However, these changes in host defences may not actually reflect the loss of or regaining of an adaptation, but may represent phenotypic flexibility related to the risk of parasitism perceived in the absence or presence of brood parasites (Zuñiga and Redondo 1992, Brooke et al. 1998, Rothstein 2001). Alternatively, a decline in an adaptation in the absence of current selection may occur if that adaptation is costly to maintain (Byers 1997).

Black-billed Magpies (*Pica hudsonia*) of North America apparently have retained relic egg-recognition behaviour (Bolen et al. 2000). There is no evidence of current parasitism on Black-billed Magpies by any interspecific brood parasite (Trost 1999). Old World magpies *P. pica*, hereafter Eurasian Magpies, are major hosts of Great Spotted Cuckoos (*Clamator glandarius*) throughout Europe and Africa and have been recorded as hosts of Asian Koels (*Eudynamys scolopacea*) in southeast Asia (Baker 1942, Johnsgard 1997). In Europe, Great Spotted Cuckoo eggs mimic only eggs of Eurasian Magpies, their primary host (Soler 1990). Eurasian Magpies eject varying frequencies of non-mimetic and mimetic eggs (Soler et al. 1999). This variability appears to be related to the

duration of sympatry with cuckoos, geographic distance between magpie populations, and gene flow between sympatric and allopatric populations (Soler 1990, Soler and Møller 1990, Soler et al. 1999). Black-billed Magpies, previously considered conspecific with Eurasian Magpies (Trost 1999), may have retained egg recognition if their ancestral population was from an area of sympatry or if they retained egg recognition in allopatry. However, a taxonomic reclassification of Black-billed Magpies as a species distinct from Eurasian Magpies (American Ornithologists' Union 2000) based on differences in behaviour, vocalizations, and genetics (Birkhead 1991, Enggist-Düblin and Birkhead 1992, Zink et al. 1995) suggests that these two species have been isolated for a long time. Thus, ejection frequencies of non-mimetic and mimetic eggs, if retained through speciation, may have declined in Black-billed Magpies in comparison to Eurasian Magpies.

Recently, Bolen et al. (2000) tested egg-recognition abilities of Black-billed Magpies in Idaho and Yellow-billed Magpies (*P. nuttalli*) in California. Both species ejected all non-mimetic eggs added to their nests and Yellow-billed Magpies ejected 11 % of conspecific eggs. Bolen et al. (2000) concluded that Black-billed Magpies have retained egg-recognition capabilities that originally evolved in Eurasian Magpies to counter parasitism by Old World cuckoos. Ejection in Yellow-billed Magpies was considered to be a plesiomorphic trait inherited from Black-billed Magpies (Bolen et al. 2000). However, an alternative hypothesis that egg-recognition abilities in both North American species of magpie evolved initially (or has been maintained) in response to the threat of conspecific parasitism has not been tested in Black-billed Magpies. There is no evidence of conspecific parasitism in Yellow-billed Magpies (Reynolds 1995, Bolen

1999), but there is anecdotal evidence for Black-billed Magpies. Trost and Webb (1986) documented the movement of a few marked eggs between magpie nests that possibly represents a strategy for conspecific parasitism involving the transfer of eggs in the bill (e.g. Brown and Brown 1988). In addition, neither North American magpie has been tested for recognition of artificial mimetic eggs, which would provide a relative comparison of these species' recognition capabilities to Eurasian Magpies.

In this study, I determined whether an additional population of Black-billed Magpies, at the eastern edge of this species' range in North America, has retained egg recognition in the absence of brood parasitism. I also determined the ability of Black-billed Magpies to recognize mimetic eggs and tested the alternative hypothesis that egg recognition is an adaptation to counter conspecific parasitism. For comparison, I tested American Crows (*Corvus brachyrhynchos*), which I predicted would accept foreign eggs. North American *Corvus* species are not known to host any brood parasite (but see Hatch 1967 for an incidental cowbird parasitism record). More importantly, although other *Corvus* species host brood parasites in Europe, Africa, and Asia (Johnsgard 1997), there is no evidence that any species ejects foreign eggs and all species experimentally tested are accepters (Yom-Tov 1976, Soler 1990).

METHODS

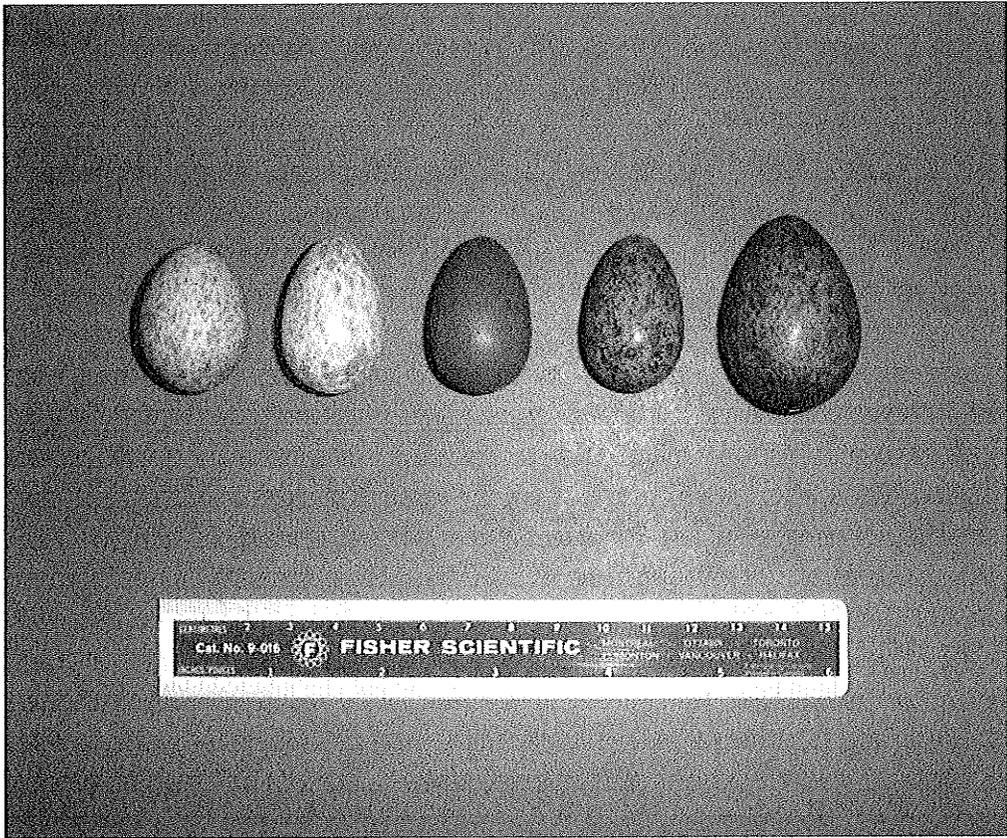
General

This study was conducted in and around Winnipeg, Manitoba, Canada (49° 53' N, 97° 8' W). In April and May 1999, randomly assigned non-mimetic and mimetic eggs were added to magpie and crow nests during laying and incubation. I added eggs to nests

throughout the entire incubation period because the exact day of incubation was unknown at the time of experimental parasitism. A single experimental egg was added to each nest without the removal of a 'host' egg. I inspected each nest daily to determine whether the experimental egg was ejected, the time until ejection, and to detect damaged or missing host eggs. If the experimental egg was in the nest after 5 days and the nest was still active, I considered the egg accepted and removed it. Because the retention of a behaviour is influenced by its cost (Byers 1997), I calculated the cost of ejection (i.e. number of damaged or missing host eggs/foreign egg ejected) and the frequency of egg recognition errors. Recognition errors are of two forms, ejection errors or true recognition errors (Røskoft et al. 2002). Ejection errors occur when a host ejects one of its own eggs in a parasitized nest instead of a parasitic egg (e.g. Davies and Brooke 1988), whereas true egg recognition errors occur when a host ejects one of its own eggs in an unparasitized nest (e.g. Marchetti 1992). I only calculated the frequency of ejection errors because unmanipulated nests were not monitored. I assumed that any magpie egg damaged or missing from an experimentally parasitized nest was the result of an ejection cost or an ejection error. Finally, the influence of nest stage was considered because some hosts of Old World cuckoos respond differently to parasitic eggs depending on the stage of the nest at the time of parasitism (e.g. Davies and Brooke 1988, 1989a). Nest stage was determined by recording egg laying between daily nest checks or backdating from the hatching date.

Experimental eggs were made of wood and painted with non-toxic acrylic paints (Folk Art Acrylic Paint by Plaid®; colours and product numbers to follow). Non-mimetic eggs were painted blue (Blue Ribbon 719; Figure 5.1). Mimetic eggs were

Figure 5.1. Experimental egg treatments added to Black-billed Magpie and American Crow nests. Eggs are (from left to right) real magpie egg, artificial magpie egg (mimetic), artificial egg (non-mimetic), artificial crow egg (mimetic), and real crow egg.



painted to match the appearance of Black-billed Magpie or American Crow eggs (Figure 5.1). For mimetic magpie eggs, a base colour of beige (Tapioca CA903) was used with spots of light brown (Butter Pecan CA939) and dark brown (a 1:1:1 mixture of Butter Pecan CA939, Coffee Bean 940, and Honeycomb CA942). For mimetic crow eggs, a base colour of light green (a 5:1:1:0.5 mixture of Basil Green 645, Olive Green 449, Mushroom 472, and Yellow Light 918) was used with spots of black (Licorice 938), olive green (a 8:2:1 mixture of Olive Green 449, Coffee Bean 940, and Yellow Light 918), and brown (a 1:1:1 mixture of Coffee Bean 940, Olive Green 449, and Mushroom 472). Experimental eggs approximated the size of Great Spotted Cuckoo eggs, 31.2 x 23.5 mm, but real cuckoo eggs are slightly heavier, at 9.5 g (Soler 1990). Measurements of 25 experimental eggs averaged 34.0 x 22.3 mm ($\pm 0.03 \times 0.04$ SE) and mass averaged 6.0 g (± 0.08 SE). Experimental eggs were similar in size to real magpie eggs, which average 33.5 x 23.5 mm, and slightly lighter than real magpie eggs, which weigh 9.4 g (Trost 1999). However, experimental eggs were smaller than American Crow eggs, which average 41.4 x 29.1 mm (Harrison 1975). Most hosts show similar levels of rejection or acceptance of artificial wooden eggs as they do of real eggs (Peer et al. 2000).

Conspecific egg recognition – Black-billed Magpies

In April and May 2000, I tested the ability of Black-billed Magpies to recognize conspecific eggs. Eggs were collected from four magpie nests at which no experimentation occurred. One conspecific egg was added to each experimental nest during laying or incubation, without the removal of a 'host' egg. At the time of addition, each host egg was numbered sequentially with a non-toxic, black marker. Numbers given to foreign conspecific eggs were varied sequentially for each additional nest to

remove any possible bias (i.e., a number that provided a larger mark). Nests were inspected daily through day 5 to determine whether the conspecific egg was ejected, the time until ejection, and to detect damaged or missing host eggs. After day 5, each nest was inspected again on days 8 and 11. Using the same criteria as the general tests for egg recognition in magpies, I also calculated the cost of conspecific egg ejection and the frequency of ejection errors.

The degree of similarity between the foreign conspecific egg and each egg of the host clutch was qualitatively assessed for each of ground colour, spot pattern, and size. Each host egg was assessed at the time of addition as were any host eggs laid after egg addition. A similarity index was generated by assigning a score to each conspecific egg in terms of the number of host eggs it visually matched for each of the three parameters. The sum of these scores was then divided by the host clutch size to calculate the value for the index at a given nest. For example, if a conspecific egg matched 3 of 6 host eggs in ground colour, 2 of 6 host eggs in spot pattern, and 6 of 6 host eggs in size, its similarity index was $(3 + 2 + 6)/6 = 1.83$. Thus, the similarity index potentially ranges from 0.0 (egg matched no host eggs in any parameter) to 3.0 (egg matched each host egg in all parameters). With the similarity index, I compared how well a conspecific egg matched host eggs at nests where magpies accepted versus ejected foreign conspecific eggs.

In addition, I used Davies et al.'s (1996) model to estimate the level of conspecific parasitism that would select for conspecific egg ejection in Black-billed Magpies. This model predicts the threshold level of parasitism above which it is more profitable for a host to reject parasitism than to accept it based on the cost of ejection, the probability of making recognition errors, and the cost of acceptance. Data for seven

parameters were required to run the Davies et al. (1996) model: 1) probability of correctly ejecting a parasitic egg, 2) cost of ejection, 3) probability of making an ejection error, 4) cost of an ejection error, 5) cost of accepting parasitism, 6) probability of making a true egg recognition error, and 7) cost of making a true egg recognition error. The first four parameters were calculated from data collected in the experimental tests of conspecific egg recognition. Because true egg recognition errors are extremely difficult to detect and the cost of conspecific parasitism in Black-billed Magpies is unknown, I estimated the values for the final three parameters based on information from the literature.

Analysis

Fisher exact tests were used to compare the proportion of non-mimetic to mimetic eggs ejected. These tests were one-tailed because I predicted more non-mimetic eggs would be ejected than mimetic eggs. Two-tailed Fisher exact tests were used to compare the proportion of eggs ejected by nest stage and two-tailed Mann-Whitney U tests were used to compare time to ejection. For all tests, I used a significance level of $\alpha = 0.05$.

RESULTS

General egg recognition – Black-billed Magpies

Three magpie nests (5 %) were depredated before a result was recorded: two before the first inspection was made on day 1 and one on day 3 of acceptance. Depredations on day 1 do not bias results toward ejection or acceptance and are not included in any analyses. Exclusion of depredated nests that were accepted for more than one day could bias results toward ejections (e.g. Davies and Brooke 1988). However,

including the single depredated nest as an acceptance did not alter the significance of the observed trends. Therefore, these data are presented without this nest. No magpie nests were deserted.

There was no significant difference in ejection frequency of non-mimetic eggs by nest stage (Fisher exact test, two-tailed, $P = 1.0$), whereas ejection frequency according to nest stage for mimetic eggs differed significantly (Fisher exact test, two-tailed, $P = 0.05$). Thus, I analyzed these data separately for each nest stage and combined across nest stages when non-mimetic and mimetic eggs were compared.

Across nest stages, magpies ejected all non-mimetic eggs, whereas about half of the mimetic eggs were ejected (Table 5.1). Significantly more non-mimetic eggs than mimetic eggs were ejected (Fisher exact test, one-tailed, $P < 0.0001$). However, for eggs ejected, there was no difference in time to ejection for non-mimetic versus mimetic eggs (Table 5.2). No eggs were damaged or missing after magpies ejected non-mimetic eggs ($n = 26$), but there was a low cost of ejection for mimetic eggs, 0.06 eggs damaged or missing/ejection ($n = 16$). For magpies that accepted mimetic eggs, there was no evidence for ejection errors because no eggs were damaged or missing from these clutches ($n = 10$).

Regardless of nest stage, magpies ejected all non-mimetic eggs (Table 5.1). There was no significant difference in time to ejection of non-mimetic eggs by nest stage (Table 5.2). Magpies ejected half of the mimetic eggs during laying, whereas all mimetic eggs were ejected during incubation (Table 5.1). Of the mimetic eggs ejected, there was no significant difference in time to ejection by nest stage (Table 5.2). Significantly more

Table 5.1. Percent of experimental eggs ejected by Black-billed Magpies and American Crows.

Species	Egg type	Laying (n)	Incubation (n)	Overall (n)
Black-billed Magpie	non-mimetic	100 (10)	100 (16)	100 (26)
	mimetic	50 (20)	100 (6)	62 (26)
	conspecific ^a	0 (11)	0 (9)	0 (20)
American Crow	non-mimetic ^b	33 (9)	0 (5)	21 (14)
	mimetic ^b	13 (8)	0 (4)	8 (12)
	non-mimetic ^c	33 (9)	17 (6)	27 (15)
	mimetic ^c	22 (9)	20 (5)	21 (14)

^a 5-day acceptance criterion.

^b Ejection frequency does not include desertions.

^c Rejection frequency includes desertions.

Table 5.2. Time to ejection (days) of experimental eggs by Black-billed Magpies by nest stage. P is the significance value for Mann-Whitney U test, two-tailed.

Comparison	Laying \pm SE (n)	Incubation \pm SE (n)	Stages Combined \pm SE (n)
Non-mimetic	1.19 \pm 0.14 (16) ^a	1.00 \pm 0.00 (10) ^a	1.12 \pm 0.08 (26)
Mimetic	1.90 \pm 0.48 (10) ^b	1.33 \pm 0.33 (6) ^b	1.69 \pm 0.33 (16)
Non-mimetic	U = 63.5	U = 25.0	U = 169.0
Vs. Mimetic	P = 0.21	P = 0.20	P = 0.10

^a U = 70.0, P = 0.25

^b U = 25.0, P = 0.48

non-mimetic eggs were ejected than mimetic eggs during laying (Fisher exact test, one-tailed, $P < 0.01$). However, the response to the two egg types during incubation did not differ significantly (Fisher exact test, one-tailed, $P = 1.0$). Time to ejection of non-mimetic versus mimetic eggs was not significantly different by nest stage (Table 5.2).

General egg recognition – American Crows

No American Crow nests were depredated before a response was recorded. Crows deserted three nests, one containing a non-mimetic egg and two with mimetic eggs. In some species, desertion may be a response to natural parasitism (Hosoi and Rothstein 2000, but see Hill and Sealy 1994). However, hosts rarely desert experimentally parasitized nests without clutch reduction (e.g. no desertions in response to experimental parasitism in five corvid species; Soler 1990). Furthermore, American Crows are known to occasionally desert unmanipulated nests in response to human visitation (e.g. McGowan 2001). Because I did not test a group of nests to control for desertion responses, I analyzed these data with and without desertion responses. Nest stage did not significantly influence crows' response to non-mimetic eggs (Fisher exact tests, two-tailed, $P = 0.26$ excluding desertions or $P = 0.60$ including desertions) or mimetic eggs (Fisher exact tests, two-tailed, $P = 1.0$ excluding or including desertions). Therefore, data were pooled across nest stages for further analysis.

American Crows infrequently ejected non-mimetic eggs and rarely ejected mimetic eggs (Table 5.1). Including desertion as a response, rejection frequencies of non-mimetic and mimetic eggs increased slightly (Table 5.1). Unlike magpies, crows did not eject or reject (including desertion) significantly more non-mimetic than mimetic eggs (Fisher exact tests, one-tailed, $P = 0.36$ excluding desertion or $P = 0.54$ including

desertion). There was no cost of ejection for crows that ejected non-mimetic eggs ($n = 3$) or mimetic eggs ($n = 1$). At nests where crows accepted eggs, no eggs were missing from nests that were parasitized with non-mimetic eggs ($n = 11$) or mimetic eggs ($n = 11$). Thus, there was no evidence of ejection errors.

Conspecific egg recognition – Black-billed Magpies

Four magpie nests (17 %) parasitized with conspecific eggs were depredated before a 5-day result was recorded. Two nests were depredated on the first day a response could be recorded and one each on days 2 and 3 of acceptance. Two nests were depredated between days 5 and 8, and one nest was depredated between days 8 and 11. Thus, these results may be biased slightly toward a higher ejection frequency.

All conspecific eggs were accepted through day 5 ($n = 20$), whereas 2 conspecific eggs were ejected by day 8 (11.1 % ejected, $n = 18$) and no additional eggs were ejected by day 11 ($n = 17$, one nest was checked on day 10 instead of day 11 because of logistic constraints). No host eggs were damaged or missing at the two nests where conspecific eggs were ejected. At nests where conspecific eggs were accepted through day 8 ($n = 16$), single host eggs were missing from each of two magpie nests providing evidence of ejection errors. There was no significant difference in ejection (8-day criterion) of conspecific eggs based on nest stage (Fisher exact test, two-tailed, $P = 0.18$). The similarity index for conspecific eggs that were accepted (8-day criterion) was 1.71 (± 0.16 SE, $n = 16$), whereas the indices for the two ejected conspecific eggs were 1.83 and 2.71. This indicates that ejected conspecific eggs appeared to be more similar to host eggs than the average conspecific egg that was accepted, although both values fell within the range of similarity indices of accepted conspecific eggs (range = 0.80 – 3.0).

The following data were used as parameter estimates for the Davies et al. (1996) model. Magpies ejected four conspecific eggs, two correctly and two incorrectly (probability of correctly ejecting = 0.5 and probability of making an ejection error = 0.5). To estimate the cost of ejection of conspecific eggs, I used the cost of ejection for all egg types (0.023 eggs/ejection; total $n = 44$ for non-mimetic, mimetic, and conspecific eggs) because of the very small sample of conspecific eggs ejected. The mean number of host eggs lost per ejection error was 1.0 eggs/error. This represents the cost of an ejection error because no further production loss is expected with a conspecific egg in the nest after the loss of a host egg. I assumed that the cost of accepting parasitism was a lowering of nest production by 33 % because Högstedt (1980) found that Eurasian Magpies with a clutch size of seven eggs, the mean clutch size in my study (Underwood unpublished data), produced 33 % fewer offspring when a single conspecific egg was added to their nests. However, this cost estimate may be high because predation was significantly higher on enlarged clutches in this study (Högstedt 1980). The probability of making a true recognition error is more difficult to determine or estimate. Therefore, I followed Davies et al.'s (1996) approach and used two estimates. The first assumed that a host always ejects the oddest egg in their nest (probability = 1.0) and the second assumed the same probability for true recognition errors as there were for ejection errors (probability = 0.5). Finally, I assumed that the cost of a recognition error was the same as for an ejection error (1.0 egg/error).

Using these parameter estimates, Davies et al.'s (1996) model predicts that either 21.8 % or 35.7 % of magpie nests must be parasitized by conspecifics to favour conspecific egg ejection, depending on the probability of true egg recognition errors.

However, this estimate is based on a fairly high cost of accepting parasitism. If a conspecific parasite removes a host egg at the time of parasitism as do most obligate brood parasites (Wyllie 1981, Sealy 1992) and some conspecific parasites (Lombardo et al. 1989), then the cost of parasitism should be only that of the loss of the host egg removed by the parasite (similar to the cost of an ejection error). If we assume that magpies removed a single host egg from one-third of the nests they parasitized (as some conspecific parasites do; Lombardo et al. 1989), the cost of parasitism overall would be lower. Using this lower cost of parasitism, the model predicts that either 26.8 % or 42.3% of magpie nests must be parasitized by conspecifics to favour conspecific egg ejection, depending on the probability of true egg recognition errors.

DISCUSSION

Black-billed Magpies in Manitoba ejected all non-mimetic eggs, responded intermediately to mimetic eggs during laying, and ejected all mimetic eggs during incubation. American Crows accepted most non-mimetic and mimetic eggs. These results extend those of Bolen et al. (2000) in support of the hypothesis that Black-billed Magpies retained egg-recognition behaviour in the long absence of a selection pressure of interspecific brood parasitism. The ability of magpies to recognize some mimetic eggs shows that these abilities have remained relatively refined. The inability of most American Crows to recognize either egg type reveals that egg recognition in magpies is not likely related to nest sanitation behaviour or the predatory nature of corvids (e.g. Yom-Tov 1976, Moskát et al. 2003). The limited recognition abilities of American

Crows were similar to their European congeners, which are infrequent hosts of Great Spotted Cuckoos (Soler 1990).

Surprisingly, Black-billed Magpies ejected more mimetic eggs added during incubation than laying. Parasitic eggs laid during incubation present a lower risk because they are less likely to hatch. Other rejecter species that respond differently to parasitism by nest stage have a higher rejection frequency during laying, e.g. Cedar Waxwings (*Bombycilla cedrorum*; Rothstein 1976) and Yellow Warblers (*Dendroica petechia*; Sealy 1995). However, Davies and Brooke (1988) found that Reed Warblers (*Acrocephalus scirpaceus*) were more likely to reject Common Cuckoo (*Cuculus canorus*) eggs later in the nest cycle and suggested that hosts may inspect clutches more closely after incubation has begun. Indeed, attentiveness of female Black-billed Magpies supports this idea. Percent of time females spent at nests was 23 %, on the first day of laying but steadily increased to 90 % by the seventh day where it remained until hatching (Buitron 1988).

Little evidence was found to support an alternative hypothesis that egg recognition in Black-billed Magpies has been maintained by conspecific parasitism. A low level (11 %) of conspecific recognition was found that was likely slightly inflated due to a few depredated nests before a result was obtained. Ejection of only one out of 10 parasitic eggs would not provide much of a benefit against the potential cost of parasitism. Black-billed Magpies also were just as likely to make ejection errors as they were to correctly eject the conspecific egg. Thus, conspecific egg recognition is not well refined in this species, especially compared to the high levels of ejection of non-mimetic and mimetic eggs. Similarly low levels of conspecific egg ejection have been found in

other species where evidence for no conspecific parasitism is strong (Peer and Sealy 2000). Furthermore, conspecific egg recognition is rare (Lyon 2003), especially in passerines (Underwood and Sealy 2002). A few passerines, such as *Ploceus* weaverbirds recognize conspecific eggs (Victoria 1972, Jackson 1998, Lahti and Lahti 2002), but weaverbirds are also parasitized by Diederik Cuckoos (*Chrysococcyx caprius*) that lay mimetic eggs (Rowan 1983). Whether egg recognition in weaverbirds resulted from selection from conspecific parasitism (Jackson 1998) or interspecific parasitism (Victoria 1972) has not been conclusively demonstrated (Underwood and Sealy 2002).

In Black-billed Magpies, only anecdotal evidence exists for conspecific parasitism, by egg moving, in one population, but this may have been related to human disturbance (Trost and Webb 1986). Of the three magpie species, Yellow-billed Magpies are most likely to experience conspecific parasitism because they nest in small colonies and at the highest density (Birkhead 1991), both conditions that favour conspecific parasitism (Yom-Tov 2001). However, DNA fingerprinting found no conspecific parasitism in Yellow-billed Magpies (Bolen 1999) and conspecific parasitism has not been recorded in Eurasian Magpies (Birkhead 1991). In contrast to the lack of evidence for conspecific parasitism in the three species of magpies, the predictions of Davies et al.'s (1996) model suggest a relatively high level of conspecific parasitism (21.8 % to 42.3 %) would be required for conspecific egg ejection to be favoured over acceptance. In passerines, frequencies of conspecific parasitism only occur at these levels in some colonial or dense-nesting species (Lombardo 1988, Lombardo et al. 1989, Brown and Brown 1989) and, for some colonies or colonial species, conspecific parasitism falls well short of these levels (e.g. Brown and Brown 1989, Alves and Bryant 1998). Black-billed Magpies and

Eurasian Magpies are not colonial nesters and most populations are not very dense (Birkhead 1991). Thus, it is unlikely that conspecific parasitism is high enough in Black-billed Magpies to cross the threshold level that favours conspecific egg ejection. This further supports retention of recognition in the absence of interspecific parasitism.

Based on fossil evidence, Black-billed Magpies probably arrived in North America across the Bering Sea land bridge and were present by at least the Pleistocene (Trost 1999), but may have become extinct and recolonized North America from Asia after the last glacial period (Voous 1960). However, a mitochondrial DNA difference of 3.9 % between Black-billed Magpies in North America and the Russian subspecies of the Eurasian Magpie *P. p. camtschatica* (Zink et al. 1995) implies a separation of approximately 780,000 to 2.4 million years, depending on the molecular clock estimate used (Klicka and Zink 1998). This does not support a scenario of recent recolonization. If genetic separation and molecular clock estimates are correct, this extends the retention time for a behaviour over that found in previous studies, which have suggested retention up to 300,000 years (e.g. Coss 1993).

A long absence of selection for egg recognition with no reduction in ejection behaviour is not surprising if there is little or no cost associated with the behaviour. However, ejection frequencies of non-mimetic eggs (100 %) in the two North American populations are higher than some Eurasian Magpie populations, even those sympatric with cuckoos (this study, Bolen et al. 2000, Soler et al. 1999). The ejection frequency of mimetic eggs (50 %) in North America during the laying period was similar to those of Eurasian Magpies sympatric with cuckoos, but higher than that of Eurasian Magpies in allopatry (Soler et al. 1999). Small differences in ejection frequencies may be attributed

to the experimental eggs used (i.e. different paints), but our results are consistent with those of Bolen et al. (2000) for non-mimetic eggs, although differences in experimental mimetic eggs are likely to have a somewhat greater influence on ejection frequency. Conspecific egg recognition does not explain these high levels of ejection in Black-billed Magpies and Yellow-billed Magpies (this study, Bolen et al. 2000) nor can gene flow because of the degree of genetic separation (Zink et al. 1995) and large geographic distance from potential source populations. Relatively high ejection frequencies in Black-billed Magpies compared to some Eurasian Magpie populations are somewhat surprising. However, a few allopatric populations of Eurasian Magpies, such as in Norway, eject a large proportion (58 – 100 %) of non-mimetic eggs and a small proportion (7 – 26 %) of mimetic eggs, which suggests that the lack of any egg recognition in Sweden (Soler and Møller 1990) was an anomalous result (Rothstein 2001).

One additional factor that may explain some of the discrepancy in ejection frequencies between Black-billed Magpies and Eurasian Magpies is the ‘mafia’-like behaviour of Great Spotted Cuckoos. Soler et al. (1995b) found that Great Spotted Cuckoos depredate Eurasian Magpie nests from which their egg has been ejected. Accepting a cuckoo egg may be a trade-off against the potential penalty of ejection and may not represent a lack of egg recognition. Thus, observed ejection frequencies in some populations of Eurasian Magpies may not be commensurate with their egg-recognition abilities.

Summary

Egg ejection in a Manitoba population of Black-billed Magpies supports the hypothesis that this behaviour has persisted in the absence of a current selection pressure, interspecific brood parasitism. Little support was found for conspecific parasitism selecting for egg recognition. Black-billed Magpies ejected a low frequency of conspecific eggs and Davies et al.'s (1996) model predicted a relatively high level of conspecific parasitism would be required before conspecific egg ejection would be favoured. However, conspecific parasitism cannot be completely ruled out as a potential selection pressure until Black-billed Magpie clutches or broods are examined genetically. Ejection behaviour has been retained at levels comparable to Eurasian Magpies sympatric with cuckoos. Future research on Old World subspecies of the Eurasian Magpie, especially the Asian subspecies *camtschatica*, *leucoptera* and *sericea*, may clarify the retention time of this behaviour and the degree of isolation from interspecific parasitism by Black-billed Magpies in North America.

LITERATURE CITED

- Altshuler, D. L. 2001. Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest. *Evolutionary Ecology Research* 3:767-778.
- Alvarez, F., and L. Arias de Reyna. 1974. Mecanismos de parasitización por *Clamator glandarius* y defensa por *Pica pica*. Doñana, *Acta Vertebrata* 1:43-65.
- Alvarez, F., L. Arias de Reyna, and M. Segura. 1976. Experimental brood parasitism of the magpie (*Pica pica*). *Animal Behaviour* 24:907-916.
- Alves, M. A. S., and D. M. Bryant. 1998. Brood parasitism in the Sand Martin, *Riparia riparia*: evidence for two parasitic strategies in a colonial passerine. *Animal Behaviour* 56:1323-1331.
- American Ornithologists' Union. 1957. Check-list of North American Birds, 5th edition. American Ornithologists' Union, Washington, D.C.
- American Ornithologists' Union. 1998. Check-list of North American Birds, 7th edition. American Ornithologists' Union, Washington, D.C.
- American Ornithologists' Union. 2000. Forty-second supplement to the American Ornithologists' Union Check-list of North American Birds. *Auk* 117:847-858.
- Amundsen, T., P. T. Brobakken, A. Moksnes, and E. Røskaft. 2002. Rejection of Common Cuckoo *Cuculus canorus* eggs in relation to female age in the Bluethroat *Luscinia svecica*. *Journal of Avian Biology* 33:366-370.
- Andersson, M. 1978. Optimal egg shape in waders. *Ornis Fennica* 55:105-109.
- Andersson, S., and T. Amundsen. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proceedings of the Royal Society of London B* 264:1587-1591.

- Andersson, S., J. Örnborg, and M. Andersson. 1998. Ultraviolet sexual dimorphism and assortative mating in Blue Tits. *Proceedings of the Royal Society of London B* 265:445-450.
- Baichich, P. J., and C. J. O. Harrison. 1997. *A Guide to the Nests, Eggs, and Nestlings of North American Birds*, 2nd edition. Academic Press, San Diego, CA.
- Baerends, G. P., and R. H. Drent. 1982. The Herring Gull and its egg Part II, the responsiveness to egg-features. *Behaviour* 82:1-416.
- Baker, E. C. S. 1942. *Cuckoo Problems*. H. F. & B. Witherby, London, UK.
- Baltz, M. E., and D. E. Burhans. 1998. Rejection of artificial parasite eggs by Gray Kingbirds in the Bahamas. *Condor* 100:566-568.
- Banks, A. N. 2001. For your eyes only? The role of UV in mate choice. *Trends in Ecology & Evolution* 16:473-474.
- Barta, Z., and T. Székely. 1997. The optimal shape of avian eggs. *Functional Ecology* 11:656-662.
- Bennett, A. T. D., and I. C. Cuthill. 1994. Ultraviolet vision in birds: what is its function? *Vision Research* 34:1471-1478.
- Bennett, A. T. D., I. C. Cuthill, J. C. Partridge, and E. J. Maier. 1996. Ultraviolet vision and mate choice in Zebra Finches. *Nature* 380:433-435.
- Bent, A. C. 1950. *Life Histories of North American Wagtails, Shrikes, Vireos, and Their Allies*. United States National Museum, Bulletin 197, Smithsonian Institution, Washington, D.C.

- Bent, A. C. 1958. Life Histories of North American Blackbirds, Orioles, Tanagers, and Allies. United States National Museum, Bulletin 211, Smithsonian Institution, Washington, D.C.
- Birkhead, T. R. 1991. The Magpies. T & A D Poyser, London, UK.
- Blake, E. R. 1968. Family Vireonidae. Pages 103-138 in Check-list of Birds of the World, Volume 14 (R. A. Paynter, Jr., Ed.). Museum of Comparative Zoology, Cambridge, MA.
- Blankespoor, G. W., J. Oolman, and C. Uthe. 1982. Eggshell strength and cowbird parasitism of Red-winged Blackbirds. *Auk* 99:363-365.
- Bolen, G. M. 1999. Extra-pair Behavior in Yellow-billed Magpies (*Pica nuttalli*). Ph.D. Thesis, University of California, Berkeley, CA.
- Bolen, G. M., S. I. Rothstein, and C. H. Trost. 2000. Egg recognition in Yellow-billed and Black-billed Magpies in the absence of interspecific parasitism: implications for parasite-host coevolution. *Condor* 102:432-438.
- Briskie, J. V., and S. G. Sealy. 1987. Responses of Least Flycatchers to experimental inter- and intraspecific brood parasitism. *Condor* 89:899-901.
- Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. *Evolution* 46:334-340.
- Brooke, M. de L., and N. B. Davies. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* 335:630-632.
- Brooke, M. de L., N. B. Davies, and D. G. Noble. 1998. Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of Reed

- Warblers in a changing world. *Proceedings of the Royal Society of London B* 265:1277-1282.
- Brooker, M. G., and L. C. Brooker. 1989. The comparative breeding behaviour of two sympatric cuckoos, Horsfield's Bronze-cuckoo *Chrysococcyx basalis* and the Shining Bronze-cuckoo *C. lucidus*, in Western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. *Ibis* 131:528-47.
- Brooker, M. G., and L. C. Brooker. 1991. Eggshell strength in cuckoos and cowbirds. *Ibis* 133:406-413.
- Brown, C. R., and M. B. Brown. 1988. A new form of reproductive parasitism in Cliff Swallows. *Nature* 331:66-68.
- Brown, C. R., and M. B. Brown. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Animal Behaviour* 37:777-796.
- Buitron, D. 1988. Female and male specialization in parental care and its consequences in Black-billed Magpies. *Condor* 90:29-39.
- Burgham, M. C. J., and J. Picman. 1989. Effect of Brown-headed Cowbirds on the evolution of Yellow Warbler anti-parasite strategies. *Animal Behaviour* 38:298-308.
- Burhans, D. E., and P. C. Freeman. 1997. Partial rejection of immaculate foreign eggs by Yellow-breasted Chats. *Auk* 114:503-506.
- Burhans, D. E. 2000. Morning nest arrivals in cowbird hosts: their role in aggression, cowbird recognition, and host response to parasitism. Pages 161-168 *in Ecology and Management of Cowbirds and Their Hosts* (J. N. M. Smith, T. L. Cook, S. I.

- Rothstein, S. K. Robinson, and S. G. Sealy, Eds.). University of Texas Press, Austin, TX.
- Burhans, D. E. 2001. Enemy recognition by Field Sparrows. *Wilson Bulletin* 113:189-193.
- Burkhardt, D. 1982. Birds, berries and UV. *Naturwissenschaften* 69:153-157.
- Byers, J. A. 1997. American Pronghorn. *Social Adaptations & the Ghosts of Predators Past*. The University of Chicago Press, Chicago, IL.
- Carter, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. *Condor* 88:11-25.
- Cavalcanti, R. B., and T. M. Pimentel. 1988. Shiny Cowbird parasitism in central Brazil. *Condor* 90:40-43.
- Chen, D.-M., J. S. Collins, and T. H. Goldsmith. 1984. The ultraviolet receptor of bird retinas. *Science* 225:337-340.
- Chen, D.-M., and T. H. Goldsmith. 1986. Four spectral classes of cone in the retinas of birds. *Journal of Comparative Physiology A* 159:473-479.
- Cherry, M. I., and A. T. D. Bennett. 2001. Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry. *Proceedings of the Royal Society of London B* 268:565-571.
- Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*). In *The Birds of North America*, No. 527 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, PA.
- Clark, K. L., and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. *Wilson Bulletin* 93:249-258.

- Coss, R. G. 1993. Evolutionary persistence of ground squirrel antisnake behavior: reflections on Burton's commentary. *Ecological Psychology* 5:171-194.
- Coss, R. G. 1999. Effects of relaxed natural selection on the evolution of behavior. Pages 180-208 in *Geographic Variation in Behavior, Perspectives on Evolutionary Mechanisms* (S. A. Foster and J. A. Endler, Eds.). Oxford University Press, Oxford, UK.
- Cruz, A., T. H. Manolis, and R. W. Andrews. 1995. History of Shiny Cowbird *Molothrus bonariensis* brood parasitism in Trinidad and Tobago. *Ibis* 137:321.
- Cruz, A., T. Manolis, and J. W. Wiley. 1985. The Shiny Cowbird: a brood parasite expanding its range in the Caribbean region. *Ornithological Monographs* 36:607-620.
- Cruz, A., and J. W. Wiley. 1989. The decline of an adaptation in the absence of presumed selection pressure. *Evolution* 43:55-62.
- Cruz, A., J. W. Wiley, T. K. Nakamura, and W. Post. 1989. The Shiny Cowbird *Molothrus bonariensis* in the West Indian region – biogeographical and ecological implications. Pages 519-540 in *Biogeography of the West Indies: Past, Present, and Future* (C. A. Woods, Ed.). Sandhill Crane Press, Inc., Gainesville, FL.
- Curson, D. R., C. B. Goguen, and N. E. Mathews. 1998. Western Wood-Pewees accept cowbird eggs. *Great Basin Naturalist* 58:90-91.
- Cuthill, I. C., A. T. D. Bennett, J. C. Partridge, and E. J. Maier. 1999. Plumage reflectance and the objective assessment of avian sexual dichromatism. *American Naturalist* 160:183-200.

- Cuthill, I. C., J. C. Partridge, A. T. D. Bennett, S. C. Church, N. S. Hart, and S. Hunt. 2000. Ultraviolet vision in birds. *Advances in the Study of Behavior* 29:159-214.
- Davies, N. B. 1999. Cuckoos and cowbirds versus hosts: co-evolutionary lag and equilibrium. *Ostrich* 70:71-79.
- Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. T & A D Poyser, London, UK.
- Davies, N. B., and M. de L. Brooke. 1988. Cuckoos versus Reed Warblers: adaptations and counteradaptations. *Animal Behaviour* 36:262-284.
- Davies, N. B., and M. de L. Brooke. 1989a. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal Ecology* 58:207-24.
- Davies, N. B., and M. de L. Brooke. 1989b. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *Journal of Animal Ecology* 58:225-236.
- Davies, N. B., and M. de L. Brooke. 1998. Cuckoos versus hosts: experimental evidence for coevolution. Pages 59-79 in *Parasitic Birds and Their Hosts, Studies in Coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.
- Davies, N. B., M. de L. Brooke, and A. Kacelnik. 1996. Recognition errors and probability of parasitism determine whether Reed Warblers should accept or reject mimetic cuckoo eggs. *Proceedings of the Royal Society of London B* 263:925-931.
- Davis, S. K., D. R. Klippenstine, and R. M. Brigham. 2002. Does egg rejection account

for the low incidence of cowbird parasitism in Chestnut-collared Longspurs (*Calcarius ornatus*)? *Auk* 119:556-560.

Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species.

Proceedings of the Royal Society of London B 205:489-511.

Dearborn, D. C. 1998. Begging behavior and food acquisition by Brown-headed Cowbird nestlings. *Behavioral Ecology and Sociobiology* 43:259-270.

Dearborn, D. C. 1999. Brown-headed Cowbird nestling vocalizations and risk of nest predation. *Auk* 116:448-457.

Dearborn, D. C., A. D. Anders, F. R. Thompson III, and J. Faaborg. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. *Condor* 100:326-334.

Deeming, D. C. 1991. Reasons for the dichotomy in egg turning in birds and reptiles. Pages 307-323 *in* *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles* (D. C. Deeming and M. W. J. Ferguson, Eds.). Cambridge University Press, Cambridge, UK.

Dunning, J. B., Jr. 1993. *CRC Handbook of Avian Masses*. CRC Press, Boca Raton, FL.

Encabo, S. I., E. Barba, J. A. Gil-Delgado, and J. S. Monrós. 2001. Fitness consequences of egg shape variation: a study on two passerines and comments on the optimal egg shape. *Ornis Fennica* 78:83-92.

Encabo, S. I., E. Barba, J. A. Gil-Delgado, and J. S. Monrós. 2002. Geographical variation in egg size of the Great Tit *Parus major*: a new perspective. *Ibis* 144:623-631.

- Enggist-Düblin, E., and T. R. Birkhead. 1992. Differences in the calls of European and North American Black-billed Magpies and the Yellow-billed Magpie. *Bioacoustics* 4:185-194.
- Erdfelder, E., F. Faul, and A. Buchner. 1996. GPOWER: a general power analysis program. *Behavior Research Methods, Instruments, & Computers* 28:1-11.
- Everitt, B. S., and G. Der. 1996. *A Handbook of Statistical Analyses Using SAS*. Chapman & Hall, London, UK.
- Finch, D. M. 1982. Rejection of cowbird eggs by Crissal Thrashers. *Auk* 99:719-724.
- Fleischer, R. C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. *Behavioral Ecology and Sociobiology* 17:91-99.
- Fleischer, T. L. 2000. Egg rejection in the absence of selection in the Florida Scrub-Jay. Abstract. 118th Meeting of the American Ornithologists' Union, St. John's, NF.
- Fleischer, T. L. 2000. Reactions of Florida Scrub-Jays (*Aphelocoma coerulescens*) to Eggs and Shams Added to Their Nests. M.Sc. Thesis, University of South Florida, Tampa, FL.
- Fraga, R. M. 1985. Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. *Ornithological Monographs* 36:829-844.
- Fraga, R. M. 1998. Interactions of the parasitic Screaming and Shiny Cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the Bay-winged Cowbird (*M. badius*). Pages 173-193 in *Parasitic Birds and Their Hosts, Studies in Coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.

- Fraga, R. M. 2002. Notes on new or rarely reported Shiny Cowbird hosts from Argentina. *Journal of Field Ornithology* 73:213-219.
- Friedmann, H. 1955. The Honey-guides. United States National Museum Bulletin No. 208, Smithsonian Institution, Washington, D.C.
- Friedmann, H., and L. F. Kiff. 1985. The parasitic cowbirds and their hosts. *Proceedings of the Western Foundation of Vertebrate Zoology* 2:225-304.
- Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A Further Contribution to Knowledge of the Host Relations of the Parasitic Cowbirds. *Smithsonian Contributions to Zoology* No. 235, Smithsonian Institution Press, Washington, D.C.
- Gardali, T., and G. Ballard. 2000. Warbling Vireo (*Vireo gilvus*). *In* The Birds of North America, No. 551 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, PA.
- Gibbs, H. L., P. Miller, G. Alderson, and S. G. Sealy. 1997. Genetic analysis of Brown-headed Cowbirds *Molothrus ater* raised by different hosts: data from mtDNA and microsatellite markers. *Molecular Ecology* 6:189-193.
- Goldsmith, T. H. 1980. Hummingbirds see near ultraviolet light. *Science* 207:786-788.
- Graham, D. S. 1988. Responses of five host species to cowbird parasitism. *Condor* 90:588-591.
- Haas, C. A., and K. H. Haas. 1998. Brood parasitism by Brown-headed Cowbirds on Brown Thrashers: frequency and rates of rejection. *Condor* 100:535-540.
- Harrison, H. H. 1975. *A Field Guide to Birds' Nests*. Houghton Mifflin Company, Boston, MA.

- Hatch, D. R. M. 1967. Cowbird egg in crow nest. *Blue Jay* 25:189.
- Hill, D. P., and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have Clay-coloured Sparrows evolved an anti-parasite defense? *Animal Behaviour* 48:1063-1070.
- Högstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* 210:1148-1150.
- Honkavaara, J., M. Koivula, E. Korpimäki, H. Siitari, and J. Viitala. 2002. Ultraviolet vision and foraging in terrestrial vertebrates. *Oikos* 98:505-511.
- Honza, M., J. Picman, T. Grim, V. Novák, M. Čapek Jr., and V. Mrlík. 2001. How to hatch from an egg of great structural strength. A study of the Common Cuckoo. *Journal of Avian Biology* 32:249-255.
- Hoover, J. P. 2003. Experiments and observations of Prothonotary Warblers indicate a lack of adaptive responses to brood parasitism. *Animal Behaviour* 65:935-944.
- Hosoi, S. A., and S. I. Rothstein. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Animal Behaviour* 59:823-840.
- Howes-Jones, D. 1985a. Relationships among song activity, context, and social behavior in the Warbling Vireo. *Wilson Bulletin* 97:4-20.
- Howes-Jones, D. 1985b. The complex song of the Warbling Vireo. *Canadian Journal of Zoology* 63:2756-2766.
- Hoy, G., and J. Ottow. 1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. *Auk* 81:186-203.
- Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk* 96:73-77.

- Hunt, S., A. T. D. Bennett, I. C. Cuthill, and R. Griffiths. 1998. Blue Tits are ultraviolet tits. *Proceedings of the Royal Society of London B* 265:451-455.
- Hunt, S., I. C. Cuthill, A. T. D. Bennett, S. C. Church, and J. C. Partridge. 2001. Is the ultraviolet waveband a special communication channel in avian mate choice? *Journal of Experimental Biology* 204:2499-2507.
- Jackson, W. M. 1988. Egg discrimination and egg-color variability in the Northern Masked Weaver. Pages 407-416 *in* *Parasitic Birds and Their Hosts, Studies in Coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.
- Jacobs, G. H. 1992. Ultraviolet vision in vertebrates. *American Zoologist* 32:544-554.
- Jacobs, G. H. 1993. The distribution and nature of colour vision among the mammals. *Biological Reviews of the Cambridge Philosophical Society* 68:413-471.
- Jamieson, I. G. 1986. The functional approach to behavior: is it useful? *American Naturalist* 127:195-208.
- Jaramillo, A. P. 1993. Parasite-host Coevolution in the Cowbirds *Molothrus rufoaxillaris* and *Molothrus badius*: Egg Mimicry in Shape and Size. M.Sc. Thesis, University of Toronto, Toronto, ON.
- Johnsgard, P. A. 1997. *The Avian Brood Parasites*. Oxford University Press, Oxford, UK.
- Johnson, L. S., J. E. Leyhe, and C. Werner. 2001. The shape of eggs in different-sized clutches of the House Wren (*Troglodytes aedon*). *Canadian Journal of Zoology* 79:1527-1531.

- Kattan, G. H. 1998. Impact of brood parasitism: why do House Wrens accept Shiny Cowbird eggs? Pages 212-222 *in* Parasitic Birds and Their Hosts, Studies in Coevolution (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.
- Kelly, C. 1987. A model to explore the rate of spread of mimicry and rejection in hypothetical populations of cuckoos and hosts. *Journal of Theoretical Biology* 125:283-299.
- Kemal, R. E., and S. I. Rothstein. 1988. Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. *Animal Behaviour* 36:175-183.
- Klicka, J., and R. M. Zink. 1998. Pleistocene speciation and the mitochondrial DNA clock. *Science* 282:1955.
- Kreithen, M. L., and T. Eisner. 1978. Ultraviolet light detection by the Homing Pigeon. *Nature* 272:347-348.
- Lahti, D. C., and A. R. Lahti. 2002. How precise is egg discrimination in weaverbirds? *Animal Behaviour* 63:1135-1142.
- Langmore, N. E., S. Hunt, and R. M. Kilner. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422:157-160.
- Lanier, G. N., Jr. 1982. A test for conspecific egg discrimination in three species of colonial passerine birds. *Auk* 99:519-525.
- Lichtenstein, G., and S. G. Sealy. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic Brown-headed Cowbird chicks in Yellow Warbler nests. *Proceedings of the Royal Society of London B* 265:249-254.

- Lokemoen, J. T., and R. R. Koford. 1996. Using candlers to determine the incubation stage of passerine eggs. *Journal of Field Ornithology* 67:660-668.
- Lombardo, M. P. 1988. Evidence of intraspecific brood parasitism in the Tree Swallow. *Wilson Bulletin* 100:126-128.
- Lombardo, M. P., H. W. Power, P. C. Stouffer, L. C. Romagnano, and A. S. Hoffenberg. 1989. Egg removal and intraspecific brood parasitism in the European Starling (*Sturnus vulgaris*). *Behavioral Ecology and Sociobiology* 24:217-223.
- Lorenzana, J. C. 1999. Fitness Costs and Benefits of Egg Ejection by Gray Catbirds. M.Sc. Thesis, University of Manitoba, Winnipeg, MB.
- Lorenzana, J. C., and S. G. Sealy. 1999. A meta-analysis of the impact of parasitism by the Brown-headed Cowbird on its hosts. *Studies in Avian Biology* 18:241-253.
- Lorenzana, J. C., and S. G. Sealy. 2001. Fitness costs and benefits of cowbird ejection by Gray Catbirds. *Behavioral Ecology* 12:325-329.
- Lotem, A., and H. Nakamura. 1998. Evolutionary equilibria in avian brood parasitism: an alternative to the "arms race-evolutionary lag" concept. Pages 223-235 *in* Parasitic Birds and Their Hosts, Studies in Coevolution (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.
- Lotem, A., H. Nakamura, and A. Zahavi. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behavioral Ecology* 3:128-132.
- Lotem, A., H. Nakamura, and A. Zahavi. 1995. Constraints on egg discrimination and cuckoo-host co-evolution. *Animal Behaviour* 49:1185-1209.

- Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*). In the Birds of North America, No. 47 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- Lowther, P. E., and W. Post. 1999. Shiny Cowbird (*Molothrus bonariensis*). In the Birds of North America, No. 399 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, PA.
- Lyon, B. E. 1997. Spatial patterns of Shiny Cowbird brood parasitism on Chestnut-capped Blackbirds. *Animal Behaviour* 54:927-939.
- Lyon, B. E. 2003. Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature* 422:495-499.
- MacKenzie, D. I. 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. *Canadian Field-Naturalist* 96:61-68.
- MacKenzie, D. I., S. G. Sealy, and G. D. Sutherland. 1982. Nest-site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. *Canadian Journal of Zoology* 60:2212-2223.
- Maddocks, S. A., S. C. Church, and I. C. Cuthill. 2001. The effects of the light environment on prey choice by Zebra Finches. *Journal of Experimental Biology* 204:2509-2515.
- Marchetti, K. 1992. Costs to host defence and the persistence of parasitic cuckoos. *Proceedings of the Royal Society of London B* 248:41-45.
- Marchetti, K. 2000. Egg rejection in a passerine bird: size does matter. *Animal Behaviour* 59:877-883.

- Martín-Vivaldi, M., M. Soler, and A. P. Møller. 2002. Unrealistically high costs of rejecting artificial model eggs in cuckoo *Cuculus canorus* hosts. *Journal of Avian Biology* 33:295-301.
- Mason, P. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: I. The quality of different species as hosts. *Auk* 103:52-60.
- Mason, P., and S. I. Rothstein. 1986. Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. *Evolution* 40:1207-1214.
- Massoni, V., and J. C. Reboreda. 1998. Costs of brood parasitism and the lack of defenses on the Yellow-winged Blackbird – Shiny Cowbird system. *Behavioral Ecology and Sociobiology* 42:273-280.
- Massoni, V., and J. C. Reboreda. 2002. A neglected cost of brood parasitism: egg punctures by Shiny Cowbirds during inspection of potential host nests. *Condor* 104:407-412.
- May, R. M., and S. K. Robinson. 1985. Population dynamics of avian brood parasitism. *American Naturalist* 126:475-494.
- McGowan, K. J. 2001. Demographic and behavioral comparisons of suburban and rural American Crows. Pages 365-381 in *Avian Ecology and Conservation in an Urbanizing World* (J. M. Marzluff, R. Bowman, and R. Donnelly Eds.). Kluwer Academic Press, Norwell, MA.
- Mermoz, M. E., and G. J. Fernández. 1999. Low frequency of Shiny Cowbird parasitism on Scarlet-headed Blackbirds: anti-parasite adaptations or nonspecific host life-history traits? *Journal of Avian Biology* 30:15-22.

- Mermoz, M. E., and J. C. Reboreda. 1994. Brood parasitism of the Shiny Cowbird, *Molothrus bonariensis*, on the Brown-and-Yellow Marshbird, *Pseudoleistes virescens*. *Condor* 96:716-721.
- Moksnes, A. 1992. Egg recognition in chaffinches and bramblings. *Animal Behaviour* 44:993-995.
- Moksnes, A., and E. Røskaft. 1995. Egg-morphs and host preferences in the Common Cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *Journal of Zoology, London* 236:625-648.
- Moksnes, A., E. Røskaft, and A. T. Braa. 1991. Rejection behavior by Common Cuckoo hosts towards artificial brood parasite eggs. *Auk* 108:348-354.
- Moksnes, A., E. Røskaft, and M. Mørkved Solli. 1994. Documenting puncture ejection of parasitic eggs by Chaffinches *Fringilla coelebs* and Blackcaps *Sylvia atricapilla*. *Fauna Norvegica, Series C, Cinclus* 17:115-118.
- Moksnes, A., E. Røskaft, and T. Tysse. 1995. On the evolution of blue cuckoo eggs in Europe. *Journal of Avian Biology* 26:13-19.
- Morton, E. S., and S. M. Farabaugh. 1979. Infanticide and other adaptations of the nestling Striped Cuckoo *Tapera naevia*. *Ibis* 121:212-213.
- Moskát, C., T. Székely, T. Kisbenedek, Z. Karcza, and I. Bártol. 2003. The importance of nest cleaning in egg rejection behaviour of Great Reed Warblers *Acrocephalus arundinaceus*. *Journal of Avian Biology* 34:16-19.
- Nickell, W. P. 1958. Variations in engineering features of the nests of several species of birds in relation to nest sites and nesting materials. *Butler University Botanical Studies* 13:121-139.

- Nickell, W. P. 1965. Habitats, territory, and nesting of the catbird. *American Midland Naturalist* 73:433-478.
- Olsen, P. D., R. B. Cunningham, and C. F. Donnelly. 1994. Avian egg morphometrics: allometric models of egg volume, clutch volume and shape. *Australian Journal of Zoology* 42:307-321.
- Ortega, C. P. 1998. *Cowbirds and Other Brood Parasites*. University of Arizona Press, Tucson, AZ.
- Ortega, C. P., and A. Cruz. 1988. Mechanisms of egg acceptance by marsh-dwelling blackbirds. *Condor* 90:349-358.
- Ortega, C. P., and A. Cruz. 1991. A comparative study of cowbird parasitism in Yellow-headed Blackbirds and Red-winged Blackbirds. *Auk* 108:16-24.
- Ortega, C. P., and J. C. Ortega. 2003. Brown-headed Cowbird (*Molothrus ater*) parasitism on Warbling Vireos (*Vireo gilvus*) in southwest Colorado. *Auk* 120:759-764.
- Ortega, J. C., C. P. Ortega, and A. Cruz. 1993. Does Brown-headed Cowbird egg colouration influence Red-winged Blackbird responses towards nest contents? *Condor* 95:217-219.
- Parrish, J. W., J. A. Ptacek, and K. L. Will. 1984. The detection of near-ultraviolet light by nonmigratory and migratory birds. *Auk* 101:53-58.
- Payne, R. B. 1997. Avian brood parasitism. Pages 338-369 *in* Host-parasite Evolution (D. H. Clayton and J. Moore, Eds.). Oxford University Press, Oxford, UK.

- Payne, R. B., and L. L. Payne. 1998. Brood parasitism by cowbirds: risks and effects on reproductive success and survival in Indigo Buntings. *Behavioral Ecology* 9:64-73.
- Peer, B. D. 1998. An Experimental Investigation of Egg Rejection Behavior in the Grackles (*Quiscalus*). Ph.D. Thesis, University of Manitoba, Winnipeg, MB.
- Peer, B. D., and E. K. Bollinger. 1997. Explanations for the infrequent cowbird parasitism on Common Grackles. *Condor* 99:151-161.
- Peer, B. D., and E. K. Bollinger. 1998. Rejection of cowbird eggs by Mourning Doves: a manifestation of nest usurpation? *Auk* 115:1057-1062.
- Peer, B. D., and S. G. Sealy. 1999. Parasitism and egg puncture behaviour by Bronzed and Brown-headed Cowbirds in sympatry. *Studies in Avian Biology* 18:235-240.
- Peer, B. D., and S. G. Sealy. 2000a. Conspecific brood parasitism and egg rejection in Great-tailed Grackles. *Journal of Avian Biology* 31:271-7.
- Peer, B. D., and S. G. Sealy. 2000b. Responses of Scissor-tailed Flycatchers (*Tyrannus forficatus*) to experimental cowbird parasitism. *Bird Behavior* 13:63-67.
- Peer, B. D., and S. G. Sealy. 2001. Mechanism of egg recognition in the Great-tailed Grackle (*Quiscalus mexicanus*). *Bird Behavior* 14:71-73.
- Peer, B. D., K. Ellison, and S. G. Sealy. 2002. Intermediate frequencies of egg ejection by Northern Mockingbirds (*Mimus polyglottos*) sympatric with two cowbird species. *Auk* 119:855-858.
- Peer, B. D., S. K. Robinson, and J. R. Herkert. 2000. Egg rejection behavior by grassland hosts: has the Brown-headed Cowbird evolved a mimetic egg? *Auk* 117:892-901.

- Petit, K. E., L. J. Petit, and D. R. Petit. 1989. Fecal sac removal: do the pattern and distance of dispersal affect the chance of nest predation? *Condor* 91:479-482.
- Phillips, A. R. 1991. *The Known Birds of North and Middle America. Part II.* Allen R. Phillips, Denver, CO.
- Picman, J. 1989. Mechanism of increased puncture resistance of eggs of Brown-headed Cowbirds. *Auk* 106:577-583.
- Picman, J. 1997. Are cowbird eggs unusually strong from the inside? *Auk* 114:66-73.
- Picman, J., and S. Pribil. 1997. Is greater eggshell density an alternative mechanism by which parasitic cuckoos increase the strength of their eggs? *Journal für Ornithologie* 138:531-541.
- Picman, J., S. Pribil, and A. K. Picman. 1996. The effect of intraspecific egg destruction on the strength of Marsh Wren eggs. *Auk* 113:599-607.
- Post, W., T. K. Nakamura, and A. Cruz. 1990. Patterns of Shiny Cowbird parasitism in St. Lucia and southwestern Puerto Rico. *Condor* 92:461-469.
- Poulsen, H. 1953. A study of incubation responses and some other behaviour patterns in birds. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening* 115:1-131.
- Pribil, S., and J. Picman. 1997. Parasitism of House Wren nests by Brown-headed Cowbirds: why is it so rare? *Canadian Journal of Zoology* 75:302-307.
- Rahn, H., L. Curran-Everett, and D. T. Booth. 1988. Eggshell differences between parasitic and nonparasitic Icteridae. *Condor* 90:962-964.
- Regosin, J. V. 1994. Scissor-tailed Flycatchers eject Brown-headed Cowbird eggs. *Journal of Field Ornithology* 65:508-511.

- Rensch, B. 1925. Verhalten von Singvögeln bei Aenderung des Geleges. Ornithologische Monatsberichte 33:169-173.
- Reynolds, M. D. 1995. Yellow-billed Magpie (*Pica nuttalli*). In The Birds of North America, No. 180 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- Rich, T., and S. I. Rothstein. 1985. Sage Thrashers reject cowbird eggs. Condor 87:561-562.
- Rising, J. D., and N. J. Flood. 2000. Baltimore Oriole (*Icterus galbula*). In The Birds of North America, No. 384 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, PA.
- Robert, M., & Sorici, G. 1999. Rapid increase of host defence against brood parasites in a recently parasitized area: the case of Village Weavers in Hispaniola. Proceedings of the Royal Society of London B 266:941-946.
- Rohwer, S., and C. D. Spaw. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evolutionary Ecology 2:27-36.
- Rohwer, S., C. D. Spaw, and E. Røskaft. 1989. Costs to Northern Orioles of puncture-ejecting parasitic cowbird eggs from their nests. Auk 106:734-738.
- Røskaft, E., A. Moksnes, D. Meilvang, V. Biciík, J. Jemelíková, and M. Honza. 2002. No evidence for recognition errors in *Acrocephalus* warblers. Journal of Avian Biology 33:31-38.

- Røskaft, E., S. Rohwer, and C. D. Spaw. 1993. Cost of puncture ejection compared with costs of rearing cowbird chicks for Northern Orioles. *Ornis Scandinavica* 24:28-32.
- Rothstein, S. I. 1970. An Experimental Investigation of the Defenses of the Hosts of the Parasitic Brown-headed Cowbird (*Molothrus ater*). Ph.D. Thesis, Yale University, New Haven, CT.
- Rothstein, S. I. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. *Auk* 91:796-807.
- Rothstein, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250-271.
- Rothstein, S. I. 1975b. Mechanisms of avian egg-recognition: do birds know their own eggs? *Animal Behaviour* 23:268-278.
- Rothstein, S. I. 1975c. Evolutionary rates and host defenses against avian brood parasitism. *American Naturalist* 109:161-176.
- Rothstein, S. I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. *Auk* 93:675-691.
- Rothstein, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. *Wilson Bulletin* 89:21-32.
- Rothstein, S. I. 1978. Mechanisms of avian egg-recognition: additional evidence for learned components. *Animal Behaviour* 26:671-677.
- Rothstein, S. I. 1982a. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. *American Zoologist* 22:547-560.

- Rothstein, S. I. 1982b. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? *Behavioral Ecology and Sociobiology* 11:229-239.
- Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics* 21:481-508.
- Rothstein, S. I. 1992. Brood parasitism, the importance of experiments and host defences of avifaunas on different continents. Pages 521-535 *in* Proceedings of the VII Pan-African Ornithological Congress.
- Rothstein, S. I. 2001. Relic behaviours, coevolution and the retention versus loss of host defences after episodes of avian brood parasitism. *Animal Behaviour* 61:95-107.
- Rothstein, S. I., and S. K. Robinson. 1998. The evolution and ecology of avian brood parasitism: an overview. Pages 3-56 *In* Parasitic Birds and Their Hosts, Studies in Coevolution (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.
- Rowan, M. K. 1983. The Doves, Parrots, Louries and Cuckoos of Southern Africa. David Phillip, Capetown, South Africa.
- Rutilia, J., R. Latja, and K. Koskela. 2002. The Common Cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? *Journal of Avian Biology* 33:414-419.
- Rydell, J., Roininen, H., & Philip, K. W. 2000. Persistence of bat defence reactions in high Arctic moths (Lepidoptera). *Proceedings of the Royal Society of London B* 267:553-557.

- Sallabanks, R., and F. C. James. 1999. American Robin (*Turdus migratorius*). In *The Birds of North America*, No. 462 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, PA.
- Schaefer, V. H. 1974. Geographic Variation in the Placement and Structure of the Nests of Three Taxa of North American Orioles. M.Sc. Thesis, University of Toronto, Toronto, ON.
- Schlotzhauer, S. D., and R. C. Littell. 1997. SAS[®] System for Elementary Statistical Analysis, 2nd edition. SAS Institute, Cary, NC.
- Sealy, S. G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. *Canadian Field-Naturalist* 94:154-158.
- Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. *Condor* 94:40-54.
- Sealy, S. G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. *Animal Behaviour* 49:877-889.
- Sealy, S. G. 1996. Evolution of host defenses against brood parasitism: implications of puncture-ejection by a small passerine. *Auk* 113:346-355.
- Sealy, S. G. 1999. Cowbird parasitism on Lark Buntings: frequency, acceptance, and fledging. *Journal of Field Ornithology* 70:182-186.
- Sealy, S. G., and R. C. Bazin. 1995. Low frequency of observed cowbird parasitism on Eastern Kingbirds: host rejection, effective nest defence, or parasite avoidance? *Behavioral Ecology* 6:140-145.
- Sealy, S. G., and D. L. Neudorf. 1995. Male Northern Orioles eject cowbird eggs: implications for the evolution of rejection behavior. *Condor* 97:369-375.

- Sealy, S. G., and J. C. Lorenzana. 1998. Yellow Warblers (*Dendroica petechia*) do not recognize their own eggs. *Bird Behavior* 12:57-66.
- Sealy, S. G., and T. J. Underwood. Submitted. Rejecters and accepters of cowbird parasitism among the New World orioles (*Icterus* spp.). *Ornitologia Neotropical*
- Sealy, S. G., D. L. Neudorf, K. A. Hobson, and S. A. Gill. 1998. Pages 194-211 in *Parasitic Birds and Their Hosts, Studies in Coevolution* (S. I. Rothstein and S. K. Robinson, Eds.). Oxford University Press, Oxford, UK.
- Sealy, S. G., A. J. Banks, and J. F. Chace. 2000. Two subspecies of Warbling Vireo differ in their responses to cowbird eggs. *Western Birds* 31:190-194.
- Sealy, S. G., D. G. McMaster, and B. D. Peer. 2002. Tactics of obligate brood parasites to secure suitable incubators. Pages 254-269 in *Avian Incubation: Behaviour, Environment and Evolution* (D. C. Deeming, Ed.). Oxford University Press, Oxford, UK.
- Sibley, C. G., and J. E. Ahlquist. 1982. The relationship of the vireos (Vireoninae) as indicated by DNA-DNA hybridization. *Wilson Bulletin* 94:114-128.
- Smart, I. H. M. 1991. Egg-shape in birds. Pages 101-116 in *Egg Incubation: Its Effects on Embryonic Development in Birds and Reptiles* (D. C. Deeming and M. W. J. Ferguson, Eds.). Cambridge University Press, Cambridge, UK.
- Soler, J. J., J. G. Martinez, M. Soler, and A. P. Møller. 1999. Genetic and geographic variation in rejection behavior of cuckoo eggs by European magpie populations: an experimental test of rejecter-gene flow. *Evolution* 53:947-956.
- Soler, M. 1990. Relationships between the Great Spotted Cuckoo *Clamator glandarius* and its corvid hosts in a recently colonized area. *Ornis Scandinavica* 21:212-223.

- Soler, M., and A. P. Møller. 1990. Duration of sympatry and coevolution between the Great Spotted Cuckoo and its magpie host. *Nature* 343:748-750.
- Soler, M., J. G. Martinez, J. J. Soler, and A. P. Møller. 1995a. Preferential allocation of food by magpies *Pica pica* to Great Spotted Cuckoo *Clamator glandarius* chicks. *Behavioral Ecology and Sociobiology* 37:7-13.
- Soler, M., J. J. Soler, J. G. Martinez, and A. P. Møller. 1995b. Magpie host manipulation by Great Spotted Cuckoos: evidence for an avian mafia? *Evolution* 49:770-775.
- Soler, M., J. G. Martinez, and J. J. Soler. 1996. Effects of brood parasitism by the Great Spotted Cuckoo on the breeding success of the magpie host: an experimental study. *Ardeola* 43:87-96.
- Soler, M., J. J. Soler, and J. G. Martinez. 1997. Great Spotted Cuckoos improve their reproductive success by damaging magpie host eggs. *Animal Behaviour* 54:1227-1233.
- Soler, M., M. Martín-Vivaldi, and T. Pérez-Contreras. 2002. Identification and sex responsible for recognition and the method of ejection of parasitic eggs in some potential Common Cuckoo hosts. *Ethology* 108:1093-1101.
- Spaw, C. D., and S. Rohwer. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. *Condor* 89:307-318.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2000. *Categorical Data Analysis Using the SAS System*. 2nd edition. SAS Institute, Cary, NC.

- Stokke, B. G., M. Honza, A. Moksnes, E. Røskaft, and G. Rudolfsen. 2002. Costs associated with recognition and rejection of parasitic eggs in two European passerines. *Behaviour* 139:629-644.
- Stokke, B. G., A. Moksnes, E. Røskaft, G. Rudolfsen, and M. Honza. 1999. Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among Reed Warblers (*Acrocephalus scirpaceus*). *Proceedings of the Royal Society of London B* 266:1483-1488.
- Stokke, B. G., A. Moksnes, and E. Røskaft. 2002. Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution* 56:199-205.
- Strausberger, B. M., and D. E. Burhans. 2001. Nest desertion by Field Sparrows and its possible influence on the evolution of cowbird behavior. *Auk* 118:770-776.
- Swynnerton, C. F. M. 1918. Rejections by birds of eggs unlike their own: with remarks on some of the cuckoo problems. *Ibis (Series 10)* 6:127-54.
- Tewksbury, J. J., T. E. Martin, S. J. Hejl, M. J. Kuehn, and J. W. Jenkins. 2002. Parental care of a cowbird host: caught between the costs of egg-removal and nest predation. *Proceedings of the Royal Society of London B* 269:423-429.
- Tinbergen, N., G. J. Broekhuysen, F. Feekes, J. C. W. Houghton, H. Kruuk, and E. Szulc. 1962. Egg shell removal by the Black-headed Gull, *Larus ridibundus* L.; a behaviour component of camouflage. *Behaviour* 19:74-117.
- Tovée, M. J. 1995. Ultra-violet photoreceptors in the animal kingdom: their distribution and function. *Trends in Ecology & Evolution* 10:455-460.

- Trost, C. H. 1999. Black-billed Magpie (*Pica pica*). In *The Birds of North America*, No. 389 (A. Poole and F. Gill, Eds.). The Birds of North America, Inc., Philadelphia, PA.
- Trost, C. H., and C. L. Webb. 1986. Egg moving by two species of corvid. *Animal Behaviour* 34:294-295.
- Tschanz, B. 1959. Zur Brutbiologie der Trottellumme (*Uria aalge aalge* Pont.). *Behaviour* 14:1-100.
- Tschanz, B., P. Ingold, and H. Lengacher. 1969. Eiform und bruterfolg bei Trottellummen *Uria aalge aalge* Pont. *Der Ornithologische Beobachter* 66:25-42.
- Underwood, T. J., and S. G. Sealy. 2002. Adaptive significance of egg colouration, Chapter 19. Pages 280-298 in *Avian Incubation: Behaviour, Environment and Evolution* (D. C. Deeming, Ed.). Oxford University Press, Oxford, UK.
- Underwood, T. J., S. G. Sealy, and C. M. McLaren. In Press. Eastern Wood-Pewees as Brown-headed Cowbird hosts: accepters but infrequently parasitized. *Journal of Field Ornithology*
- Victoria, J. K. 1972. Clutch characteristics and egg discriminative ability of the African Village Weaverbird *Plocues cucullatus*. *Ibis* 114:367-376.
- Viitala, J., E. Korpimäki, P. Palokangas, M. Koivula. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* 373:425-427.
- Voous, K. H. 1960. *Atlas of European Birds*. Thomas Nelson and Sons Limited, London, UK.

- Ward, D., and J. N. M. Smith. 2000. Brown-headed Cowbird parasitism results in a sink population in Warbling Vireos. *Auk* 117:337-344.
- Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*. Academic Press, London, UK.
- Walters, M. 2000. Shape of avian eggs: a response to Barta and Székely. *Bulletin of the British Ornithologists' Club* 120:63-64.
- Welbergen, J., J. Komdeur, R. Kats, and M. Berg. 2001. Egg discrimination in the Australian Reed Warbler (*Acrocephalus australis*): rejection response toward model and conspecific eggs depending on timing and mode of artificial parasitism. *Behavioral Ecology* 12:8-15.
- Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 68:35-59.
- Willson, M. F., and C. J. Whelan. 1989. Ultraviolet reflectance of fruits of vertebrate-dispersed plants. *Oikos* 55:341-348.
- Witmer, M. C., D. J. Mountjoy, and L. Elliot. 1997. Cedar Waxwing (*Bombycilla cedrorum*). In *The Birds of North America*, No. 309 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.
- Woolfenden, B. E., H. L. Gibbs, S. G. Sealy, and D. G. McMaster. 2003. Host use and fecundity of individual female Brown-headed Cowbirds. *Animal Behaviour* 66:95-106.
- Wyllie, I. 1981. *The Cuckoo*. Universe Books, New York, NY.

- Yom-Tov, Y. 1976. Recognition of eggs and young by the Carrion Crow (*Corvus corone*). Behaviour 59:247-251.
- Yom-Tov, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis 143: 133-143.
- Zink, R. M., S. Rohwer, A. V. Adreev, and D. L. Dittmann. 1995. Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. Condor 97:639-649.
- Zuñiga, J. M., and T. Redondo. 1992. No evidence for variable duration of sympatry between the Great Spotted Cuckoo and its magpie host. Nature 359: 410-411.

APPENDICES

Appendix 1. Response of host species to real or artificial Brown-headed Cowbird (*Molothrus ater*) eggs experimentally added to their nests. Data are from studies where nests were experimentally parasitized with eggs present and considered 5 days as the acceptance criterion, unless otherwise noted.

Species	Method ^a	% rejected	n	Reference
Rejecters				
Cassin's Kingbird (<i>Tyrannus vociferans</i>)	unk	100.0	unk	Rothstein in Peer and Sealy (2000b)
Western Kingbird (<i>Ty. verticalis</i>)	E	100.0	2	Rothstein (1975a)
	E	100.0	7	Rowher et al. (1989)
Eastern Kingbird (<i>Ty. tyrannus</i>)	E	100.0	33	Rothstein (1975a)
	E	98.7	88	Sealy and Bazin (1995)
Scissor-tailed Flycatcher (<i>Ty. forficatus</i>)	E	100.0	3	Regosin (1994)
	E	100.0	20	Peer and Sealy (2000b)
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	E	100.0	21	Rothstein (2001)
Warbling Vireo (<i>Vireo gilvus gilvus</i>)	E (96.7), D	100.0	30	Sealy (1996), Sealy et al. (2000)
Blue Jay (<i>Cyanocitta cristata</i>)	E (92.0), D	100.0	25	Rothstein (1975a)
Florida Scrub-Jay (<i>Aphelocoma coerulescens</i>)	E (73.1), D	92.3 ^b	26	Fleischer (2000)
Western Scrub-Jay (<i>Ap. californica</i>)	unk	100.0	unk	Rothstein in Peer (1998)

American Robin (<i>Turdus migratorius</i>)	E (82.6), D	97.8	46	Rothstein (1975a)
	E (96.0), D	100.0	25	Briskie et al. (1992)
	E	66.7	18	Briskie et al. (1992)
Gray Catbird (<i>Dumetella carolinensis</i>)	E	94.3	53	Rothstein (1975a)
	E	96.0	94	Lorenzana (1999)
Sage Thrasher (<i>Oreoscoptes montanus</i>)	E (90.9), D	100.0	11	Rich and Rothstein (1985)
Brown Thrasher (<i>Toxostoma rufum</i>)	E	96.3	26	Rothstein (1975a)
		57.8 ^c	64	Haas and Haas (1998)
Crissal Thrasher (<i>To. crissale</i>)	E	100.0	9	Finch (1982)
Cedar Waxwing (<i>Bombycilla cedorum</i>)	E (42.4 ^d), D, P	87.8	33	Rothstein (1975a)
	E (27.6 ^d), D, P	69.0	58	Rothstein (1976)
Western Meadowlark (<i>Sturnella neglecta</i>)	unk	77.8 ^c	18	Peer et al. (2000)
Great-tailed Grackle (<i>Quiscalus mexicanus</i>)	E	100.0	80	Peer (1998)
Baltimore Oriole (<i>Icterus galbula</i>)	E	100.0	16	Sealy and Neudorf (1995)
Bullock's Oriole (<i> Ic. bullockii</i>)	E (100 ^d), P	100.0	20	Rothstein (1977)
Intermediates				
Mourning Dove (<i>Zenaida macroura</i>)	E(6.3), D	31.2	16	Rothstein (1975a)
	E (28.8 ^d), D, P	53.4	73	Peer and Bollinger (1998)

Northern Mockingbird (<i>Mimus polyglottos</i>)	E	25.0	4	Rothstein (1975a)
	unk	50.0 ^f	20 ^f	Mason in Friedmann and Kiff (1985)
	E	60.0	30	Peer et al. (2002)

Accepters

Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	E (16.7), D	41.7	12	Rothstein (1975a)
Western Wood-Pewee (<i>Contopus sordidulus</i>)	E	20.0	10	Curson et al. (1998)
Eastern Wood-Pewee (<i>Con. virens</i>)		0.0	12	Underwood et al. (in press)
Alder Flycatcher (<i>Empidonax alnorum</i>)	B	33.3	3	Sealy unpublished data
Least Flycatcher (<i>Em. minimus</i>)		0.0 ^g	27	Briskie and Sealy (1987)
Eastern Phoebe (<i>Sayornis phoebe</i>)	P, B	6.0	50	Rothstein (1975a)
Yellow-throated Vireo (<i>Vi. flavifrons</i>)		0.0	2	Underwood unpublished data
Warbling Vireo (<i>Vi. gilvus swainsoni</i>)	E	25.0	8	Sealy et al. (2000)
Red-eyed Vireo (<i>Vi. olivaceus</i>)	E	33.3	3	Rothstein (1975a)
		0.0	12	Underwood unpublished data
N. Rough-winged Swallow (<i>Stelgidopteryx serripennis</i>)		0.0	2	Rothstein (1975a)
Barn Swallow (<i>Hirundo rustica</i>)	E	7.7	13	Rothstein (1975a)
House Wren (<i>Troglodytes aedon</i>)		0.0	5	Pribil and Picman (1997)

Wood Thrush (<i>Hylocichla mustelina</i>)		0.0	6	Rothstein (1975a)
California Thrasher (<i>To. redivivum</i>)		unk	unk	Rothstein in Rich and Rothstein (1985)
Le Conte's Thrasher (<i>To. lecontei</i>)		unk	unk	Rothstein in Rich and Rothstein (1985)
European Starling (<i>Sturnus vulgaris</i>)		0.0	2	Rothstein (1975a)
Yellow Warbler (<i>Dendroica petechia</i>)		0.0	16	Rothstein (1975a)
	D, B	100.0	3	Burgham and Picman (1989)
		0.0	29	Briskie et al. (1992)
	E (5.1), D, B	11.4 ^h	158 ^h	Sealy (1995)
Prairie Warbler (<i>Dendroica discolor</i>)		0.0	2	Rothstein (1975a)
Prothonotary Warbler (<i>Protonotaria citrea</i>)		0.0 ^h	10 ^h	Hoover (2003)
Yellow-breasted Chat (<i>Icteria virens</i>)	E	9.1	11	Burhans and Freeman (1997)
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)		0.0	2	Rothstein (1975a)
Chipping Sparrow (<i>Spizella passerina</i>)	D	15.8	19	Rothstein (1975a)
Clay-colored Sparrow (<i>Spize. pallida</i>)		0.0	67	Hill and Sealy (1994)
Field Sparrow (<i>Spize. pusilla</i>)		0.0 ^e	3	Peer et al. (2000)
		0.0	29	Strausberger and Burhans (2001)
Vesper Sparrow (<i>Pooecetes gramineus</i>)		0.0	3	Rothstein (1975a)
		0.0 ^e	4	Peer et al. (2000)
Lark Sparrow (<i>Chondestes grammacus</i>)		0.0 ^e	2	Peer et al. (2000)
Lark Bunting (<i>Calamospiza melanocorys</i>)	E	20.0	5	Sealy (1999)

Savannah Sparrow (<i>Passerculus sandwichensis</i>)		0.0	2	Sealy unpublished data
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)		0.0 ^e	10	Peer et al. (2000)
Song Sparrow (<i>Melospiza melodia</i>)	E	11.1	9	Rothstein (1975a)
Chestnut-collared Longspur (<i>Calcarius ornatus</i>)		0.0	23	Davis et al. (2002)
Northern Cardinal (<i>Cardinalis cardinalis</i>)	E	14.3	7	Rothstein (1975a)
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)		0.0	4	Rothstein (1975a)
Dickcissel (<i>Spiza americana</i>)	unk	11.1 ^e	9	Peer et al. (2000)
Bobolink (<i>Dolichonyx oryzivorus</i>)		0.0	2	Sealy unpublished data
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	E (3.3 ^d), P	3.3	92	Rothstein (1975a)
		0.0	19	Ortega and Cruz (1988)
Eastern Meadowlark (<i>Sturnella magna</i>)	D	33.3	3	Rothstein (1975a)
	unk	35.7 ^e	14	Peer et al. (2000)
Yellow-headed Blackbird (<i>Xanthocephalus xanthocephalus</i>)		0.0	2	Rothstein (1975a)
	E	7.3	55	Ortega and Cruz (1988)
		0.0	23	Ortega and Cruz (1991)

Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)	E (9.1 ^d), D, P	21.2	33	Sealy unpublished data
Common Grackle (<i>Quisicalus quiscula</i>)	E (7.1), D	11.4	70	Rothstein (1975a)
	E, D, P, B	12.3 ^h	154 ^h	Peer and Bollinger (1997)
Orchard Oriole (<i>Ic. spurius</i>)		0.0	26	Sealy and Underwood (submitted)
Hooded Oriole (<i>Ic. cucullatus</i>)		0.0	~10	Friedmann et al. (1977), Rothstein pers. comm.
House Finch (<i>Carpodacus mexicanus</i>)		0.0	2	Rothstein (1975a)
American Goldfinch (<i>Carduelis tristis</i>)	D, P	20.0	10	Rothstein (1975a)

^a Methods of rejection: E = ejection, D = nest desertion, P = pecking, B = egg burial. Numbers in parentheses are the percent of total eggs that were rejected by ejection where more than one method of rejection was used.

^b A 12-day acceptance criterion was used.

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

^d 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 incapable of being puncture-ejected.

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

^f Sample size and rejection frequency are approximate.

^g A 3-day acceptance criterion was used.

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

Appendix 2. Response of host species to real or artificial Bronzed Cowbird (*Molothrus aeneus*) eggs experimentally added to their nests. Data are from studies where nests were experimentally parasitized with eggs present and considered 5 days as the acceptance criterion, unless otherwise noted.

Species	% rejected ^a	n	Reference
Rejecters ^b			
Scissor-tailed Flycatcher (<i>Tyrannus forficatus</i>)	95.2	21	Peer and Sealy (2000)
Couch's Kingbird (<i>Ty. couchii</i>)	100.0	4	Carter (1986)
Northern Mockingbird (<i>Mimus polyglottos</i>)	68.8	32	Peer et al. (2002)
Curve-billed Thrasher (<i>Toxostoma curvirostre</i>)	100.0	4	Carter (1986)
Boat-tailed Grackle (<i>Quiscalus major</i>)	100.0	19	Peer (1998)
Great-tailed Grackle (<i>Q. mexicanus</i>)	100.0	4	Carter (1986)
	100.0	93	Peer (1998)

^a Method of rejection was ejection for all species considered.

^b Few potential Bronzed Cowbird hosts have been tested for their response to parasitism. The few species that have been tested represent a biased sample. These species were chosen for testing because of their low frequencies of parasitism and/or their close phylogenetic relationship to known rejecters of Brown-headed Cowbird eggs (see Appendix 1).

Appendix 3. Response of host species to real or artificial Shiny Cowbird (*Molothrus bonariensis*) eggs experimentally added to their nests. Data are from studies where nests were experimentally parasitized with eggs present and considered 5 days as the acceptance criterion, unless otherwise noted.

Species	Egg Morph ^a	Method ^b	% rejected	n	Reference
Rejecters					
Rufous Hornero (<i>Furnarius rufus</i>)	I	E	80.0	5	Mason (1986)
	S	E	83.3	6	Mason (1986)
	S	E	62.5	8	Mason and Rothstein (1986)
Brown Cacholote (<i>Pseudoseisura lophotes</i>)	I	E	100.0 ^c	1	Fraga (2002)
	S	E	100.0 ^c	5	Fraga (2002)
Gray Kingbird (<i>Tyrannus dominicensis</i>)	S	unk	85.7	21	Cruz et al. (1985, 1989)
	S	unk	100.0	13	Post et al. (1990)
	S	E	85.0	20	Baltz and Burhans (1998)
Fork-tailed Flycatcher (<i>Ty. savana</i>)	I	E	100.0	3	Mason (1986)
	S	E	100.0	2	Mason (1986)
	S		0.0 ^d	7	Cavalcanti and Pimentel (1988)
Red-legged Thrush (<i>Turdus plumbeus</i>)	S	unk	100.0	3	Cruz et al. (1985, 1989)

Northern Mockingbird (<i>Mimus polyglottos</i>)	S	unk	77.7	9	Cruz et al. (1985, 1989)
	S	unk	100.0	9	Post et al. (1990)
Chalk-browed Mockingbird (<i>Mi. saturninus</i>)	I	E	100.0 ^e	10	Fraga (1985)
	S	E (33.3), P	17.6 ^e	17	Fraga (1985)
	I	E (87.5), D	72.7	11	Mason (1986)
	S	E (50.0), D	20.0	10	Mason (1986)
	S		0.0 ^d	1	Cavalcanti and Pimentel (1988)
Pearly-eyed Thrasher (<i>Margarops fuscatus</i>)	S	unk	81.0	21	Cruz et al. (1985, 1989)
Bananaquit (<i>Coereba flaveola</i>)	S	unk	64.3	14	Cruz et al. (1985, 1989)
Stripe-headed Tanager (<i>Spindalis zena</i>)	S	unk	100.0	2	Cruz et al. (1985, 1989)
Brown-and-Yellow Marshbird (<i>Pseudoleistes virescens</i>)	I	E	83.3	6	Mermoz and Reboreda (1994)
Greater Antillean Grackle (<i>Quiscalus niger</i>)	S	unk	88.8	36	Cruz et al. (1985, 1989)
	S	unk	76.9	13	Post et al. (1990)
Carib Grackle (<i>Qu. lugubris</i>)	unk	unk	88.9	9	Cruz et al. (1995)
	S	unk	63.3	30	Post et al. (1990)
Yellow Oriole (<i>Icterus nigrogularis</i>)	unk	unk	100.0	1	Cruz et al. (1995)
Village Weaver (<i>Ploceus cucullatus</i>)	S	unk	13.8	58	Cruz and Wiley (1989)
	S	unk	89.3 ^d	56	Robert and Sorci (1999)

Accepters

Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	S		0.0	4	Post et al. (1990)
Mangrove Cuckoo (<i>Coc. minor</i>)	S		0.0	6	Post et al. (1990)
Tufted Tit-Spinetail (<i>Leptasthenura platensis</i>)	I		0.0	1	Mason (1986)
	S		0.0	4	Mason (1986)
Wren-like Rushbird (<i>Phleocryptes melanops</i>)	I		0.0	5	Mason 1986
	S		0.0	7	Mason 1986
Short-billed Canastero (<i>Asthenes baeri</i>)	unk		0.0	3	Fraga (2002)
Little Thornbird (<i>Phacellodomos sibilatrix</i>)	S		0.0	1	Mason (1986)
	unk		0.0	3	Fraga (2002)
Freckle-breasted Thornbird (<i>Phac. striaticollis</i>)	S		0.0	1	Mason (1986)
Firewood-gatherer (<i>Anumbius annumbi</i>)	S		0.0	6	Mason (1986)
White-crested Tyrannulet (<i>Serpophaga subcristata</i>)	S		0.0	1	Mason (1986)
Vermilion Flycatcher (<i>Pyrocephalus rubinus</i>)	I		0.0	6	Mason (1986)
	S		0.0	6	Mason (1986)
Yellow-browed Tyrant (<i>Satrapa icterophrys</i>)	I	D	33.3	3	Mason (1986)
	S		0.0	2	Mason (1986)
Cattle Tyrant (<i>Machetornis rixosus</i>)	I		0.0	2	Mason (1986)
Caribbean Elaenia (<i>Elaenia martinica</i>)	S		0.0	8	Post et al. (1990)

Puerto Rican Flycatcher (<i>Myiarchus antillarum</i>)	S		0.0	10	Cruz et al. (1985, 1989)
	S		0.0	5	Post et al. (1990)
Great Kiskadee (<i>Pitangus sulphuratus</i>)	I		0.0	4	Mason (1986)
	S	E	50.0	2	Mason (1986)
Black-whiskered Vireo (<i>Vireo altiloquus</i>)	S	unk	33.3	3	Cruz et al. (1985, 1989)
	S	unk	0.0	10	Post et al. (1990)
Brown-chested Martin (<i>Phaeoprogne tapera</i>)	S		0.0	1	Mason (1986)
Caribbean Martin (<i>Progne dominicensis</i>)	S	unk	14.3	7	Post et al. (1990)
White-rumped Swallow (<i>Tachycineta leucorrhoa</i>)	S		0.0	3	Mason (1986)
House Wren (<i>Troglodytes aedon</i>)	I		0.0	3	Mason (1986)
	S		0.0	8	Kattan (1998)
Masked Gnatcatcher (<i>Polioptila dumicola</i>)	I		0.0	1	Mason (1986)
Creamy-bellied Thrush (<i>Tu. amaurochalinus</i>)	I		0.0	1	Mason (1986)
Tropical Mockingbird (<i>Mi. gilvus</i>)	S	unk	14.3	14	Post et al. (1990)
Scaly-breasted Thrasher (<i>Mar. fuscus</i>)	S		0.0	4	Post et al. (1990)
Yellow Warbler (<i>Dendroica petechia</i>)	S		0.0	20	Cruz et al. (1985, 1989)
	S		15.4	13	Post et al. (1990)
Adelaide's Warbler (<i>De. adelaidae</i>)	S		0.0	5	Post et al. (1990)
Blue-and-yellow Tanager (<i>Thraupis bonariensis</i>)	I		0.0	1	Mason (1986)

Black-faced Grassquit (<i>Tiaris bicolor</i>)	S		0.0	10	Cruz et al. (1985, 1989)
Puerto Rican Bullfinch (<i>Loxigilla portoricensis</i>)	S		0.0	1	Cruz et al. (1985, 1989)
Unknown finches (<i>Lox. spp.</i>)	S		0.0	10	Post et al. (1990)
Saffron Finch (<i>Sicalis flaveola</i>)	I		0.0	4	Mason (1986)
	S		0.0	8	Mason (1986)
Grassland Yellow-Finch (<i>Si. luteola</i>)	I		0.0	2	Mason (1986)
Grassland Sparrow (<i>Ammodramus humeralis</i>)	I		0.0	1	Mason (1986)
Rufous-collared Sparrow (<i>Zonotrichia capensis</i>)	I	D	33.3	6	Mason (1986)
	S	D	20.0	5	Mason (1986)
Streaked Saltator (<i>Saltator albicollis</i>)	S	unk	28.6	7	Post et al. (1990)
Scarlet-headed Blackbird (<i>Amblyramphus</i>	I		0.0	3	Mermoz and Fernández (1999)
<i>holosericeus</i>)	S		0.0	6	Mermoz and Fernández (1999)
Saffron-cowled Blackbird (<i>Agelaius flavus</i>)	I		0.0	2	Fraga (2002)
	S		0.0	1	Fraga (2002)
Chestnut-capped Blackbird (<i>Ag. ruficapillus</i>)	I		0.0 ^f	3	Lyon (1997)
	S		0.0 ^f	3	Lyon (1997)
Yellow-winged Blackbird (<i>Ag. thilius</i>)	I		0.0	5	Massoni and Reboreda (1998)
	S		0.0	7	Massoni and Reboreda (1998)
Yellow-shouldered Blackbird (<i>Ag. xanthomus</i>)	S	unk	9.1	11	Cruz et al. (1985, 1989)
	S		0.0	6	Post et al. (1990)

Bay-winged Cowbird (<i>Molothrus badius</i>)	I	0.0	6	Mason (1986)
Black-cowled Oriole (<i>Ic. prothemelas</i>)	S	0.0	7	Cruz et al. (1985, 1989)
Nutmeg Mannikin (<i>Lonchura punctulata</i>)	S	0.0	15	Cruz et al. (1985, 1989)
Hooded Siskin (<i>Carduelis magellanica</i>)	S	0.0	1	Mason (1986)
House Sparrow (<i>Passer domesticus</i>)	I	0.0	1	Mason (1986)
	S	0.0	1	Mason (1986)

^a In some areas of their range, populations of Shiny Cowbirds lay dimorphic eggs and produce an immaculate egg morph and/or a spotted egg morph (Ortega 1998): I = immaculate, S = spotted.

^b Methods of rejection: E = ejection, D = nest desertion, P = pecking, B = egg burial. Numbers in parentheses are the percent of total eggs that were rejected by ejection where more than one method of rejection was used.

^c A 2-day acceptance criterion was used.

^d A 1-day acceptance criterion was used.

^e Some nests were tested with more than one egg type, i.e. only 16 nests in total experimentally parasitized. Immaculate eggs included two dove eggs and spotted eggs included five Screaming Cowbird (*Molothrus rufoaxillaris*) eggs, but responses to these were not differentiated.

^f An 8-day acceptance criterion was used.