

**REPORTED BLACK-BILLED AND YELLOW-BILLED CUCKOO HOSTS'  
RESPONSES TO A DUMMY BLACK-BILLED CUCKOO  
AND CUCKOO-LIKE EGGS**

BY

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A thesis submitted to the Faculty of Graduate Studies in partial fulfilment of the  
requirements for the degree of

Master of Science

Department of Zoology

University of Manitoba  
Winnipeg, Manitoba  
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## ABSTRACT

Nest defence was examined in two putative Black-billed and Yellow-billed cuckoo (*Coccyzus erythrophthalmus* and *C. americanus*) hosts, the Red-winged Blackbird (*Agelaius phoeniceus*) and Yellow Warbler (*Dendroica petechia*) at Delta Marsh, Manitoba. The objectives were to determine whether Red-winged Blackbirds and Yellow Warblers responded differentially to the Black-billed Cuckoo at the laying and nestling stages and if their responses revealed specific recognition of the cuckoo as a brood parasite. Red-winged Blackbirds and Yellow Warblers were presented with taxidermic mounts of a Black-billed Cuckoo, a Common Grackle (*Quiscalus quiscula*; an egg and nestling predator), and an American Robin (*Turdus migratorius*; control) at the laying and nestling stages in 2001. Red-winged Blackbirds responded to the cuckoo at laying, but less aggressively than they did to the grackle, and their responses increased between stages. Thus, Red-winged Blackbirds did not perceive the cuckoo as a brood parasite but may have recognized it as a predator. In 2002, Red-winged Blackbirds were presented with a Eurasian Blackbird (*Turdus merula*), with which they had no previous experience. Their responses to the cuckoo were similar to their responses to the Eurasian Blackbird, which suggested that they likely responded to the cuckoo as they would to an unfamiliar intruder. Yellow Warblers responded similarly to the cuckoo and robin, indicating that they did not recognize the cuckoo as a specific threat.

Because Yellow Warblers lay smaller eggs than the cuckoo, they may not be suitable Black-billed Cuckoo hosts. Both model cuckoo eggs and real cuckoo-sized eggs (American Robin eggs) were placed in Yellow Warbler nests to determine if they would

accept, and if so, whether they could incubate Black-billed Cuckoo eggs. Yellow Warblers accepted 63% of cuckoo-sized eggs. However, 10/27 Yellow Warblers deserted parasitized nests. Rejected nests had smaller volumes than accepted nests. Robin eggs placed in Yellow Warbler nests developed blood vessels and embryos as quickly as robin eggs placed in conspecific nests. Thus, Yellow Warblers are potentially suitable Black-billed Cuckoo hosts. However, their acceptance of model eggs and lack of nest defence behaviour in response to the dummy cuckoo suggests that Yellow Warblers were not previously Black-billed Cuckoo hosts.

For Jessy, Sonja, Mike and Hector

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## GENERAL INTRODUCTION

Black-billed and Yellow-billed cuckoos (*Coccyzus erythrophthalmus* and *C. americanus*) are facultative brood parasites, or, birds that usually build nests and rear their young but sometimes lay in other birds' nests. Recently, there has been some debate about how facultative parasitism arose in these *Coccyzus* cuckoos. While molecular phylogenies agree that the family Cuculidae is divided into three major clades, with parasitic species in each of these clades (Aragon et al. 1999, Sorenson and Payne 2002), the question of whether parasitism evolved independently in each group or whether all of the groups evolved from a single parasitic ancestor and some secondarily lost this parasitic behaviour remains unresolved. Hughes (1996, 1997, 1999) has suggested that the facultative parasitism exhibited by Black-billed and Yellow-billed Cuckoos is a remnant of an ancestral breeding strategy and that the Black-billed and Yellow-billed Cuckoos were themselves once obligate brood parasites. Hughes (1997) has also suggested that Black-billed and Yellow-billed Cuckoo eggs match or mimic the eggs of many of their reported non-cuckoo hosts. Both theoretical and experimental objections have been raised in response to Hughes' host egg mimicry hypothesis, including criticisms of Hughes' quantification of egg mimicry (Lorenzana and Sealy 2002) and questions about the plausibility of an obligate brood parasite evolving an independent breeding strategy (Payne 1997, Poaini 1997). Furthermore, Hughes' host egg mimicry hypothesis assumes that the 30 records for Black-billed and Yellow-billed Cuckoos' parasitism of non-cuckoo species, dating from 1877 until the present, are representative of the cuckoos' past host use. However, many of these records are unconfirmed and there is little evidence to suggest that these instances of parasitism



reflect anything more than opportunistic laying by the cuckoos. Also, many of the reported hosts lay eggs that are less than 35% the volume of Black-billed and Yellow-billed Cuckoo eggs and thus, these reported host species seem too small to be hosts. Davies and Brooke (1989), as well as Moksnes et al. (1990) have suggested that whether a potential host species has been previously parasitized by a brood parasite, may be determined by examining the potential host's reactions to model cuckoo eggs placed in their nests and to taxidermic mounts of the brood parasite. Hosts previously parasitized by the European Common Cuckoo (*Cuculus canorus*) often recognize the cuckoo as a brood parasite and/or reject its eggs from their nests (Davies and Brooke 1989, Moksnes et al. 1990). Similarly, if reported Black-billed and Yellow-billed Cuckoo hosts were more frequently parasitized in the past, anti-parasite defences may have been selected for and retained. My study examined the reactions of two reported Black-billed and Yellow-billed Cuckoo hosts, the Red-winged Blackbird (*Agelaius phoeniceus*) and Yellow Warbler (*Dendroica petechia*), to a model Black-billed Cuckoo placed near their nest and determined whether the Yellow Warbler, which lays small eggs relative to the cuckoos, would accept and incubate Black-billed Cuckoo-sized eggs.

When Black-billed and Yellow-billed Cuckoos do lay in other birds nests, it is most frequently those of conspecifics (Fleischer et al. 1985) or the other cuckoo species (i.e., Black-billed Cuckoos lay in Yellow-billed Cuckoos nests and vice versa; Nolan and Thompson 1975), but rarely in the nests of non-cuckoo species (Hughes 2001). In addition to their occasional brood-parasitic behaviour, Black-billed and Yellow-billed cuckoos have other life history traits that seem atypical of nesting species. They have 10-day incubation periods (Johnsgard 1997), which are shorter than expected for their egg

size (Davies and Brooke 1988). Some brood parasites, like the Brown-headed Cowbird (*Molothrus ater*), have an incubation period shorter than what is expected for their egg size (Briskie and Sealy 1990) or, some cuckoos, retain the egg in their oviduct prior to laying to advance incubation (Payne 1974). Both strategies increase the probability that the parasitic egg will hatch before the host's eggs (McMaster and Sealy 1998). Also, the timing of Black-billed and Yellow-billed cuckoos' nest construction and laying is not always sequential—Black-billed and Yellow-billed cuckoos sometimes lay their first egg prior to lining the nest and nest construction may continue during incubation (Hughes 2001). This differs from other nesting species that usually complete their nests prior to laying their first egg. Nolan and Thompson (1975) found that Black-billed and Yellow-billed Cuckoos' parasitic behaviour primarily occurred in years of high food abundance resulting from cicada outbreaks. They suggested that, if cuckoo egg production is sensitive to food availability, then in years of high food abundance Black-billed and Yellow-billed Cuckoos may produce eggs either in excess of their nest's capacity or when they have no nest (Nolan and Thompson 1975). This, in turn, leads to the cuckoo laying its eggs in the nests of other birds. Also, unlike most other nesting species that typically lay an egg every 24 hours until the laying of the penultimate egg, Black-billed and Yellow-billed cuckoo laying patterns are less predictable because they sometimes skip one to several days (Hughes 2001, Sealy 2003). Two other members of the genus, the Dwarf Cuckoo (*C. pumilus*) and Dark-billed Cuckoo (*C. melacoryphus*) also occasionally exhibit parasitic behaviour (Ralph 1975, Sick 1993) but there is relatively little information available on their ecology.

The *Coccyzus* cuckoos belong to the behaviourally, morphologically and distributionally diverse family Cuculidae. Recently, there has been debate about the relationships within and between various family members, including *Coccyzus*' relation to other parasitic genera, as well as when brood parasitism evolved. One previously accepted classification system (Peters 1940) divided the cuckoo family into 6 subfamilies and placed parasitic and non-parasitic cuckoos in separate subfamilies: Cuculinae (the parasitic cuckoos), Phaenicophaeinae (the non-parasitic cuckoos including *Coccyzus*), Neomorphinae (the roadrunners or "ground cuckoos"), Crotophaginae (anis and guira), Centropodinae (coucals), and Couinae (couas). Following this arrangement brood parasitism would have evolved at least twice, in Cuculinae and Neomorphinae (parasitic *Tapera* and *Dromococcyx*) and, what could be considered a third time, in Phaenicophaeinae (*Coccyzus*). However, Peters' criteria used to group the cuckoos are not entirely clear and some of his proposed groupings have been re-examined.

A molecular phylogeny, based on sequences of the mitochondrial ND2 (NADH dehydrogenase subunit 2) gene, divides the cuckoos into three major clades: Cuculinae (includes most Old World parasitic cuckoos), Phaenicophinae (includes the parasitic genus *Clamator*, *Coccyzus* and the nesting cuckoos), and Neomorphinae-Crotophaginae (includes the New World parasitic cuckoos *Dromococcyx* and *Tapera* plus the ground cuckoos; Sorenson and Payne 2002). Sorenson and Payne (2002) argued that obligate brood parasitism evolved independently in each of the three lines. Aragon et al. (1999) proposed a phylogeny, based on mitochondrial cytochrome b sequences, that also supported the monophyly of these 3 major clades but, argued that all three clades likely evolved from a common parasitic ancestor and that some members of Phaenicophaeinae

had either lost or partially lost this ancestral parasitic behaviour. Hughes (1996, 2000) similarly concluded that brood parasitism evolved only once in the cuckoos, however, her phylogenetic analyses, based on osteological (Hughes 2000), behavioural and ecological characters (Hughes 1996) placed all parasitic cuckoos, plus *Coccyzus*, in a single subfamily. Both Hughes (1996, 2000) and Aragon et al. (1999) argued that given the rarity of obligate parasitism among birds (1% of birds are obligate brood parasites), it seems unlikely for parasitism to have evolved three times in a single family. Hughes (1996, 1997) further suggested that not only did Black-billed and Yellow-billed Cuckoos evolve from an obligately parasitic ancestor but that they themselves were once obligate brood parasites that have subsequently evolved a more independent breeding strategy.

Hughes (1997) characterized Black-billed and Yellow-billed cuckoos' blue-green eggs as "matching" more than 70% of their reported host species. This proportion is significantly higher than would be expected if hosts were selected randomly from a pool of 64 (Yellow-billed Cuckoo) and 63 (Black-billed Cuckoo) potential host species with which the cuckoos' ranges overlap. Thus, Black-billed and Yellow-billed cuckoos have parasitized significantly more hosts that lay blue-green eggs than would be expected if hosts were chosen randomly. Hughes (1997) suggested that this supported a hypothesis of host-egg mimicry between cuckoos and their reported host species. She rationalized that because egg mimicry evolves in response to the selective pressure placed on parasites by egg-discriminating hosts (Davies and Brooke 1988), and since egg-discrimination has only been observed in species that are or have been frequently parasitized (Davies and Brooke 1989), there was once a historically intense parasitic relationship between the Black-billed and Yellow-billed cuckoos and their reported hosts.

Both theoretical and empirical objections have been raised to Hughes' hypothesis. Based on the hypothesis that Black-billed and Yellow-billed cuckoos evolved blue-green eggs to minimize host discrimination, Lorenzana and Sealy (2002) predicted that American Robins (*Turdus migratorius*) and Gray Catbirds (*Dumetella carolinensis*) should eject white (non-mimetic) cuckoo eggs and accept blue-green (mimetic) eggs. Contrary to prediction, American Robins accepted a high proportion of both white and blue-green eggs, whereas Gray Catbirds ejected both egg types (Lorenzana and Sealy 2002). Thus, parasitism on robins by Black-billed and Yellow-billed cuckoos did not provide the selective pressure for cuckoos to evolve a blue-green egg because robins accepted the white egg. On the other hand, if parasitism on catbirds selected for the cuckoos' blue-green colour egg, a more precise mimic should be expected (Lorenzana and Sealy 2002). However, some rarely used but suitable common cuckoo (*Cuculus canorus*) hosts, whose eggs are closely matched by Common Cuckoo's eggs, have refined discrimination abilities and reject Common Cuckoo eggs at frequencies of nearly 100% (Moksnes et al. 1990, Welbergen et al. 2001). Similarly, if cuckoo parasitism on Gray Catbirds previously affected catbird reproductive success, catbirds may discriminate between their eggs and the closely matching blue-green cuckoo eggs. Other studies of egg mimicry have quantified similarities between parasite and host eggs on a five-degree scale, which enables the researcher to assess mimicry along a gradient (e.g., perfect mimicry, good mimicry, moderate mimicry and so on; Moksnes and Røskaft 1995, Sealy et al. 1996). Hughes (1997) scored host eggs as a "match" or "no match" (Table 1). Thus, an immaculate blue-green egg (e.g., Wood Thrush

Table 1. Descriptions of eggs of Black-billed and Yellow-billed cuckoos and those of their reported hosts.

Species	Match <sup>1</sup>	Egg description	Egg vol. relative to Black-billed Cuckoo egg <sup>2</sup>	Egg vol. relative to Yellow-billed Cuckoo egg	Reject <sup>3</sup>	References <sup>4</sup>
Black-billed Cuckoo ( <i>Coccyzus erythrophthalmus</i> )	M	Light blue to light green, immaculate	1	0.71	yes	Rothstein (1975), Hughes (2001)
Yellow-billed Cuckoo ( <i>C. americanus</i> )	M	Light blue to light green (greener than Black-billed Cuckoo egg), immaculate	1.40	1	yes	Rothstein (1975), Hughes (1999)
Mourning Dove ( <i>Zenaida macroura</i> )	N	White, immaculate	1.10	0.80	n/a <sup>a</sup>	Mirarchi and Baskett (1994)
Eastern Wood-Pewee ( <i>Contopus virens</i> )	M	Creamy-white to pale yellow, speckled with chestnut	0.34	0.24	no	McCarty (1996)
Blue Jay ( <i>Cyanocitta cristata</i> )	—	Greenish, buff or bluish with brown spots	1	0.71	yes	Rothstein (1975), Tarvin and Woolfenden (1999)
Veery ( <i>Catharus fuscescens</i> )	M	Medium blue, sometimes with brown spots	0.56	0.40	no	Moskoff (1995)
Wood Thrush ( <i>Hylocichla mustelina</i> )	M	Light blue, immaculate	0.78	0.56	no	Rothstein (1975), Baicich and Harrison (1997)

Table 1 continued.

Species	Match	Egg description	Egg vol. relative to Black-billed Cuckoo egg	Egg vol. relative to Yellow-billed Cuckoo egg	Reject	References
American Robin ( <i>Turdus migratorius</i> )	M	Light blue, immaculate	1.05	0.75	yes <sup>b</sup>	Rothstein (1982), Sallabanks and James (1999)
Gray Catbird ( <i>Dumetella carolinensis</i> )	M	Deep blue or greenish blue, immaculate	0.64	0.46	yes <sup>c</sup>	Rothstein (1982), Cimprich and Moore (1995)
Cedar Waxwing ( <i>Bombycilla cedrorum</i> )	M	Pale or grayish blue, spotted with black and gray	0.46	0.33	yes	Rothstein (1975), Witmer et al. (1997)
Yellow Warbler ( <i>Dendroica petechia</i> )	N	White or creamy-white with brown and/or gray spots	0.17	0.13	mixed	Sealy (1995), Lowther et al. (1999)
Yellow-breasted Chat ( <i>Icteria virens</i> )	—	White or creamy-white with chestnut spots	0.54	0.39	?	Baicich and Harrison (1997)
Northern Cardinal ( <i>Cardinalis cardinalis</i> )	N	White or slightly greenish, speckled with brown, purple or gray	0.75	0.53	no	Graham (1988), Halkin and Linville (1999)
Eastern Towhee ( <i>Pipilo erythrophthalmus</i> )	N	Gray or creamy-white, with brown spots	0.57	0.41	no	Rothstein (1975), Greenlaw (1996)
Chipping Sparrow ( <i>Spizella passerina</i> )	M	Lightly blue, sparsely marked with black, brown or lilac	0.25	0.18	no	Graham (1988), Middleton (1998)

Table 1. continued.

Species	Match	Egg description	Egg vol. relative to Black-billed Cuckoo egg	Egg vol. relative to Yellow-billed Cuckoo egg	Reject	References
Dickcissel ( <i>Spiza americana</i> )	M	Light blue, immaculate	0.46	0.33	no	Baicich and Harrison (1997)
Red-winged Blackbird ( <i>Agelaius phoeniceus</i> )	M	Pale blue scrawled with brown or purple or gray marking	0.67	0.48	no	Yasukawa and Searcy (1995)
House Finch ( <i>Carpodacus mexicanus</i> )	—	Very pale blue, sometimes with black or purple speckles	0.32	0.23	n/a <sup>a</sup>	Hill (1993)

<sup>1</sup>The “match” column refers to Hughes’ (1997) designation of Black-billed or Yellow-billed cuckoo egg as “matching” the egg of the respective putative host species (M = match, N = non-match, — = not included in Hughes’ analysis). Classifications of cuckoo eggs as a match or non-match to their respective reported hosts’ eggs were inferred from Hughes (1997; Hughes presented egg mimicry data for Black-billed and Yellow-billed cuckoos and their hosts at the family and subfamily levels).

<sup>2</sup>Volumes calculated using the formula  $V=kLB^2$ , where a general k value of 0.51 (value from which most bird egg volumes can be determined) was used (Hoyt 1979).

<sup>3</sup>The “reject” column refers to whether the host species rejects Brown-headed Cowbird eggs.

<sup>4</sup>References for the egg descriptions, volume measurements and the host species status as an acceptor or rejector of cowbird eggs.

<sup>a</sup>Unsuitable cowbird host because of nestling diet.

<sup>b</sup>American Robins accept model Black-billed Cuckoo eggs placed in their nest (Lorenzana and Sealy 2002).

<sup>c</sup>Gray Catbirds reject model Black-billed Cuckoo eggs placed in their nest (Lorenzana and Sealy 2002).



*Hylocichla mustelina* egg) and a maculated egg with blue-green ground colour (e.g., Red-winged Blackbird *Agelaius phoeniceus* egg) were classified as equal matches for Black-billed and/or Yellow-billed cuckoo eggs. However, some ejectors distinguish egg types on the basis of maculation alone (Rothstein 1982). Lorenzana and Sealy (2002) argued that Black-billed and Yellow-billed cuckoo eggs matched only five of their reported host species' eggs. Furthermore, although Hughes suggested that the Black-billed and Yellow-billed cuckoo eggs match the eggs of the Wood Thrush and Veery (*Catharus fuscescens*), both species accept non-mimetic eggs (Rothstein 1975, Sealy unpublished) and thus it is unlikely that host discrimination selected for Black-billed or Yellow-billed cuckoos that laid more mimetic eggs. Lorenzana and Sealy (2002) also pointed out that Hughes (1997) did not include the House Finch (*Carpodacus mexicanus*) or the Yellow-breasted Chat (*Icteria virens*)—neither of whose eggs match those of the Black-billed or Yellow-billed cuckoo—among the list of cuckoo hosts used for her analysis. Including them would mean that Black-billed and Yellow-billed cuckoo eggs “match” less than 50 %, rather than 70%, of their reported host species eggs. Lastly, Hughes did not consider egg size when she categorized eggs as matching or non-matching. Parasitic cuckoos and their hosts generally lay eggs roughly similar in size, although parasitic eggs are often slightly larger (Moksnes and Røskaft 1995, Johnsgard 1997). However, some of the Black-billed and Yellow-billed cuckoos' reported host species, like the Yellow Warbler (*Dendroica petechia*) and the Eastern Wood-Pewee (*Contopus virens*), lay eggs that are considerably smaller than Black-billed and Yellow-billed cuckoo eggs (Table 1).

Also contentious is the mechanism by which an obligate brood parasite would evolve an independent breeding strategy because this would be the only instance where nesting had been lost and evolved again (Payne 1997). Hughes (1997) suggested that because Black-billed and Yellow-billed cuckoos have parasitized some of the same species that Brown-headed Cowbirds commonly use for hosts, they may have been outcompeted by cowbirds for host nests, thus forcing the cuckoos evolve an independent breeding strategy. However, it is difficult to imagine a non-parasitic breeding strategy invading a population of obligate brood parasites because independent breeders probably would fall prey to still-parasitic conspecifics (Poiani 1997). Additionally, there is little information available on previous ranges and evolutionary divergence times for *Coccyzus* species. Sequence divergence between Black-billed and Yellow-billed cuckoos suggests they diverged 4.5 million years ago (Pruett et al. 2001). Late Pleistocene (0.5 m.y.a.) and Holocene (100 000 y.a.) Brown-headed Cowbird fossils have been identified from deposits in several south central states in the United States (Lowther 1993). However, prior to European settlement in the late 18<sup>th</sup> century the cowbirds' range was restricted primarily to the short and mixed-grass prairies of the Great Plains (Mayfield 1965, Rothstein 1994). Because little is known of the historic ranges occupied by Black-billed and Yellow-billed cuckoos, the hypothesis that cowbirds outcompeted cuckoos for hosts cannot be evaluated. Other factors that might have limited cuckoo host availability, such as the development of anti-parasite defences by commonly used hosts, are also plausible.

Hughes' host egg mimicry hypothesis assumes that the records for Black-billed and Yellow-billed cuckoo parasitism reflect past host use. There are 11 and 19 records of parasitism by Black-billed and Yellow-billed cuckoos for 11 and 13 non-cuckoo hosts, respectively, from 1877 until the present (Table 2). Most of these records include little supporting documentation (e.g., description of eggs in nest) to confirm these species were previously parasitized. Black-billed or Yellow-billed cuckoo young have been found in the nests of Yellow Warblers, Eastern Towhees, Red-winged Blackbirds and Mourning Doves (the latter was likely the result of a nest usurption because Mourning Doves feed their young crop milk which is unsuitable for the more insectivorous cuckoo; Wolfe 1994). As well, some reported hosts, like the Yellow Warbler, lays eggs smaller than cuckoo's, yet an important characteristic of a suitable host species is that their eggs and the parasite's eggs are similar in size to facilitate incubation (Sealy et al. 2002). Species too small to incubate *Coccyzus* eggs are too small to be hosts. Many of the records of Black-billed and Yellow-billed cuckoo parasitism on non-cuckoo species were published in the late 19<sup>th</sup> century. Some of these earlier records may have been cases of mistaken identity where oologists, more familiar with the Common Cuckoo, mistook Brown-headed Cowbird eggs (which are similar in size and maculation to some Common Cuckoo eggs) for Black-billed or Yellow-billed Cuckoo eggs (Sealy and Stewart unpublished). This would also explain why fewer records have been published in the last century. More, recent records of Black-billed and Yellow-billed cuckoo parasitism may actually reflect opportunistic laying or even "egg-dumping" rather than past host use.

Table 2. Records of parasitism by Black-billed and Yellow-billed cuckoos on non-cuckoo species.

	Date	Locality	Nest contents <sup>1</sup>	Status <sup>2</sup>	Evidence <sup>3</sup>	Source
<u>Black-billed Cuckoo hosts</u>						
Eastern Wood-Pewee	—	—	—	U	1	Bendire (1895)
Veery	—	—	—	U	1	Roberts (1932)
Cedar Waxwing	19 Jul 1874	New York	1/4	U	1	Bagg (1877)
Yellow Warbler	—	Ontario	1/—	U	1	Clarke (1890)
Yellow-breasted Chat	6 Jun 1944	Virginia	1/4	C	3-6	Thomas (1995)
Chipping Sparrow	—	Ontario	1/—	U	1	Clarke (1890)
	—	Ontario	1/—	U	1	Clarke (1890)
American Robin	—	—	—	U	1	Dawson (1903)
Gray Catbird	—	—	—	U	1	Bent (1940)
Wood Thrush	—	—	—	U	1	Bent (1940)
Northern Cardinal	—	—	—	U	1	Bent (1940)
<u>Yellow-billed Cuckoo hosts</u>						
Mourning Dove	1993	Oklahoma	—	U	1	Wolfe (1994)

Table 2 continued.

	Date	Locality	Nest contents <sup>1</sup>	Status <sup>2</sup>	Evidence <sup>3</sup>	Source
<u>Yellow-billed Cuckoo</u>						
<u>hosts</u>						
Mourning Dove	11 Jul 1994	Oklahoma	1/2	C	7	Wolfe (1994)
American Robin	—	Massachusetts	—	U	1	Allen (1877)
	—	New York	2/1/1	N <sup>4</sup>		Davison (1887)
	2 Jul 1902	Connecticut	1/2	C	3,4	Edwards (1903)
Wood Thrush	—	Massachusetts	—	U	1	Allen (1877)
	—	Ohio	—	U		Dawson (1903)
Cedar Waxwing	10 May 1885	Maine	1/5	U	1	Anonymous (1888)
Gray Catbird	20 May 1892	—	1/3	U	1	Webster (1892)
	4 Jun 1881	Missouri	1/1(1)	U	1	Widmann (1882)
Northern Cardinal	1932	Pennsylvania	1/2	P	2	Jacobs (1934)
	17 Jun 1914	Oklahoma	1/3	U	1	Nice (1931)
Dickcissel	1884	Texas	1/5	U	1	Attwater (1892)
	9 Jun 1961	Oklahoma	1/1/2	C	8	Wiens (1965)
Eastern Towhee	30 May 1947	South Carolina	1/—	U	1	Sprunt and Chamberlain (1949)

Table 2 continued.

	Date	Locality	Nest contents <sup>1</sup>	Status <sup>2</sup>	Evidence <sup>3</sup>	Source
<u>Yellow-billed Cuckoo</u>						
<u>hosts</u>						
Eastern Towhee	15 Jul 1973	Indiana	1/3	C	7,8	Nolan and Thompson (1975)
Black-throated Sparrow	1885	Texas	1/3	U	1	Attwater (1892)
Red-winged Blackbird	2 Jun 1953	Michigan	1/3(1)	C	4,6,7	Nickell (1954)
	—	Iowa	—	U	1	Black (1992)
House Finch	—	—	—	U	1	Ryser (1985)
<u>Unidentified cuckoo hosts</u>						
Blue Jay	—	Illinois	1/1	U	1	Darwin (1859)

<sup>1</sup> Number of cuckoo eggs/number of host eggs or number of cuckoo eggs/number of cowbird eggs/number of host eggs. Brackets indicate the number of host eggs found on the ground below the nest.

<sup>2</sup> C = confirmed record, U = unconfirmed, P = probable parasitism. If a record is unconfirmed, the laying of a cuckoo in a non-cuckoo species nest is mentioned without any other supporting documentation. If parasitism is confirmed, there is some supporting documentation (see criteria 3-7 listed below). If parasitism is considered probable, the record was highly suggestive of cuckoo parasitism but documentation was inadequate.

<sup>3</sup> 1. Mention of a Black-billed Cuckoo or Yellow-billed cuckoo laying in the nest of a non-cuckoo species, unaccompanied by any documentation; 2. nest contents indicated (i.e. number of cuckoo eggs and host eggs, shape of cuckoo egg or colour of host eggs); 3. measurement of cuckoo egg(s) and possibly host eggs; 4. colour of cuckoo egg recorded (e.g. light greenish blue, dark greenish blue, immaculate); 5. photograph of parasitized clutch *in situ*; 6. parasitized clutch preserved in museum; 7. cuckoo hatched from egg when nest was discovered, or description of a young cuckoo with cuckoo species assumed on the basis of one or the other cuckoo species in the vicinity or geographic area; 8. identification of host species with indication of cuckoo(s) present in the area and/or cuckoo nest in the vicinity (indicating familiarity with the species and its eggs).

<sup>4</sup>American Robin nest apparently usurped by Yellow-billed Cuckoo, then usurped again by Mourning Dove. Author mentioned that a cuckoo and dove were present on the nest simultaneously when the nest was collected. This does not constitute a record of brood parasitism.

Davies and Brooke (1989), as well as Moksnes et al. (1990) and Moksnes and Røskoft (1992), suggested that whether a potential Common Cuckoo host has been previously parasitized can be determined by examining their reactions to mimetic model cuckoo eggs and taxidermic mounts of a Common Cuckoo. Previously parasitized hosts often recognize the cuckoo as a brood parasite and reject mimetic cuckoo eggs from their nests which indicates these species are ahead of the cuckoo in a coevolutionary arms race (Davies and Brooke 1989, Moksnes et al. 1990). Unsuitable hosts or hosts that have not been previously parasitized typically do not recognize the brood parasite as a threat and do not reject parasitic eggs because there has been no selective pressure to do so (Moksnes and Røskoft 1988). Similarly, if reported Black-billed Cuckoo hosts were also previously parasitized at higher frequencies then parasite recognition and nest defence strategies possibly were selected for and retained. Alternatively, if Black-billed Cuckoo hosts were not previously parasitized, or, if they were parasitized but anti-parasite defences were costly to retain, then anti-parasite nest defence strategies in response to the cuckoo may not have been selected for or may have been lost in the absence of parasitism. Furthermore, if parasite recognition is learned then it may not be a suitable candidate for retention. My first objective was to determine whether Red-winged Blackbirds and/or Yellow Warblers responded differentially to the Black-billed Cuckoo at the laying and nestling stages and, if so, whether their responses revealed specific recognition of the Black-billed Cuckoo as a brood parasite (Chapter 1). My second objective was to test whether Yellow Warblers are a suitable Black-billed Cuckoo host. I determined whether Yellow Warblers accepted model Black-billed Cuckoo eggs and real



cuckoo-sized eggs (American Robin eggs) experimentally placed in their nests, and if Yellow Warblers could incubate cuckoo-sized eggs (Chapter 2).

## CHAPTER 1

RED-WINGED BLACKBIRDS AND YELLOW WARBLERS DO NOT RECOGNIZE  
THE BLACK-BILLED CUCKOO AS A SPECIFIC THREAT

## INTRODUCTION

Because parasitism often reduces the number of host young fledged (Burgham and Picman 1989, Weatherhead 1989, Røskoft et al. 1990, Sealy 1992, Øien et al. 1998, Lorenzana and Sealy 1999), host anti-parasite defences should be selected for to reduce the impacts of parasitism. While some species reject parasitic eggs through egg ejection or nest desertion (Rothstein 1975, Rothstein 1982, Rohwer and Spaw 1988, Davies and Brooke 1989), birds can also reduce the negative impacts of parasitism by preventing parasitism from occurring in the first place through nest defence behaviours (Moksnes et al. 1990, Sealy et al. 1998, Strausberger and Burhans 2001). The benefits of defending a nest from initial parasitism can be substantial, because parasites often remove a host egg when they lay their own egg (Sealy 1992) and both the laying of the parasitic egg and the removal of host eggs may damage other eggs in the nest (Davies and Brooke 1989, Moksnes et al. 1990). Raising a parasitic chick may be costly (Lorenzano and Sealy 2001), particularly if the parasite evicts host young or is larger than the host species because of the increased food demands that the parasite places on host parents and the parasite's increased ability to outcompete host young (Braden et al. 1997, Lichtenstein and Sealy 1998).

However, nest defence behaviour may be costly in terms of energy expenditure or risk of injury to the parent, such that specific enemy recognition should be selected so

parents maximize their fitness by responding only to enemies that threaten the nest (Patterson et al. 1980, Regelman and Curio 1983, Neudorf and Sealy 1992, Sealy et al. 1998) or themselves. The intensity with which nest owners respond should vary over the course of the nesting cycle with nest owners' responses corresponding to an enemy's potential effect on their nesting success (Patterson et al. 1980). For example, White-crowned Sparrows (*Zonotrichia leucophrys*) defended their nests aggressively from western garter snakes (*Thamnophis elegans*) during the nestling stage when the threat of predation was greatest but responded little toward garter snakes during the incubation and fledgling stages because garter snakes do not prey on eggs or fledglings (Patterson et al. 1980). Similarly, some birds parasitized by Brown-headed Cowbirds respond more intensely to the brood parasite during laying and early incubation when the threat of successful parasitism is great but respond less intensely later in the nesting cycle when parasitic eggs would not likely hatch (Folkers and Lowther 1985, Briskie and Sealy 1989, Neudorf and Sealy 1992, Gill and Sealy 1996). Nest defence behaviour is not likely to evolve in Black-billed Cuckoo hosts under current selection pressures because most members of a population will never be parasitized and those that are, will likely reproduce the following year (Moksnes et al. 1990). However, if Black-billed and Yellow-billed cuckoos once parasitized host species more regularly, as Hughes' host-egg mimicry hypothesis suggests, common hosts may have evolved nest defence behaviours against Black-billed Cuckoos.

Many traits in animals today can be attributed to past, rather than current, selection pressures (Byers 1997, Coss 1999, Peer and Sealy 2000, Rothstein 2001).

Pronghorns' (*Antilocapa americana*) running speed and endurance far exceed the running abilities of any present-day predators (Byers 1997). Byers (1997) argued that the pronghorn's running ability reflects past selection pressures brought about by more formidable predators with whom pronghorns were sympatric prior to the end of the late Pleistocene, thus their running ability is a "relic" behaviour or a behaviour that was previously selected for and is currently maintained despite the absence of current selection pressures.

Because the selection pressures are strong in parasite-host systems (Davies 1999), the adaptations and counter-adaptations associated with parasitism are suitable candidates for retention (Rothstein 2001). If in the absence of brood parasitism these anti-parasite traits are adaptively neutral and their maintenance is cost-free for the host, then these traits may be retained (Peer 1998). For example, Gray Catbirds (*Dumetella carolinensis*) on Bermuda are not presently parasitized by Brown-headed Cowbirds but they ejected 83% of non-mimetic eggs placed in their nests (Rothstein 2001). Rothstein suggested that this behaviour has been retained from the catbirds' North American ancestors that were parasitized by cowbirds prior to colonizing Bermuda. Similarly, both Loggerhead Shrikes (*Lanius ludovicianus*) and Yellow-billed Magpies (*Pica nuttali*) ejected non-mimetic eggs at frequencies near 100% despite having never, or rarely (there are 3 records of cowbird parasitism on shrikes), been parasitized by brood parasites (Bolen et al. 2000, Rothstein 2001). These authors argued that the Loggerhead Shrikes' egg recognition and ejection behaviour most likely has been retained from their Old World relatives that are frequent cuckoo hosts (Nakamura et al. 1998, Moskát and Fuisz 1999).

Thus, egg ejection by Gray Catbirds, Loggerhead Shrikes and Yellow-billed Magpies is a relic behaviour selected for by host/parasite interactions and maintained for several hundred years in the absence of parasitism or, in the case of the Loggerhead Shrike and Yellow-billed Magpie, through speciation events (Bolen et al. 2000, Rothstein 2001).

Retained anti-parasite behaviours are not limited to egg ejection behaviours. The Black Tit (*Petroica macrocephala dannefaerdi*) is endemic to the Snares Islands where it has likely been genetically isolated from mainland New Zealand tit (*P. macrocephala*) populations since the Pleistocene glaciations (1.6 to 0.1 m.y.a; McLean and Maloney 1998). While mainland populations are parasitized by the Long-tailed Cuckoo (*Eudynamys taitensis*), the Black Tits on the Snares Islands have no enemies. However, despite their lack of experience with natural enemies, when presented with a Long-tailed Cuckoo and a predator, Black Tits responded similarly to parasitized mainland tit populations (McLean and Maloney 1998). McLean and Maloney's research demonstrated that brood parasite recognition may be, in part, genetically based and has the potential to be retained in the absence of current selection pressure.

On the other hand, costly traits are likely lost when selection is released. For example, the retention of egg rejection behaviours could be costly if unparasitized hosts mistakenly reject one or more of their own eggs (Marchetti 1992, Davies et al. 1996, Peer and Bollinger 1997, Marchetti 2000). Five percent (10/190) of Yellow-browed Leaf Warblers (*Phylloscopus inornatus*) mistakenly ejected their own eggs at unparasitized nests (Marchetti 1992) and Davies et al. (1996) found that under low parasitism rates (19-41%), Reed Warblers accept mimetic cuckoo eggs because the potential for recognition

errors is high. Parasite recognition and nest defence behaviours may be good candidates for retention because their retention is not likely costly (i.e., will not lead to the rejection of the hosts' own eggs). If reported interspecific Black-billed and Yellow-billed cuckoo hosts were previously parasitized at higher frequencies in the past, then parasite recognition and nest defence strategies may have been selected for and retained.

My objectives were to determine whether Red-winged Blackbirds and/or Yellow Warblers responded differentially to the Black-billed Cuckoo at the laying or nestling stage and, if so, whether the nature of their responses revealed specific recognition of the Black-billed Cuckoo as a brood parasite or if they responded to the cuckoo in a more generalized way. I tested Red-winged Blackbirds' and Yellow Warblers' recognition of the Black-billed Cuckoo, rather than the Yellow-billed Cuckoo, because Black-billed Cuckoos nest sporadically in the study area (Delta Marsh, Manitoba; Sealy 1978, Sealy in press) and also because salvaged Black-billed Cuckoo specimens were available (previously collected by S. G. Sealy) to make the models needed for examining hosts' behavioural responses.

Both Yellow Warblers and Red-winged Blackbirds have been recorded as *Coccyzus* cuckoo hosts that have hatched *Coccyzus* young (in the case of the Red-winged Blackbird this parasitism was confirmed, see Table 2). Also, Yellow Warblers and Red-winged Blackbirds both respond to another brood parasite, the Brown-headed Cowbird, significantly more intensely during laying and early incubation ("laying" hereafter), when the threat of parasitism is greatest (Folkers and Lowther 1985, Burgham and Picman 1989, Hobson and Sealy 1989, Neudorf and Sealy 1992, Gill and Sealy 1996). Thus,

they may have the capacity to recognize another brood parasite, the Black-billed Cuckoo, as well. Furthermore, both species accept non-mimetic eggs in their nests (Sealy 1995, Ortega and Cruz 1988) and thus nest defence is their most likely anti-parasite strategy (Neudorf and Sealy 1992). If Yellow Warblers and Red-winged Blackbirds recognize the Black-billed Cuckoo as a parasitic threat they should similarly respond more strongly to the Black-billed Cuckoo during laying. Also, Yellow Warblers exhibit two other responses to Brown-headed Cowbirds that are not elicited by other predator or control models: (1) a “seet” call that differs from the “chip”, “metallic chip” and “warble” that Yellow Warblers utter when presented with predator or control models, and (2) a nest-protection behaviour in which the female “rushes” to and sits on her nest (Hobson and Sealy 1989, Gill and Sealy 1996). Unlike incubation behaviour, this nest sitting is apparently used to block parasites from gaining access to their nest (Hobson and Sealy 1989, Uyehara and Narins 1995, Budnik et al. 2001). If Yellow Warblers perceive the Black-billed Cuckoo as a parasitic threat then they may respond with one and/or both of these behaviours. Alternatively, Red-winged Blackbirds and Yellow Warblers may perceive the Black-billed Cuckoo as a nest predator, because Black-billed Cuckoos have been observed depredated both eggs (Sealy 1994) and nestlings (Bent 1940). If Red-winged Blackbirds and Yellow Warblers perceive the cuckoo as a nest predator they should respond strongly at both the laying and nestling stages.

Even if cuckoos previously parasitized or depredated Red-winged Blackbird and Yellow Warbler nests, because the size of Black-billed Cuckoo breeding populations are inconsistent between years (Hughes 2001), Red-winged Blackbirds and Yellow Warblers

may not be familiar with cuckoos on their breeding grounds, despite having encountered them along migratory routes and/or on the wintering grounds. Alternatively, even if Red-winged Blackbirds and Yellow Warblers were previously parasitized and developed anti-parasite defences these traits may have been lost if their retention was costly in the absence of cuckoo parasitism or if their recognition of the cuckoo was based on their previous experience with the cuckoo. Songbirds sometimes give a generalized nest defence response to intruders at their nest even if they have not had previous experience with a particular predator or parasite (Smith et al. 1984, Hobson et al. 1988, Gill et al. 1997, Lindholm and Thomas 2000). Responses to an unfamiliar intruder are of intermediate intensity between control and predator models (Bazin and Sealy 1993) and the intensity of the nest owners' responses varies little over the course of the nesting cycle (Hobson et al. 1988, Bazin and Sealy 1993). If Red-winged Blackbirds and Yellow Warblers are not familiar with the Black-billed Cuckoo as either a brood parasite or nest predator then they should give a generalized response of intermediate intensity and that should vary little over the course of the nesting cycle.

## METHODS

### **Study site**

Fieldwork was conducted out of the Delta Marsh Field Station (University of Manitoba) on Lake Manitoba's south shore (50°11'N, 98°19' W), during May to July 2001-2002. The site consists of a dune-ridge forest, approximately 80 m wide (MacKenzie 1982), which, extends along the southern shore of the lake. Yellow



Warblers nested densely in this area. South of the ridge is marsh, where Red-winged Blackbirds nest densely, primarily within the 100 m of the ridge or north edge of the marsh (see Mackenzie (1982) for further study site details). Nests were numbered with flagging tape tied to vegetation 1-2 m from the nests and their contents were inspected every 1-3 days prior to testing.

### **Model presentations**

Model presentations were done in 2001 and 2002 to determine whether Red-winged Blackbirds and Yellow Warblers recognized the Black-billed Cuckoo as a brood parasite (2001) and whether the Red-winged Blackbirds' response to the Black-billed Cuckoo was similar to their response to an unfamiliar nest intruder (2002). Yellow Warblers' responses to a novel species were not tested because they have been previously quantified in two studies involving different novel stimuli (Hobson et al. 1988, Gill et al. 1997).

To determine whether Red-winged Blackbirds and Yellow Warblers recognized the Black-billed Cuckoo as a brood parasite behavioural responses were quantified by presenting taxidermic or freeze-dried mounts of a Black-billed Cuckoo, Common Grackle (a positive control) and American Robin (a negative control) at 47 and 42 Red-winged Blackbird nests and 39 and 48 Yellow Warbler nests during the laying and nestling periods, respectively. The robin is similar in size to the Black-billed Cuckoo and Common Grackle and does not threaten either species at either nesting stage. On the other hand, because Common Grackles prey on songbird eggs and nestlings (Bent 1958,

Sealy 1994) and are threats throughout the nesting cycle, Red-winged Blackbirds and Yellow Warblers should respond to them with equal intensity throughout nesting or with increasing intensity as their reproductive investment increases (Montgomerie and Weatherhead 1988, Neudorf and Sealy 1992, Gill and Sealy 1996).

To quantify Red-winged Blackbird's nest defence responses to a species with which they have had no prior experience in May and June 2002, taxidermic and freeze-dried mounts of a male Eurasian Blackbird (*Turdus merula*; novel species), a Black-billed Cuckoo and an American Robin (negative control) were presented at 45 and 45 Red-winged Blackbird nests at laying and at the nestling stages, respectively. The Eurasian Blackbird is a robin-shaped thrush and males are all black except for a bright orange-yellow bill and eye-ring. It is found throughout much of Europe, as well as, parts of North Africa and Asia and has been introduced to Australia and New Zealand (Harrison and Greensmith 1993). Red-winged Blackbirds, whose range is restricted to North and South America, have had no prior contact or experience with the Eurasian Blackbird and thus by presenting them with the Eurasian Blackbird at their nests their response to a novel nest intruder could be quantified. The 2001 and 2002 model presentations were done separately rather than presenting all four models (cuckoo, robin, grackle and Eurasian Blackbird) in a single trial to prevent Red-winged Blackbirds from habituating to the models over the course of the trial (Sealy et al. 1998).

Each nest was tested once, at the laying or nestling stage, to avoid habituation of hosts to the models (Sealy et al. 1998). As well, for the polygynous Red-winged Blackbird, only one nest per harem was tested to avoid testing the same male more than

once. Red-winged Blackbirds nests that were within 30 of one another (Strausberger 2001) and were visibly defended by a single male were considered part of one harem. Models were presented between 0700 hr (after laying) and 2200 hr CDT at both stages of the nesting cycle. Presentation order was determined by drawing model names from a hat before each trial. Each model was presented for 5 minutes with at least 15 minutes between successive presentations to reduce carry-over aggression and habituation to the models (Sealy et al. 1998). Trials began when the first adult returned to within 2 m of the model.

Models were attached to wooden stakes painted to blend with the surrounding vegetation and placed level with the nest rim facing the nest from approximately 0.5 m to simulate an intrusion. Defensive responses to the models were observed with binoculars from a blind approximately 5 m from the nest and observations were spoken into a portable cassette recorder and later transcribed. Blinds were set up at least 20 minutes before the beginning of the first trial. The responses recorded were: (a) vocalizations for Red-winged Blackbirds: checks, chinks, growls, screams, female chatter calls, male song, see calls, ree calls (Orians and Christman 1968); for Yellow Warblers: seet calls, chips, metallic chips, warbles (Hobson and Sealy 1989, Gill and Sealy 1996), (b) close passes and hovers above the model, (c) songspread, tailspread and wingspread displays (Red-winged Blackbird), (d) contacts or strikes on the model, (e) attacks (continuous pecking of the model), (f) perch changes, (g) displacement (bill wipes, preening, foraging), (g) distraction displays, (h) nest sitting, (i) host distance from the model (recorded in categories: < 2 m, 2-5 m, > 5 m), and (j) time spent out of sight/departures. Screams,

attacks, preening, and distraction displays were recorded as the amount of time nest owners spent performing each behaviour during the 5 minute trial and all other behaviours were recorded as the number of times they were performed within the test period.

### **Statistical Analyses**

The data for each host species and year were analysed separately unless otherwise indicated. A non-parametric rank F test was done to determine whether a difference existed in the behaviour elicited by each of the three models. Nest defence responses were ranked within each nest (blocks) and a one-way ANOVA was then performed on the ranks. The rank F test statistic,  $F_R$ , is equivalent to the test statistic for a non-parametric Friedman test (Neter et al. 1996) and this test has been called a modified Friedman test by other researchers (Neudorf and Sealy 1992, Bazin and Sealy 1993, Gill and Sealy 1996). Blocking by nest reduces variance caused by the influence of secondary characteristics of nest owners (e.g., age) because the secondary characters are held constant among stimuli. When a significant difference was found, a Bonferroni pairwise comparison test was performed on mean within-nest ranks to identify the model(s) that elicited significantly different responses from the hosts. Paired t-tests were performed on within-nest ranks to determine whether models elicited significantly different responses from males and females. This test is a modified Wilcoxon-Mann-Whitney test (Neudorf and Sealy 1992) and Levene's test for homogeneity of variance were used prior to analysis to ensure that the ranked data had equal variances. Mann-

Whitney U tests were used to determine whether differences existed in the responses elicited by the models between the laying and nestling stages, as well as to compare between-year responses for the Black-billed Cuckoo and American Robin models. The number of individuals that responded among models and stages were compared using Chi-square tests.

## RESULTS

### **Red-winged Blackbirds 2001**

#### *Laying*

Red-winged Blackbirds responded more aggressively towards the grackle and less aggressively towards the robin during laying (Table 3). Red-winged Blackbirds responded to the cuckoo with an intensity intermediate between the grackle and robin. Red-winged Blackbirds spent significantly more time within 2 m of the grackle and uttered significantly more checks, growls, screams and ree calls, performed significantly more tailspreads, made significantly more perch changes, and hovered above and hit the grackle significantly more than the cuckoo or robin. The cuckoo and grackle elicited significantly more chatter calls, songspreads, passes, and wingspreads than the robin. Also, the cuckoo elicited significantly more hovers, tailspreads and perch changes than the robin. The time Red-winged Blackbirds spent attacking the cuckoo did not differ significantly from the time spent attacking the grackle or robin, but Red-winged Blackbirds attacked the grackle model significantly more than the robin.

Table 3. Red-winged Blackbirds' behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models at laying. Mean  $\pm$  SE, as well as mean within-nest ranks  $\pm$  SE (in brackets), are presented (N = 47 nests tested).

Response <sup>1</sup>	Model			P <sup>2</sup>
	Cuckoo	Robin	Grackle	
Check	20.09 $\pm$ 4.00 <sup>b</sup> (1.85 $\pm$ 0.11)	20.06 $\pm$ 3.67 <sup>b</sup> (1.85 $\pm$ 0.11)	35.53 $\pm$ 4.64 <sup>a</sup> (2.30 $\pm$ 0.11)	0.005
Growl	0.02 $\pm$ 0.02 <sup>b</sup> (1.96 $\pm$ 0.02)	0.02 $\pm$ 0.02 <sup>b</sup> (1.97 $\pm$ 0.04)	0.87 $\pm$ 0.59 <sup>a</sup> (2.07 $\pm$ 0.43)	0.031
♀ Song	4.87 $\pm$ 0.79 <sup>a</sup> (2.04 $\pm$ 1.04)	3.83 $\pm$ 0.73 <sup>b</sup> (1.63 $\pm$ 0.10)	7.53 $\pm$ 1.26 <sup>a</sup> (2.32 $\pm$ 0.11)	0.000
♀ Scream (min)	0.13 $\pm$ 0.09 <sup>b</sup> (1.86 $\pm$ 0.05)	0.02 $\pm$ 0.01 <sup>c</sup> (1.76 $\pm$ 0.54)	0.61 $\pm$ 0.17 <sup>a</sup> (2.37 $\pm$ 0.08)	0.000
♂ Song	0.46 $\pm$ 0.16 (1.91 $\pm$ 0.08)	1.02 $\pm$ 0.32 (2.14 $\pm$ 0.08)	0.91 $\pm$ 0.38 (1.95 $\pm$ 0.07)	0.074
♂ See	1.26 $\pm$ 0.67 (2.00 $\pm$ 0.05)	1.62 $\pm$ 1.04 (1.96 $\pm$ 0.06)	3.40 $\pm$ 1.79 (2.03 $\pm$ 0.06)	0.740
♂ Ree	1.38 $\pm$ 0.58 <sup>b</sup> (1.87 $\pm$ 0.07)	1.68 $\pm$ 0.69 <sup>b</sup> (1.90 $\pm$ 0.09)	4.47 $\pm$ 1.29 <sup>a</sup> (2.22 $\pm$ 0.09)	0.005
♂ Chink	1.36 $\pm$ 1.11 (2.03 $\pm$ 0.04)	0 (1.96 $\pm$ 0.18)	0.21 $\pm$ 0.17 (2.01 $\pm$ 0.16)	0.144
♂ Songsread	0.11 $\pm$ 0.05 <sup>a</sup> (2.07 $\pm$ 0.07)	0 <sup>b</sup> (1.77 $\pm$ 0.05)	0.30 $\pm$ 0.11 <sup>a</sup> (2.14 $\pm$ 0.07)	0.000
Hover	2.40 $\pm$ 0.78 <sup>b</sup> (2.00 $\pm$ 0.09)	0.28 $\pm$ 0.12 <sup>c</sup> (1.56 $\pm$ 0.08)	2.83 $\pm$ 0.44 <sup>a</sup> (2.43 $\pm$ 0.61)	0.000
Pass	1.06 $\pm$ 0.28 <sup>a</sup> (2.11 $\pm$ 0.08)	0.21 $\pm$ 0.10 <sup>b</sup> (1.67 $\pm$ 0.06)	1.74 $\pm$ 0.40 <sup>a</sup> (2.22 $\pm$ 0.09)	0.000
Hit	4.04 $\pm$ 1.08 <sup>b</sup> (1.95 $\pm$ 0.08)	1.57 $\pm$ 1.13 <sup>b</sup> (1.65 $\pm$ 0.09)	10.57 $\pm$ 2.09 <sup>a</sup> (2.38 $\pm$ 0.10)	0.000

Table 3 continued.

Response	Model			P
	Cuckoo	Robin	Grackle	
Attack (min)	0.10 ± 0.06 <sup>a,b</sup> (2.00 ± 0.07)	0.05 ± 0.03 <sup>b</sup> (1.77 ± 0.06)	0.44 ± 0.12 <sup>a</sup> (2.22 ± 0.08)	0.000
Tailsread	0.74 ± 0.17 <sup>b</sup> (2.07 ± 0.09)	0.23 ± 0.08 <sup>c</sup> (1.62 ± 0.06)	1.19 ± 0.21 <sup>a</sup> (2.30 ± 0.09)	0.000
Wingsread	0.51 ± 0.14 <sup>a</sup> (2.05 ± 0.08)	0.13 ± 0.07 <sup>b</sup> (1.74 ± 0.07)	0.74 ± 0.17 <sup>a</sup> (2.20 ± 0.07)	0.000
Perch change	9.02 ± 1.28 <sup>b</sup> (2.02 ± 0.10)	5.40 ± 1.13 <sup>c</sup> (1.50 ± 0.09)	12.49 ± 1.69 <sup>a</sup> (2.47 ± 0.11)	0.000
Preen	0.17 ± 0.10 (1.98 ± 0.06)	0.16 ± 0.10 (1.98 ± 0.07)	0.03 ± 0.01 (2.04 ± 0.07)	0.749
Bill wipe	—	—	—	—
< 2 m (min)	6.12 ± 0.25 <sup>b</sup> (1.84 ± 0.11)	5.54 ± 0.29 <sup>b</sup> (1.68 ± 0.69)	7.50 ± 0.30 <sup>a</sup> (2.47 ± 0.67)	0.000

<sup>1</sup> Screams, attacks and time spent within two metres are reported as the mean amount of time that nest owners spent performing each of these behaviours within the five-minute trial period. All other means are based on the number of times that nest owners performed the behaviour within the five-minute trial. The combined response of the nesting pair is presented except where the behaviour is only elicited in one member of the nesting pair (e.g., only males “ree” call).

<sup>2</sup>P-values from a one-way ANOVA on rank.

<sup>a,b,c</sup> Results of Bonferroni comparison between mean ranks. Means with different superscripts are significantly different with “a” denoting the highest value, “b” denoting the next highest value and so on. Means with 2 superscripts (e.g., <sup>a,b</sup>) do not differ significantly from either of the mean responses elicited by the other two models.

*Nestling stage*

Red-winged Blackbirds responded more aggressively to the grackle than to the cuckoo or robin at the nestling stage (Table 4). They uttered significantly more growls and screams and made significantly more hovers, passes, hits, attacks, wingspreads and perch changes in response to the grackle than in response to either the robin or cuckoo. Red-winged Blackbirds spent significantly more time within 2 m of the nest when presented with the grackle and robin than when presented with the cuckoo. With the exception of time spent within 2 m, responses to the cuckoo and the robin were similar.

*Differences in female and male responses*

There were a few differences in female and male Red-winged Blackbirds' responses to each of the three models (Table 5). During laying, Red-winged Blackbird females uttered significantly more checks, made more close passes and struck the cuckoo significantly more than males. During the nestling stage, males uttered significantly more checks in response to the cuckoo than females. The cuckoo elicited similar responses from both sexes in all other behavioural categories. Female Red-winged Blackbirds struck the robin significantly more than males at the laying stage. No significant differences were found between the male and female Red-winged Blackbirds' response to the robin at the nestling stage. Males and females responded to the grackle similarly during laying although males hit the grackle significantly more than females and males preened significantly more. Females gave significantly more wingspreads in



Table 4. Red-winged Blackbirds' behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models at the nestling stage. Means  $\pm$  SE, as well as mean within-nest ranks  $\pm$  SE (in brackets), are presented (N = 42 nests tested). Conventions as in Table 3.

Response	Model			P
	Cuckoo	Robin	Grackle	
Check	60.05 $\pm$ 8.46 (1.81 $\pm$ 0.13)	70.74 $\pm$ 8.68 (2.13 $\pm$ 0.13)	69.7 $\pm$ 8.12 (2.06 $\pm$ 0.12)	0.162
Growl	2.83 $\pm$ 0.85 <sup>b</sup> (1.76 $\pm$ 0.10)	2.07 $\pm$ 0.50 <sup>b</sup> (1.75 $\pm$ 0.10)	7.12 $\pm$ 1.67 <sup>a</sup> (2.49 $\pm$ 0.10)	0.000
♀ Song	3.74 $\pm$ 0.83 (2.01 $\pm$ 0.11)	4.10 $\pm$ 0.68 (2.11 $\pm$ 0.12)	3.62 $\pm$ 0.81 (1.88 $\pm$ 0.12)	0.386
♀ Scream	0.22 $\pm$ 0.13 <sup>b</sup> (1.90 $\pm$ 0.08)	0.08 $\pm$ 0.04 <sup>b</sup> (1.80 $\pm$ 0.07)	0.87 $\pm$ 0.23 <sup>a</sup> (2.30 $\pm$ 0.09)	0.000
♂ Song	0.62 $\pm$ 0.21 (2.08 $\pm$ 0.68)	0.31 $\pm$ 0.18 (1.96 $\pm$ 0.06)	0.31 $\pm$ 0.18 (1.95 $\pm$ 0.06)	0.296
♂ See	6.33 $\pm$ 3.16 (1.95 $\pm$ 0.07)	7.45 $\pm$ 2.58 (2.08 $\pm$ 0.08)	3.10 $\pm$ 1.19 (1.96 $\pm$ 0.07)	0.396
♂ Ree	7.83 $\pm$ 2.33 (1.91 $\pm$ 0.10)	8.36 $\pm$ 2.19 (1.99 $\pm$ 0.10)	11.36 $\pm$ 2.55 (2.09 $\pm$ 0.11)	0.463
♂ Chink	2.02 $\pm$ 1.04 (2.04 $\pm$ 0.07)	4.52 $\pm$ 2.30 (2.07 $\pm$ 0.07)	0.07 $\pm$ 0.05 (1.88 $\pm$ 0.04)	0.071
♂ Songsread	0.17 $\pm$ 0.07 (2.04 $\pm$ 0.05)	0.05 $\pm$ 0.05 (2.01 $\pm$ 0.04)	0.19 $\pm$ 0.10 (1.94 $\pm$ 0.04)	0.739
Hover	2.45 $\pm$ 0.57 <sup>b</sup> (1.85 $\pm$ 0.10)	2.02 $\pm$ 0.45 <sup>b</sup> (1.76 $\pm$ 0.10)	4.07 $\pm$ 0.72 <sup>a</sup> (2.38 $\pm$ 0.11)	0.000
Pass	0.52 $\pm$ 0.14 <sup>b</sup> (1.83 $\pm$ 0.08)	0.83 $\pm$ 0.23 <sup>b</sup> (1.90 $\pm$ 0.10)	1.83 $\pm$ 0.46 <sup>a</sup> (2.26 $\pm$ 0.91)	0.002
Hit	5.90 $\pm$ 1.70 <sup>b</sup> (1.79 $\pm$ 0.12)	7.60 $\pm$ 1.57 <sup>b</sup> (1.76 $\pm$ 0.09)	28.02 $\pm$ 4.14 <sup>a</sup> (2.44 $\pm$ 0.11)	0.000
Attack	0.12 $\pm$ 0.04 <sup>b</sup> (1.73 $\pm$ 0.09)	0.16 $\pm$ 0.04 <sup>b</sup> (1.80 $\pm$ 0.08)	0.63 $\pm$ 0.14 <sup>a</sup> (2.46 $\pm$ 0.09)	0.000

Table 4 continued.

Response	Model			P
	Cuckoo	Robin	Grackle	
Tailsread	0.31 ± 0.10 (2.01 ± 0.08)	0.17 ± 0.18 (1.88 ± 0.07)	0.43 ± 0.13 2.11 ± 0.08	0.116
Wingspread	0.33 ± 0.11 <sup>a,b</sup> (2.02 ± 0.08)	0.14 ± 0.07 <sup>b</sup> (1.85 ± 0.07)	0.50 ± 0.16 <sup>a</sup> (2.12 ± 0.08)	0.045
Perch change	12.7 ± 1.85 <sup>b</sup> (1.86 ± 0.13)	11.57 ± 1.20 <sup>b</sup> (1.77 ± 0.12)	15.26 ± 1.40 <sup>a</sup> (2.37 ± 0.11)	0.001
Preen	0.06 ± 0.03 (2.06 ± 0.08)	0.05 ± 0.04 (2.02 ± 0.08)	0.03 ± 0.02 (1.91 ± 0.07)	0.418
Billwipe	1.33 ± 0.47 (2.10 ± 0.09)	0.62 ± 0.23 (1.95 ± 0.08)	0.57 ± 0.22 (1.95 ± 0.09)	0.399
< 2 m	5.47 ± 0.47 <sup>b</sup> (1.57 ± 0.10)	6.55 ± 0.37 <sup>a</sup> (2.10 ± 0.12)	7.16 ± 0.40 <sup>a</sup> (2.33 ± 0.12)	0.011

Table 5. Male and female Red-winged Blackbird behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models at the laying (L) and nestling (N) stages. Mean responses  $\pm$  SE, as well as mean within-nest ranks  $\pm$  SE (in brackets), are presented (N = 47 and 42 nests for the laying and nestling stages, respectively).

Response <sup>1</sup>		Cuckoo			Robin			Grackle		
		Female	Male	P <sup>2</sup>	Female	Male	P	Female	Male	P
Checks	L	5.74 $\pm$ 2.28 (2.06 $\pm$ 0.09)	16.02 $\pm$ 3.21 (1.77 $\pm$ 0.10)	0.031	2.70 $\pm$ 1.21 (1.66 $\pm$ 0.08)	17.68 $\pm$ 3.65 (1.94 $\pm$ 0.11)	0.045	10.89 $\pm$ 3.45 (2.27 $\pm$ 0.86)	26.45 $\pm$ 3.79 (2.30 $\pm$ 0.11)	0.478
	N	37.95 $\pm$ 8.33 (2.07 $\pm$ 0.12)	27.67 $\pm$ 4.68 (1.65 $\pm$ 0.11)	0.013	32.55 $\pm$ 6.88 (1.95 $\pm$ 0.12)	38.19 $\pm$ 4.97 (2.13 $\pm$ 0.13)	0.239	27.21 $\pm$ 7.21 (1.98 $\pm$ 0.12)	42.52 $\pm$ 5.45 (2.32 $\pm$ 0.10)	0.14
Growl	L	0.13 $\pm$ 0.13 (1.97 $\pm$ 0.01)	0.02 $\pm$ 0.02 (2.04 $\pm$ 0.08)	1.0	0.02 $\pm$ 0.02 (2.0 $\pm$ 0.03)	0 (1.96 $\pm$ 0.03)	0.290	0.19 $\pm$ 0.19 (2.00 $\pm$ 0.03)	0.68 $\pm$ 0.56 (2.06 $\pm$ 0.04)	1.0
	N	2.40 $\pm$ 0.83 (1.88 $\pm$ 0.11)	0.45 $\pm$ 0.19 (1.85 $\pm$ 0.06)	0.757	2.07 $\pm$ 0.50 (1.80 $\pm$ 0.09)	0.36 $\pm$ 0.18 (1.87 $\pm$ 0.08)	0.529	5.76 $\pm$ 1.69 (2.32 $\pm$ 0.10)	5.76 $\pm$ 1.69 (2.29 $\pm$ 0.09)	0.797
Hover	L	1.32 $\pm$ 0.50 (2.04 $\pm$ 0.08)	1.09 $\pm$ 0.38 (1.98 $\pm$ 0.09)	0.402	0.13 $\pm$ 0.07 (1.68 $\pm$ 0.06)	0.17 $\pm$ 0.10 (1.64 $\pm$ 0.07)	0.592	1.28 $\pm$ 0.28 (2.28 $\pm$ 0.09)	1.55 $\pm$ 0.28 (2.38 $\pm$ 0.08)	0.000
	N	1.43 $\pm$ 0.36 (2.01 $\pm$ 0.09)	1.05 $\pm$ 0.30 (1.81 $\pm$ 0.08)	0.052	0.76 $\pm$ 0.18 (1.80 $\pm$ 0.10)	1.26 $\pm$ 0.42 (1.80 $\pm$ 0.08)	1.0	1.76 $\pm$ 0.34 (2.19 $\pm$ 0.10)	2.31 $\pm$ 0.53 (2.39 $\pm$ 0.10)	0.088
Pass	L	0.62 $\pm$ 0.17 (2.20 $\pm$ 0.08)	0.47 $\pm$ 0.17 (1.94 $\pm$ 0.06)	0.005	0.09 $\pm$ 0.07 (1.72 $\pm$ 0.05)	0.19 $\pm$ 0.09 (1.81 $\pm$ 0.07)	0.323	0.48 $\pm$ 0.19 (2.05 $\pm$ 0.07)	0.48 $\pm$ 0.19 (2.25 $\pm$ 0.08)	0.002
	N	0.24 $\pm$ 0.08 (1.94 $\pm$ 0.07)	0.29 $\pm$ 0.11 (1.83 $\pm$ 0.07)	0.317	0.21 $\pm$ 0.08 (1.92 $\pm$ 0.09)	0.62 $\pm$ 0.22 (1.92 $\pm$ 0.07)	1.0	0.49 $\pm$ 0.14 (2.12 $\pm$ 0.08)	1.36 $\pm$ 0.38 (2.26 $\pm$ 0.09)	0.264

Table 5 continued.

Response		Cuckoo			Robin			Grackle		
		Female	Male	P	Female	Male	P	Female	Male	P
Hit	L	1.26 ± 0.44 (2.10 ± 0.06)	2.79 ± 0.81 (1.89 ± 0.08)	0.024	0.13 ± 0.13 (1.80 ± 0.05)	1.47 ± 1.07 (1.70 ± 0.09)	0.253	2.53 ± 0.93 (2.11 ± 0.07)	1.36 ± 0.38 (2.40 ± 0.09)	0.019
	N	5.90 ± 1.70 (1.82 ± 0.11)	2.60 ± 0.70 (1.77 ± 0.10)	0.664	3.67 ± 0.92 (1.81 ± 0.07)	3.93 ± 0.85 (1.82 ± 0.10)	0.910	14.62 ± 2.88 (2.37 ± 0.11)	13.40 ± 2.04 (2.40 ± 0.11)	0.755
Attack	L	0.01 ± 0.01 (2.02 ± 0.04)	0.08 ± 0.06 (1.94 ± 0.05)	0.128	0 (1.91 ± 0.03)	0.05 ± 0.03 (1.82 ± 0.05)	0.095	0.05 ± 0.03 (2.06 ± 0.05)	0.38 ± 0.11 (2.24 ± 0.07)	0.10
	N	0.07 ± 0.03 (1.90 ± 0.08)	0.03 ± 0.01 (1.74 ± 0.07)	0.128	0.06 ± 0.02 (1.79 ± 0.07)	0.10 ± 0.04 (1.93 ± 0.07)	0.135	0.26 ± 0.09 (2.31 ± 0.09)	0.38 ± 0.01 (2.33 ± 0.08)	0.819
Perch Change	L	6.68 ± 0.84 (2.18 ± 0.11)	2.60 ± 0.70 (1.89 ± 0.09)	0.015	4.17 ± 0.88 (1.56 ± 0.10)	1.26 ± 0.37 (1.69 ± 0.10)	0.385	8.43 ± 1.42 (2.25 ± 0.10)	4.51 ± 0.68 (2.41 ± 0.10)	0.287
	N	4.67 ± 0.93 (1.93 ± 0.14)	4.67 ± 0.93 (1.81 ± 0.11)	0.463	6.98 ± 0.74 (1.89 ± 0.11)	5.14 ± 0.77 (1.87 ± 0.11)	0.885	8.38 ± 0.95 (2.18 ± 0.12)	6.90 ± 0.98 (2.32 ± 0.11)	0.366
< 2 m	L	4.67 ± 0.11 (2.07 ± 0.09)	1.45 ± 0.25 (1.68 ± 0.09)	0.008	4.18 ± 0.23 (1.97 ± 0.09)	1.36 ± 0.267 (1.72 ± 0.10)	0.090	7.50 ± 0.21 (1.95 ± 0.09)	3.26 ± 0.26 (2.59 ± 0.09)	0.175
	N	3.64 ± 0.29 (1.76 ± 0.10)	1.82 ± 0.29 (1.62 ± 0.11)	0.290	4.21 ± 0.23 (2.11 ± 0.09)	2.34 ± 0.28 (2.01 ± 0.11)	0.476	4.22 ± 0.23 (2.13 ± 0.10)	4.22 ± 0.23 (2.37 ± 0.12)	0.091

<sup>1</sup>Screams, attacks and time spent within two metres are reported as the mean amount of time that nest owners spent performing each of these behaviours within the five-minute trial period. All other means are based on the number of times that nest owners performed the behaviour within the five-minute trial.

<sup>2</sup>P-values are from student t-tests performed on within-nest ranks.

response to the grackle at laying than did males. All responses to the grackle at the nestling stage were similar.

#### *Laying and nestling stages compared*

The Red-winged Blackbirds' responses to all three models generally increased or remained the same between stages.

#### BLACK-BILLED CUCKOO

Females uttered significantly more checks and growls, wiped their bill significantly more, plus hovered above and hit the cuckoo significantly more at the nestling stage (Table 6). However, females spent significantly less time within 2 m of the cuckoo at the nestling stage. Males uttered significantly more growls and ree calls and wiped their bills significantly more in response to the cuckoo at the nestling stage. However, males performed significantly fewer tailspreads in response to the cuckoo at the nestling stage.

#### COMMON GRACKLE

Females uttered significantly more checks and growls, hit the grackle significantly more and wiped their bills significantly more in response to the grackle at the nestling stage. Females uttered significantly fewer chattercalls in response to the grackle at the nestling stage. Males also uttered significantly more checks and growls, performed significantly more tailspreads, made significantly more perch changes, and

Table 6. Comparison of Red-winged Blackbirds' behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models presented at their nests during laying and the nestling stage.

Sex	Response	Cuckoo		Robin		Grackle	
		Change <sup>1</sup>	P <sup>2</sup>	Change	P	Change	P
Female	Checks	+	0.000	+	0.000	+	0.001
	Screams	=	ns	=	ns	=	ns
	Growls	+	0.000	+	0.000	+	0.000
	Song	=	ns	=	ns	-	0.021
	Hover	+	0.042	+	0.000	=	ns
	Pass	=	ns	=	ns	=	ns
	Hit	+	0.03	+	0.000	+	0.000
	Wingspread	=	ns	=	ns	=	ns
	Tailsread	=	ns	=	ns	=	ns
	Billwipe	+	0.001	+	0.031	+	0.016
	Preen	=	ns	=	ns	=	ns
	Perch change	=	ns	+	0.000	=	ns
	< 2 m	-	0.008	=	ns	=	ns
Male	Checks	=	ns	+	0.001	+	0.017
	Chink	=	ns	+	0.004	=	ns
	Growl	+	0.015	+	0.016	+	0.000
	Song	=	ns	-	0.025	=	ns
	See	=	ns	=	ns	=	ns
	Ree	+	0.010	+	0.001	-	0.033
	Songsread	=	ns	+	ns	=	ns
	Hover	=	ns	+	0.001	=	ns
	Pass	=	ns	=	ns	=	ns

Table 6 continued.

Sex	Response	Cuckoo		Robin		Grackle	
		Change	P	Change	P	Change	P
Male	Hit	=	ns	+	0.000	=	ns
	Wingspread	=	ns	=	ns	=	ns
	Tailsread	-	0.022	=	ns	+	0.022
	Billwipe	+	0.008	+	0.008	+	0.016
	Preen	=	ns	=	ns	=	ns
	Perch change	=	ns	+	0.000	+	0.041
	< 2 m	=	ns	+	0.017	=	ns

<sup>1</sup>A “+” indicates that the response increased from the laying to the nestling stage, a “-“ indicates a decrease in response between the stages, and “=” indicates that the mean response elicited at each stage was similar.

<sup>2</sup>P-values presented are the result of Mann-Whitney U tests; “ns” indicates a non-significant P-value (> 0.05).

wiped their bills significantly more in response to the grackle at the nestling stage. Males uttered significantly fewer ree calls in response to the grackle at the nestling stage.

#### AMERICAN ROBIN

Females uttered significantly more checks and growls, wiped their bills significantly more, changed perches significantly more, and hovered above and hit the robin significantly more at the nestling stage. Males uttered significantly more checks, chinks, growls and ree calls but sang significantly fewer songs in response to the robin at the nestling stage. Males also wiped their bills significantly more, spent significantly more time within 2 m, made significantly more perch changes and hovered above and hit the robin significantly more at the nestling stage.

#### *Number of individuals responding to models*

There was no significant difference among models in the number of members of the nesting pair that responded at laying (Table 7). Red-winged Blackbirds responded as pairs to the grackle significantly more often at the nestling stage than to the cuckoo or robin.

#### **Red-winged Blackbirds 2002**

##### *Laying*

Red-winged Blackbirds uttered significantly more checks and growls in response to the cuckoo and Eurasian Blackbird than to the robin (Table 8). Red-winged



Table 7. Number of trials in which one or both members of a Red-winged Blackbird pair responded to Black-billed Cuckoo, American Robin and Common Grackle models placed at their nests during the laying and nestling stages in May-June 2001.

Stage	Model						X <sup>2</sup>	P
	Cuckoo		Robin		Grackle			
	One	Both	One	Both	One	Both		
Laying	17	30	16	31	7	40	6.35	0.42
Nestling	13	29	9	33	1	41	11.91	0.003

Table 8. Red-winged Blackbirds' behavioural responses to Black-billed Cuckoo, American Robin and Eurasian Blackbird models at laying. Means  $\pm$  SE and mean within-nest ranks  $\pm$  SE (in brackets) are presented (N = 45 nests tested). Conventions as in Table 3.

Response	Model			P
	Cuckoo	Robin	Eurasian Blackbird	
Check	28.64 $\pm$ 4.90 <sup>a</sup> (2.15 $\pm$ 0.12)	17.78 $\pm$ 3.73 <sup>b</sup> (1.60 $\pm$ 0.11)	31.93 $\pm$ 4.45 <sup>a</sup> (2.24 $\pm$ 0.10)	0.000
Growl	0.42 $\pm$ 0.16 <sup>a</sup> (2.07 $\pm$ 0.07)	0.07 $\pm$ 0.04 <sup>b</sup> (1.84 $\pm$ 0.06)	0.40 $\pm$ 0.19 <sup>a</sup> (2.09 $\pm$ 0.07)	0.013
♀ Song	8.22 $\pm$ 1.07 (2.03 $\pm$ 0.10)	6.93 $\pm$ 0.93 <sup>b</sup> (1.68 $\pm$ 0.11)	10.53 $\pm$ 1.26 <sup>a</sup> (2.29 $\pm$ 0.11)	0.000
♀ Scream	0 (1.99 $\pm$ 0.03)	0.01 $\pm$ 0.01 (2.02 $\pm$ 0.04)	0.01 $\pm$ 0.01 (1.99 $\pm$ 0.03)	0.692
♂ Song	0.33 $\pm$ 0.15 (1.97 $\pm$ 0.06)	0.51 $\pm$ 0.32 (1.98 $\pm$ 0.06)	0.38 $\pm$ 0.13 (2.05 $\pm$ 0.08)	0.607
♂ See call	1.18 $\pm$ 0.45 (2.09 $\pm$ 0.07)	2.11 $\pm$ 0.84 (1.96 $\pm$ 0.05)	0.78 $\pm$ 0.43 (1.96 $\pm$ 0.06)	0.084
♂ Ree call	1.33 $\pm$ 0.49 <sup>a,b</sup> (2.03 $\pm$ 0.09)	1.22 $\pm$ 0.63 <sup>b</sup> (1.83 $\pm$ 0.06)	3.00 $\pm$ 0.96 <sup>a</sup> (2.13 $\pm$ 0.08)	0.025
♂ Chink	0.98 $\pm$ 0.59 (2.04 $\pm$ 0.05)	0.24 $\pm$ 0.24 (1.94 $\pm$ 0.24)	2.60 $\pm$ 2.03 (2.01 $\pm$ 0.05)	0.274
♂ Songspread	0.18 $\pm$ 0.14 (1.93 $\pm$ 0.05)	0.20 $\pm$ 0.11 (2.01 $\pm$ 0.06)	0.29 $\pm$ 0.12 (2.05 $\pm$ 0.06)	0.327
Hover	0.67 $\pm$ 0.39 (1.96 $\pm$ 0.06)	0.29 $\pm$ 0.12 (1.92 $\pm$ 0.07)	0.91 $\pm$ 0.43 (2.12 $\pm$ 0.07)	0.095
Pass	0.22 $\pm$ 0.09 <sup>b</sup> (1.83 $\pm$ 0.07)	0.20 $\pm$ 0.12 <sup>b</sup> (1.81 $\pm$ 0.06)	0.84 $\pm$ 0.19 <sup>a</sup> (2.36 $\pm$ 0.09)	0.000
Hit	1.93 $\pm$ 0.70 <sup>a,b</sup> (2.03 $\pm$ 0.08)	0.91 $\pm$ 0.50 <sup>b</sup> (1.80 $\pm$ 0.07)	3.53 $\pm$ 1.21 <sup>a</sup> (2.17 $\pm$ 0.08)	0.005
Attack	0.04 $\pm$ 0.04 (1.94 $\pm$ 0.06)	0.03 $\pm$ 0.02 (2.03 $\pm$ 0.06)	0.04 $\pm$ 0.02 (2.02 $\pm$ 0.07)	0.634

Table 8 continues.

Response	Model			P
	Cuckoo	Robin	Eurasian Blackbird	
Tailsread	1.02 ± 0.32 (2.07 ± 0.09)	0.69 ± 0.22 (1.91 ± 0.09)	0.93 ± 0.29 (2.01 ± 0.08)	0.384
Wingspread	0.67 ± 0.21 (2.09 ± 0.07)	0.27 ± 0.16 (1.88 ± 0.05)	0.47 ± 0.21 (2.03 ± 0.07)	0.061
Perch change	8.73 ± 1.04 (2.01 ± 0.12)	7.18 ± 1.16 (1.87 ± 0.12)	8.44 ± 1.06 (2.12 ± 0.12)	0.316
Preen	0.14 ± 0.06 (1.99 ± 0.06)	0.25 ± 0.11 (2.06 ± 0.09)	0.03 ± 0.02 (1.96 ± 0.07)	0.435
Billwipe	0.36 ± 0.14 (1.94 ± 0.07)	0.49 ± 0.14 (2.07 ± 0.08)	0.62 ± 0.22 (1.98 ± 0.05)	0.550
< 2 m	5.33 ± 0.36 <sup>a,b</sup> (2.00 ± 0.12)	4.76 ± 0.30 <sup>b</sup> (1.73 ± 0.12)	5.86 ± 0.33 <sup>a</sup> (2.27 ± 0.11)	0.006

Blackbirds directed significantly more close passes towards the Eurasian Blackbird than towards the cuckoo or robin. Red-winged Blackbirds uttered significantly more ree calls, hit the model significantly more and spent significantly more time within 2 m of the model in response to Eurasian Blackbird than the robin. The number of ree calls and hits, as well as the amount of time that Red-winged Blackbirds spent within 2 m of the cuckoo model, did not differ significantly from either the robin or the Eurasian Blackbird.

### *Nestling stage*

Red-winged Blackbirds hovered above the Eurasian Blackbird and cuckoo significantly more than above the robin (Table 9). They also made significantly more passes and hit and performed significantly more tailspreads and bill wipes in response to the cuckoo than the robin. Plus Red-winged Blackbirds performed significantly more tailspreads in response to the cuckoo than in response to the Eurasian Blackbird. Red-winged Blackbirds gave an intermediate number of hits, passes and bill wipes in response to the Eurasian Blackbird that did not differ significantly from the Red-winged Blackbird's response to either the robin or cuckoo.

### *Differences in female and male responses*

Females gave significantly more checks in response to the cuckoo at laying than males (Table 10). At the nestling stage, females hit the cuckoo significantly more than males but males spent significantly more time preening. Males performed significantly more tailspreads in response to the robin at laying but spent significantly less time within

Table 9. Red-winged Blackbirds' behavioural responses to Black-billed Cuckoo, American Robin and Eurasian Blackbird models at the nestling stage. Mean responses  $\pm$  SE, as well mean within-nest ranks  $\pm$  SE (in brackets), are presented (N = 45 nests tested). Conventions as in Table 3.

Response	Model			P
	Cuckoo	Robin	Eurasian Blackbird	
Check	55.98 $\pm$ 6.91 (2.03 $\pm$ 0.13)	50.69 $\pm$ 8.03 (1.90 $\pm$ 0.11)	54.16 $\pm$ 7.03 (2.07 $\pm$ 0.13)	0.592
Growl	3.09 $\pm$ 0.93 (2.08 $\pm$ 0.09)	1.18 $\pm$ 0.33 (1.91 $\pm$ 0.09)	2.53 $\pm$ 0.79 (2.01 $\pm$ 0.09)	0.435
♀ Song	5.00 $\pm$ 0.69 (2.04 $\pm$ 0.11)	4.78 $\pm$ 0.73 (2.03 $\pm$ 0.12)	4.64 $\pm$ 0.78 (1.92 $\pm$ 0.12)	0.699
♀ Scream	0.15 $\pm$ 0.08 (2.01 $\pm$ 0.04)	0.12 $\pm$ 0.08 (1.93 $\pm$ 0.06)	0.16 $\pm$ 0.07 (2.06 $\pm$ 0.07)	0.318
♂ Song	0.31 $\pm$ 0.12 (2.03 $\pm$ 0.06)	0.29 $\pm$ 0.15 (1.99 $\pm$ 0.06)	0.22 $\pm$ 0.11 (1.98 $\pm$ 0.06)	0.796
♂ See call	4.87 $\pm$ 2.37 (2.10 $\pm$ 0.07)	3.51 $\pm$ 1.55 (1.98 $\pm$ 0.06)	2.16 $\pm$ 1.05 (1.92 $\pm$ 0.07)	0.169
♂ Ree call	4.89 $\pm$ 1.33 (2.08 $\pm$ 0.10)	3.44 $\pm$ 1.18 (1.89 $\pm$ 0.09)	6.51 $\pm$ 2.04 (2.03 $\pm$ 0.08)	0.284
♂ Chink	1.29 $\pm$ 0.71 (1.98 $\pm$ 0.05)	3.29 $\pm$ 2.25 (1.99 $\pm$ 0.06)	2.71 $\pm$ 1.46 (2.03 $\pm$ 0.06)	0.724
♂ Songsread	0.18 $\pm$ 0.09 (2.04 $\pm$ 0.06)	0.07 $\pm$ 0.05 (1.93 $\pm$ 0.05)	0.13 $\pm$ 0.06 (2.02 $\pm$ 0.05)	0.306
Hover	1.69 $\pm$ 0.36 <sup>a</sup> (2.17 $\pm$ 0.11)	0.69 $\pm$ 0.18 <sup>b</sup> (1.74 $\pm$ 0.09)	1.51 $\pm$ 0.28 <sup>a</sup> (2.09 $\pm$ 0.10)	0.007
Pass	1.11 $\pm$ 0.33 <sup>a</sup> (2.13 $\pm$ 0.09)	0.51 $\pm$ 0.21 <sup>b</sup> (1.84 $\pm$ 0.07)	1.04 $\pm$ 0.37 <sup>a,b</sup> (2.09 $\pm$ 0.10)	0.041
Hit	6.38 $\pm$ 1.30 <sup>a</sup> (2.19 $\pm$ 0.11)	4.18 $\pm$ 1.40 <sup>b</sup> (1.83 $\pm$ 0.08)	6.22 $\pm$ 1.39 <sup>a,b</sup> (1.98 $\pm$ 0.10)	0.045
Attack	0.15 $\pm$ 0.06 (1.93 $\pm$ 0.06)	0.10 $\pm$ 0.05 (2.03 $\pm$ 0.07)	0.16 $\pm$ 0.06 (2.03 $\pm$ 0.07)	0.798

Table 9 continued.

Response	Model			P
	Cuckoo	Robin	Eurasian Blackbird	
Tailsread	2.98 ± 0.51 <sup>a</sup> (2.38 ± 0.10)	1.89 ± 0.42 <sup>b</sup> (1.80 ± 0.10)	1.64 ± 0.43 <sup>b</sup> (1.82 ± 0.10)	0.000
Wingspread	3.20 ± 0.55 (2.19 ± 0.12)	2.80 ± 0.66 (1.90 ± 0.11)	2.22 ± 0.53 (1.91 ± 0.09)	0.107
Perch change	13.09 ± 1.29 (2.13 ± 0.13)	9.58 ± 1.08 (1.84 ± 0.11)	11.51 ± 1.12 (2.02 ± 0.12)	0.227
Preen	0.01 ± 0.00 (1.94 ± 0.07)	0.12 ± 0.08 (2.13 ± 0.07)	0.03 ± 0.03 (1.92 ± 0.06)	0.046
Billwipe	1.11 ± 0.24 <sup>a</sup> (2.20 ± 0.08)	0.40 ± 0.15 <sup>b</sup> (1.81 ± 0.08)	0.82 ± 0.25 <sup>a,b</sup> (1.98 ± 0.08)	0.004
< 2 m	6.40 ± 0.28 (2.15 ± 0.12)	5.69 ± 0.35 (1.87 ± 0.11)	5.80 ± 0.36 (1.97 ± 0.12)	0.247

Table 10. Male and female behavioural responses to Black-billed Cuckoo, American Robin and Eurasian Blackbird models at the laying (L) and nestling (N) stages. Mean responses  $\pm$  SE, as well as mean within-nest ranks (in brackets), are presented (N = 45 and 45 nests for the laying and nestling stages, respectively). Conventions as in Table 5.

Response		Cuckoo			Robin			Eurasian Blackbird		
		Female	Male	P	Female	Male	P	Female	Male	P
Checks	L	10.13 $\pm$ 2.64 (2.30 $\pm$ 0.10)	18.51 $\pm$ 4.26 (1.97 $\pm$ 0.12)	0.024	5.73 $\pm$ 2.45 (1.69 $\pm$ 0.08)	12.04 $\pm$ 2.78 (1.71 $\pm$ 0.11)	0.854	8.20 $\pm$ 2.31 (2.01 $\pm$ 0.11)	23.73 $\pm$ 4.08 (2.32 $\pm$ 0.08)	0.025
	N	11.38 $\pm$ 3.05 (2.12 $\pm$ 0.11)	44.60 $\pm$ 5.87 (2.21 $\pm$ 0.12)	0.602	16.16 $\pm$ 5.65 (1.82 $\pm$ 0.10)	34.53 $\pm$ 6.37 (1.81 $\pm$ 0.10)	0.582	18.76 $\pm$ 5.93 (2.05 $\pm$ 0.11)	35.40 $\pm$ 5.17 (1.98 $\pm$ 0.11)	0.614
Growl	L	0.20 $\pm$ 0.08 (2.10 $\pm$ 0.06)	0.22 $\pm$ 0.10 (2.02 $\pm$ 0.05)	0.197	0.02 $\pm$ 0.02 (1.91 $\pm$ 0.04)	0.04 $\pm$ 0.03 (1.90 $\pm$ 0.05)	0.844	0.09 $\pm$ 0.04 (1.99 $\pm$ 0.03)	0.31 $\pm$ 0.18 (2.14 $\pm$ 0.06)	0.952
	N	3.00 $\pm$ 0.90 (2.17 $\pm$ 0.09)	0.20 $\pm$ 0.18 (1.87 $\pm$ 0.04)	0.002	0.89 $\pm$ 0.27 (1.91 $\pm$ 0.09)	0.29 $\pm$ 0.17 (1.99 $\pm$ 0.06)	0.382	1.71 $\pm$ 0.64 (1.91 $\pm$ 0.08)	0.82 $\pm$ 0.38 (2.13 $\pm$ 0.07)	0.221
Hover	L	0.09 $\pm$ 0.04 (2.02 $\pm$ 0.05)	0.58 $\pm$ 0.35 (1.97 $\pm$ 0.05)	0.323	0.11 $\pm$ 0.06 (2.02 $\pm$ 0.05)	0.18 $\pm$ 0.10 (1.89 $\pm$ 0.06)	0.057	0.09 $\pm$ 0.07 (1.96 $\pm$ 0.05)	0.82 $\pm$ 0.42 (2.14 $\pm$ 0.06)	0.013
	N	0.96 $\pm$ 0.28 (2.13 $\pm$ 0.10)	0.73 $\pm$ 0.21 (2.05 $\pm$ 0.09)	0.483	0.38 $\pm$ 0.12 (1.90 $\pm$ 0.08)	0.31 $\pm$ 0.09 (1.82 $\pm$ 0.09)	0.483	0.47 $\pm$ 0.15 (1.97 $\pm$ 0.09)	1.04 $\pm$ 0.25 (2.12 $\pm$ 0.09)	0.168
Pass	L	0.09 $\pm$ 0.06 (1.93 $\pm$ 0.04)	0.13 $\pm$ 0.08 (1.87 $\pm$ 0.05)	0.404	0.11 $\pm$ 0.09 (1.97 $\pm$ 0.03)	0.09 $\pm$ 0.04 (1.85 $\pm$ 0.06)	0.058	0.20 $\pm$ 0.09 (2.10 $\pm$ 0.05)	0.64 $\pm$ 0.18 (2.26 $\pm$ 0.08)	0.096
	N	0.73 $\pm$ 0.25 (2.17 $\pm$ 0.08)	0.38 $\pm$ 0.22 (1.99 $\pm$ 0.06)	0.058	0.24 $\pm$ 0.14 (1.90 $\pm$ 0.06)	0.27 $\pm$ 0.15 (1.92 $\pm$ 0.05)	0.117	0.33 $\pm$ 0.15 (1.93 $\pm$ 0.06)	0.71 $\pm$ 0.35 (2.09 $\pm$ 0.06)	0.095
Hit	L	0.18 $\pm$ 0.09 (2.02 $\pm$ 0.06)	1.76 $\pm$ 0.69 (2.02 $\pm$ 0.07)	1.0	0.13 $\pm$ 0.08 (1.94 $\pm$ 0.04)	0.78 $\pm$ 0.44 (1.83 $\pm$ 0.07)	0.124	0.24 $\pm$ 0.10 (2.03 $\pm$ 0.05)	3.29 $\pm$ 1.16 (2.14 $\pm$ 0.09)	0.215

Table 10 continued.

Response	Cuckoo			Robin			Eurasian Blackbird		
	Female	Male	P	Female	Male	P	Female	Male	P
Hit	N 4.80 ± 1.15 (2.24 ± 0.10)	1.58 ± 0.53 (1.89 ± 0.09)	0.003	1.89 ± 0.50 (1.87 ± 0.09)	2.29 ± 1.01 (1.98 ± 0.04)	0.048	3.22 ± 0.91 (1.89 ± 0.09)	3.00 ± 0.86 (2.13 ± 0.10)	0.015
Attack	L 0.04 ± 0.04 (1.97 ± 0.04)	0.01 ± 0.00 (1.96 ± 0.06)	0.800	0 (2.04 ± 0.04)	0.04 ± 0.25 (2.01 ± 0.06)	0.519	0 (1.98 ± 0.03)	0.04 ± 0.02 (2.03 ± 0.06)	0.456
	N 0.12 ± 0.05 (2.06 ± 0.06)	0.03 ± 0.02 (1.93 ± 0.06)	0.070	0.02 ± 0.01 (1.96 ± 0.06)	0.07 ± 0.04 (2.03 ± 0.07)	0.001	0.06 ± 0.04 (1.98 ± 0.06)	0.10 ± 0.04 (2.03 ± 0.07)	0.417
Tailsread	L 0.80 ± 0.23 (2.05 ± 0.08)	0.22 ± 0.08 (2.03 ± 0.07)	0.830	0.33 ± 0.17 (1.87 ± 0.07)	0.36 ± 0.12 (2.03 ± 0.07)	0.027	0.76 ± 0.27 (2.08 ± 0.08)	0.18 ± 0.07 (1.93 ± 0.06)	0.124
	N 2.82 ± 0.51 (2.31 ± 0.10)	0.16 ± 0.06 (2.07 ± 0.05)	0.057	1.82 ± 0.40 (1.87 ± 0.10)	0.07 ± 0.05 (1.91 ± 0.04)	0.083	1.53 ± 0.43 (1.82 ± 0.10)	0.11 ± 0.05 (2.01 ± 0.05)	0.136
Wingspread	L 0.62 ± 0.20 (2.08 ± 0.07)	0.04 ± 0.03 (2.02 ± 0.03)	0.430	0.24 ± 0.16 (1.89 ± 0.05)	0.02 ± 0.02 (1.99 ± 0.02)	0.083	0.44 ± 0.21 (2.03 ± 0.06)	0.02 ± 0.02 (1.99 ± 0.33)	0.511
	N 3.09 ± 0.52 (2.21 ± 0.11)	0.11 ± 0.09 (1.98 ± 0.04)	0.051	2.76 ± 0.65 (1.90 ± 0.11)	0.04 ± 0.03 (1.99 ± 0.04)	0.386	2.16 ± 0.53 (1.89 ± 0.10)	0.07 ± 0.04 (2.02 ± 0.04)	0.248
Perch Change	L 7.00 ± 0.92 (2.11 ± 0.10)	1.73 ± 0.42 (1.92 ± 0.66)	0.133	5.51 ± 0.87 (1.83 ± 0.12)	1.67 ± 0.53 (1.82 ± 0.10)	0.936	6.27 ± 0.85 (2.05 ± 0.12)	2.18 ± 0.48 (2.25 ± 0.09)	0.167
	N 9.20 ± 1.15 (2.17 ± 0.12)	3.89 ± 0.58 (2.15 ± 0.11)	0.880	6.89 ± 0.82 (1.90 ± 0.11)	2.69 ± 0.58 (1.81 ± 0.11)	0.227	7.73 ± 0.93 (1.92 ± 0.11)	3.78 ± 0.70 (2.03 ± 0.10)	0.401



Table 10 continued.

Response		Cuckoo			Robin			Eurasian Blackbird		
		Female	Male	P	Female	Male	P	Female	Male	P
Preen	L	0.14 ± 0.06 (2.0 ± 0.06)	0 (1.99 ± 0.03)	0.881	0.25 ± 0.11 (2.10 ± 0.08)	0 (1.95 ± 0.02)	0.113	0.03 ± 0.02 (1.90 ± 0.07)	0 (2.05 ± 0.04)	0.075
	N	0 (1.89 ± 0.05)	0.01 ± 0.00 (2.04 ± 0.04)	0.021	0.05 ± 0.03 (2.10 ± 0.05)	0.08 ± 0.07 (2.01 ± 0.05)	0.946	0.03 ± 0.03 (1.99 ± 0.04)	0.01 ± 0.01 (1.94 ± 0.04)	0.439
< 2 m	L	3.97 ± 0.22 (1.98 ± 0.10)	1.35 ± 0.24 (1.93 ± 0.12)	0.768	3.97 ± 0.22 (1.99 ± 0.10)	0.79 ± 0.20 (1.71 ± 0.10)	0.768	4.16 ± 0.20 (2.03 ± 0.10)	1.74 ± 0.22 (2.35 ± 0.09)	0.021
	N	4.19 ± 0.16 (2.12 ± 0.12)	2.21 ± 0.25 (2.02 ± 0.12)	0.551	3.95 ± 0.20 (1.96 ± 0.12)	1.74 ± 0.27 (1.87 ± 0.11)	0.114	3.81 ± 0.21 (1.92 ± 0.10)	1.99 ± 0.25 (2.10 ± 0.11)	0.215

2 m of the robin. Male and female Red-winged Blackbirds did not differ in their response to the robin at the nestling stage. Males hovered significantly more and uttered significantly more checks in response to Eurasian Blackbird at laying, whereas at the nestling stage, males uttered significantly more growls and hit the Eurasian Blackbird significantly more than females. Females spent significantly more time within two metres of the Eurasian Blackbird at laying.

#### *Laying and nestling stages compared*

The intensity of the Red-winged Blackbirds' responses to all three models generally increased at the nestling stage (Table 11).

#### BLACK-BILLED CUCKOO

Females made significantly more passes, hovered above the model significantly more, uttered significantly more growls, chatter calls and screams, performed significantly more tailspreads and wingspreads and directed significantly more hits and attacks at the cuckoo during the nestling stage. Females preened significantly less when presented with the cuckoo at the nestling stage. Males uttered significantly more checks, made more perch changes, spent significantly more time within 2 m, and hovered above the cuckoo significantly more at the nestling stage.

#### EURASIAN BLACKBIRD

Females uttered significantly more growls and screams, performed significantly more tailspreads, and hovered above and hit the Eurasian Blackbird significantly more at

Table 11. Comparison of Red-winged Blackbirds' responses to Black-billed Cuckoo, American Robin and Eurasian Blackbird models presented at their nests during the laying and nestling stages. Conventions as in Table 6.

Sex	Response	Cuckoo		Robin		Eurasian Blackbird	
		Change	P	Change	P	Change	P
Female	Checks	=	ns	=	ns	=	ns
	Screams	+	0.007	=	ns	+	0.015
	Growls	+	0.001	+	0.000	+	0.002
	Song	-	0.019	=	ns	-	0.000
	Hover	+	0.000	=	ns	+	0.004
	Pass	+	0.002	=	ns	=	ns
	Hit	+	0.000	+	0.000	+	0.003
	Wingspread	+	0.000	+	0.000	+	0.000
	Tailsread	+	0.000	+	0.000	+	0.020
	Perch change	=	ns	+	0.000	=	ns
	Preen	-	0.002	=	ns	=	ns
	< 2 m	=	ns	=	ns	=	ns
	Male	Checks	+	0.001	+	0.01	=
Chinks		=	ns	=	ns	=	ns
Growl		=	ns	=	ns	=	ns
Song		=	ns	=	ns	=	ns
See		=	ns	=	ns	=	ns
Ree		=	ns	+	0.050	=	ns
Songsread		=	ns	=	ns	=	ns
Hover		+	0.013	=	ns	=	ns
Pass		=	ns	=	ns	=	ns
Hit		=	ns	=	ns	=	ns

Table 11 continued.

Sex	Response	Cuckoo		Robin		Eurasian Blackbird	
		Change	P	Change	P	Change	P
Male	Wingspread	=	ns	=	ns	=	ns
	Tailsread	=	ns	+	0.024	=	ns
	Perch change	+	0.001	+	0.044	=	ns
	Preen	=	ns	=	ns	=	ns
	< 2 m	+	0.014	+	0.005	=	ns

the nestling stage. However, females uttered significantly fewer chattercalls in response to the Eurasian Blackbird at the nestling stage. Males responded to the Eurasian Blackbird with a similar intensity for all behavioural categories at the laying and nestling stages.

#### AMERICAN ROBIN

Females uttered significantly more growls, performed significantly more wingspreads and tailsreads, made significantly more perch changes and hit the robin significantly more at the nestling stage. Males uttered significantly more checks and ree calls, made significantly more perch changes, performed significantly more tailsreads and spent significantly more time within 2 m of the robin at the nestling stage.

#### *Number of individuals responding to models*

Red-winged Blackbirds responded to Eurasian Blackbird significantly more often in pairs than they did to the cuckoo or robin at laying (Table 12). The number of individuals responding singly or in pairs did not vary among models at the nestling stage.

#### **Differences between Red-winged Blackbirds responses between 2001 and 2002**

##### *Laying*

Red-winged Blackbirds sang significantly more in response to the robin and cuckoo in 2002 (Table 13). They also uttered significantly more growls in response to the cuckoo. However, Red-winged Blackbirds hovered above the cuckoo significantly less

Table 12. Number of trials in which one or both members of a Red-winged Blackbird nesting pair responded to Black-billed Cuckoo, American Robin and Eurasian Blackbird models placed at their nests during the laying and nestling stages in May-June 2002.

Stage	Model						X <sup>2</sup>	P
	Cuckoo		Robin		Eurasian Blackbird			
	one	both	one	both	one	both		
Laying	17	28	24	21	9	36	10.74	0.005
Nestling	10	35	13	32	12	33	0.54	0.763

Table 13. Red-winged Blackbirds' behavioural responses to Black-billed Cuckoo and American Robin models at the laying and nestling stages compared between 2001 and 2002 (N = 42 and 47 for the laying and nestling stages, respectively, in 2001 and N= 45 for both the laying and nestling stages in 2002).

Response <sup>1</sup>	Stage	Cuckoo			Robin		
		2001	2002	P <sup>2</sup>	2001	2002	P
Check	L	21.09 ± 4.0	28.64 ± 4.90	0.107	20.06 ± 1.21	17.78 ± 3.73	0.645
	N	60.05 ± 8.46	55.98 ± 6.91	0.959	70.74 ± 8.68	50.69 ± 8.03	0.073
Growl	L	0.02 ± 0.02	0.42 ± 0.16	0.006	0.02 ± 0.15	0.07 ± 0.04	0.289
	N	2.83 ± 0.85	3.09 ± 0.93	0.889	2.07 ± 0.50	1.18 ± 0.33	0.091
♀ Song	L	4.87 ± 0.79	8.22 ± 1.07	0.006	3.83 ± 0.73	6.93 ± 0.93	0.003
	N	3.74 ± 0.83	5.00 ± 0.68	0.038	4.10 ± 0.68	4.78 ± 0.73	0.593
♀ Scream	L	0.13 ± 0.09	0	0.056	0.02 ± 0.01	0.24 ± 0.22	0.782
	N	0.22 ± 0.13	0.15 ± 0.08	0.985	0.08 ± 0.04	0.36 ± 0.22	0.529
♂ Song	L	0.45 ± 0.16	0.33 ± 0.15	0.369	1.02 ± 0.32	0.51 ± 0.32	0.061
	N	0.62 ± 0.21	0.31 ± 0.21	0.531	0.31 ± 0.18	0.29 ± 0.15	0.921
♂ See call	L	1.26 ± 0.67	1.18 ± 0.45	0.369	1.62 ± 1.04	0.82 ± 0.40	0.942
	N	6.33 ± 3.16	4.87 ± 2.37	0.773	7.45 ± 2.58	3.51 ± 1.55	0.277
♂ Ree call	L	1.38 ± 0.58	1.33 ± 0.49	0.631	1.68 ± 0.69	1.22 ± 0.63	0.437

Table 13 continued.

Response	Stage	Cuckoo			Robin		
		2001	2002	P	2001	2002	P
♂ Ree call	N	7.83 ± 2.33	4.89 ± 1.33	0.414	8.36 ± 2.19	3.44 ± 1.18	0.035
♂ Chink	L	1.36 ± 1.11	0.98 ± 0.59	0.401	0	0.24 ± 0.24	0.307
	N	2.02 ± 1.04	1.29 ± 0.71	0.439	4.52 ± 2.30	3.29 ± 2.25	0.280
♂ Songspread	L	0.28 ± 0.08	0.18 ± 0.14	0.03	0	0.20 ± 0.11	0.038
	N	0.17 ± 0.07	0.20 ± 0.09	0.938	0.05 ± 0.05	0.07 ± 0.05	0.610
Hover	L	2.40 ± 0.78	0.67 ± 0.39	0.011	0.13 ± 0.07	0.29 ± 0.12	0.949
	N	2.45 ± 0.57	1.69 ± 0.36	0.673	2.02 ± 0.45	0.69 ± 0.18	0.002
Pass	L	1.06 ± 0.28	0.22 ± 0.09	0.002	0.09 ± 0.07	0.20 ± 0.12	0.607
	N	0.52 ± 0.14	1.11 ± 0.31	0.553	0.83 ± 0.23	0.51 ± 0.21	0.077
Hit	L	4.04 ± 1.08	1.93 ± 0.70	0.066	0.13 ± 0.08	0.91 ± 0.50	0.731
	N	10.98 ± 2.55	6.36 ± 1.30	0.993	7.60 ± 1.57	4.18 ± 1.40	0.022
Attack	L	0.10 ± 0.06	0.04 ± 0.04	0.20	0.05 ± 0.03	0.03 ± 0.02	0.201
	N	0.12 ± 0.04	0.15 ± 0.06	0.878	0.16 ± 0.04	0.10 ± 0.05	0.070
Tailsread	L	0.74 ± 0.17	1.02 ± 0.23	0.604	0.23 ± 0.08	0.69 ± 0.22	0.129
	N	0.31 ± 0.10	2.98 ± 0.51	0.000	0.17 ± 0.08	1.89 ± 0.42	0.000



Table 13 continued.

Response	Stage	Cuckoo			Robin		
		2001	2002	P	2001	2002	P
Wingspread	L	0.51 ± 0.14	0.67 ± 0.21	0.952	0.13 ± 0.08	0.27 ± 0.16	0.677
	N	0.33 ± 0.11	3.09 ± 0.52	0.000	0.14 ± 0.07	2.08 ± 0.66	0.000
Perch change	L	9.02 ± 1.28	8.73 ± 1.04	0.778	5.40 ± 1.13	7.18 ± 1.16	0.067
	N	12.69 ± 1.85	13.09 ± 1.29	0.015	5.14 ± 0.77	9.58 ± 1.08	0.326
Preen	L	0.17 ± 0.10	0.14 ± 0.06	0.395	0.16 ± 0.10	0.25 ± 0.11	0.234
	N	0.06 ± 0.03	0.01 ± 0.00	0.090	0.05 ± 0.04	0.12 ± 0.08	0.612
Bill wipe	L	0	0.36 ± 0.14	0.003	0	0.49 ± 0.14	0.000
	N	0	1.11 ± 0.24	0.342	0.62 ± 0.23	0.40 ± 0.15	0.953
< 2 m	L	6.12 ± 0.26	5.33 ± 0.36	0.371	5.54 ± 0.29	4.76 ± 0.30	0.018
	N	5.47 ± 0.47	6.41 ± 0.28	0.912	6.55 ± 0.37	5.72 ± 0.34	0.072

<sup>1</sup> Screams, attacks and time spent within two metres are reported as the mean amount of time that nest owners spent performing each of these behaviours within the five-minute trial period. All other means are based on the number of times that nest owners performed the behaviour within the five-minute trial. The combined response of the nesting pair is presented except where the behaviour is only elicited in one member of the nesting pair (e.g., only males “ree” call).

<sup>2</sup>P-values presented are the results of Mann-Whitney U tests.

and made significantly fewer close passes. They also spent significantly less time within 2 m of the robin.

### *Nestling*

Red-winged Blackbirds exhibited significantly more tailspreads and wingspreads in response to the cuckoo and robin in 2002. Red-winged Blackbirds directed significantly fewer hits to the robin and hovered above the robin significantly less. Males sang significantly more songs in response to the cuckoo but uttered significantly fewer ree calls in response to the robin. Females uttered significantly more chatter calls in response to the robin.

### **Yellow Warblers**

#### *Laying*

During laying, Yellow Warblers uttered significantly more chips and metallic chips and performed significantly more distraction displays in response to the grackle than to the cuckoo or robin (Table 14). Males sang significantly more in response to the grackle than to the robin and the number of songs uttered in response to the cuckoo did not differ significantly from either of the grackle or robin. The cuckoo elicited significantly more chips than the robin and warblers spent significantly more time within 2 m of the cuckoo and robin than the grackle. Females did not rush to sit on their nests in response to any of the models and only one female uttered a seet call in response to the cuckoo.

Table 14. Yellow Warblers' behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models at laying. Mean response  $\pm$  SE, as well as mean within-nest ranks  $\pm$  SE (in brackets), are presented (N = 39 nests tested). Conventions as in Table 3.

Response	Model			P
	Cuckoo	Robin	Grackle	
Chip	25.54 $\pm$ 5.23 <sup>b</sup> (1.94 $\pm$ 0.12)	22.03 $\pm$ 6.48 <sup>c</sup> (1.50 $\pm$ 0.10)	51.18 $\pm$ 7.65 <sup>a</sup> (2.56 $\pm$ 0.10)	0.000
Metallic Chip	0.51 $\pm$ 0.34 <sup>b</sup> (1.96 $\pm$ 0.06)	0.03 $\pm$ 0.03 <sup>b</sup> (1.87 $\pm$ 0.04)	9.31 $\pm$ 4.36 <sup>a</sup> (2.16 $\pm$ 0.07)	0.002
♂ Song	0.41 $\pm$ 0.24 <sup>a,b</sup> (1.97 $\pm$ 0.06)	0.62 $\pm$ 0.25 <sup>a</sup> (2.15 $\pm$ 0.08)	0.05 $\pm$ 0.04 <sup>b</sup> (1.87 $\pm$ 0.05)	0.008
Pass/hover	0.08 $\pm$ 0.06 (1.99 $\pm$ 0.05)	0.03 $\pm$ 0.03 (1.95 $\pm$ 0.19)	0.21 $\pm$ 0.12 (2.06 $\pm$ 0.05)	0.177
Hit	0.03 $\pm$ 0.03 (2.02 $\pm$ 0.03)	0 (1.99 $\pm$ 0.01)	0 (1.99 $\pm$ 0.01)	0.228
Distraction display	0.05 $\pm$ 0.03 <sup>b</sup> (1.88 $\pm$ 0.09)	0.04 $\pm$ 0.02 <sup>b</sup> (1.71 $\pm$ 0.06)	0.32 $\pm$ 0.10 <sup>a</sup> (2.39 $\pm$ 0.09)	0.000
♀ Tailspread	0.03 $\pm$ 0.03 (2.02 $\pm$ 0.03)	0 (1.99 $\pm$ 0.01)	0 (1.99 $\pm$ 0.01)	0.228
Perch change	26.46 $\pm$ 2.08 (2.11 $\pm$ 0.11)	27.38 $\pm$ 2.46 (2.08 $\pm$ 0.14)	21.64 $\pm$ 1.67 (1.81 $\pm$ 0.14)	0.191
♀ Bill wipe	0.28 $\pm$ 0.12 (2.06 $\pm$ 0.07)	0.36 $\pm$ 0.17 (2.03 $\pm$ 0.06)	0.08 $\pm$ 0.04 (1.91 $\pm$ 0.05)	0.201
♀ Preen	0.05 $\pm$ 0.04 (1.96 $\pm$ 0.07)	0.10 $\pm$ 0.07 (2.03 $\pm$ 0.08)	0.08 $\pm$ 0.05 (2.00 $\pm$ 0.06)	0.792
> 2m	5.13 $\pm$ 0.30 <sup>a</sup> (2.14 $\pm$ 0.13)	5.16 $\pm$ 0.25 <sup>a</sup> (2.26 $\pm$ 0.10)	4.65 $\pm$ 0.35 <sup>b</sup> (1.60 $\pm$ 0.11)	0.025

*Nestling stage*

Yellow Warblers performed significantly more distraction displays in response to the grackle than to the cuckoo or robin (Table 15). They spent significantly more time within 2 m of cuckoo and robin than the grackle. Males also sang significantly more in response to the cuckoo.

*Female and male responses*

Males and females responded similarly to the cuckoo at the laying and nestling stages (Table 16). Females performed significantly more distraction displays in response to the grackle at both stages. Females spent significantly less time within 2 m of the grackle during laying. The grackle elicited significantly more chips from males during the nestling stage. There were no other significant differences between male and female responses to the grackle at either stage. Females spent significantly more time within 2 m of the robin model at both the laying and nestling stages. Males gave significantly more metallic chips than females at laying and performed significantly more distraction displays in response to the robin at both the laying and nestling stages. Females and males did not differ in the other responses to the robin at either stage.

*Laying and nestling stages*

The intensity of the Yellow Warbler's response, as seen primarily in the amount of time engaged in distraction displays, increased between the laying and nestling stages for all three models (Table 17).

Table 15. Yellow Warblers' behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models at the nestling stage. Mean responses  $\pm$  SE, as well as mean within-nest ranks  $\pm$  SE (in brackets), are presented (N = 48 nests tested). Conventions as in Table 3.

Response	Model			P
	Cuckoo	Robin	Grackle	
Chip	33.23 $\pm$ 6.13 (1.82 $\pm$ 0.08)	37.17 $\pm$ 6.39 (2.16 $\pm$ 0.10)	41.33 $\pm$ 6.33 (1.95 $\pm$ 0.11)	0.146
Metallic chip	0 (1.96 $\pm$ 0.02)	0.75 $\pm$ 0.75 (1.99 $\pm$ 0.03)	3.40 $\pm$ 2.41 (2.05 $\pm$ 0.03)	0.073
♂ Song	2.79 $\pm$ 0.53 <sup>a</sup> (2.25 $\pm$ 0.10)	1.94 $\pm$ 0.52 <sup>b</sup> (1.89 $\pm$ 0.10)	1.83 $\pm$ 0.45 <sup>b</sup> (1.86 $\pm$ 0.10)	0.008
Pass/hover	0.27 $\pm$ 0.15 (2.01 $\pm$ 0.06)	0.17 $\pm$ 0.07 (2.00 $\pm$ 0.06)	0.15 $\pm$ 0.06 (1.99 $\pm$ 0.05)	0.969
Hit	—	—	—	—
Distraction display	0.21 $\pm$ 0.08 <sup>b</sup> (1.74 $\pm$ 0.09)	0.37 $\pm$ 0.13 <sup>b</sup> (1.67 $\pm$ 0.09)	1.18 $\pm$ 0.20 <sup>a</sup> (2.59 $\pm$ 0.08)	0.000
Tailsread	0 (1.99 $\pm$ 0.01)	0 (1.99 $\pm$ 0.10)	0.02 $\pm$ 0.02 (2.02 $\pm$ 0.14)	0.227
Perch change	35.38 $\pm$ 2.86 (2.18 $\pm$ 0.12)	30.58 $\pm$ 2.62 (1.94 $\pm$ 0.11)	27.88 $\pm$ 2.16 (1.88 $\pm$ 0.12)	0.168
Bill wipe	1.23 $\pm$ 0.29 (2.09 $\pm$ 0.09)	1.25 $\pm$ 0.41 (2.05 $\pm$ 0.09)	0.65 $\pm$ 0.18 (1.85 $\pm$ 0.09)	0.117
Preen	0.07 $\pm$ 0.03 (2.08 $\pm$ 0.06)	0.08 $\pm$ 0.05 (1.96 $\pm$ 0.07)	0.02 $\pm$ 0.01 (1.95 $\pm$ 0.07)	0.310
> 2m	6.65 $\pm$ 0.35 <sup>a</sup> (2.19 $\pm$ 0.12)	6.35 $\pm$ 0.34 <sup>a</sup> (2.11 $\pm$ 0.11)	5.70 $\pm$ 0.33 <sup>b</sup> (1.70 $\pm$ 0.12)	0.006

Table 16. Female and male Yellow Warbler behavioural responses to Black-billed Cuckoo, American Robin and Common Grackle models at the laying (L) and nestling (N) stage. Mean responses  $\pm$  SE, as well as mean within-nest ranks  $\pm$  SE (in brackets) are presented (39 and 48 nests were tested at the laying and nestling stages, respectively). Conventions as in Table 5.

Response		Cuckoo			Robin			Grackle		
		Female	Male	P	female	male	P	female	male	P
Chips	L	24.41 $\pm$ 5.23 (2.00 $\pm$ 0.12)	0.13 $\pm$ 0.05 (1.87 $\pm$ 0.08)	0.356	21.69 $\pm$ 6.48 (1.58 $\pm$ 0.10)	0.33 $\pm$ 0.19 (1.83 $\pm$ 0.06)	0.042	47.69 $\pm$ 7.63 (2.42 $\pm$ 0.12)	3.49 $\pm$ 1.36 (2.29 $\pm$ 0.09)	0.062
	N	31.23 $\pm$ 6.02 (1.90 $\pm$ 0.11)	2.00 $\pm$ 0.73 (1.80 $\pm$ 0.08)	0.489	34.27 $\pm$ 6.39 (2.16 $\pm$ 0.10)	2.90 $\pm$ 1.16 (1.90 $\pm$ 0.08)	0.058	28.96 $\pm$ 5.59 (1.95 $\pm$ 0.11)	12.38 $\pm$ 3.88 (2.30 $\pm$ 0.08)	0.01
Metallic chips	L	0.51 $\pm$ 0.34 (1.97 $\pm$ 0.06)	0 (1.99 $\pm$ 0.01)	0.838	0.03 $\pm$ 0.03 (1.88 $\pm$ 0.03)	0 (1.99 $\pm$ 0.01)	0.010	8.51 $\pm$ 4.32 (2.14 $\pm$ 0.07)	0.79 $\pm$ 0.79 (2.02 $\pm$ 0.03)	0.744
	N	0 (1.97 $\pm$ 0.02)	0 (1.98 $\pm$ 0.15)	0.569	0.75 $\pm$ 0.75 (2.0 $\pm$ 0.03)	0 (1.98 $\pm$ 0.01)	0.420	1.90 $\pm$ 1.36 (2.03 $\pm$ 0.03)	1.50 $\pm$ 1.18 (2.04 $\pm$ 0.03)	0.743
Distraction displays	L	0.04 $\pm$ 0.03 (1.83 $\pm$ 0.08)	0.01 $\pm$ 0.01 (2.00 $\pm$ 0.06)	0.119	0.02 $\pm$ 0.01 (1.79 $\pm$ 0.05)	0.02 $\pm$ 0.02 (1.94 $\pm$ 0.26)	0.010	0.26 $\pm$ 0.10 (2.37 $\pm$ 0.09)	0.06 $\pm$ 0.03 (2.06 $\pm$ 0.06)	0.719
	N	0.21 $\pm$ 0.08 (1.78 $\pm$ 0.08)	0.17 $\pm$ 0.09 (1.86 $\pm$ 0.08)	0.439	0.15 $\pm$ 0.06 (1.62 $\pm$ 0.08)	0.22 $\pm$ 0.10 (1.84 $\pm$ 0.06)	0.037	0.82 $\pm$ 0.16 (2.59 $\pm$ 0.08)	0.36 $\pm$ 0.09 (2.29 $\pm$ 0.08)	0.010
Perch changes	L	21.33 $\pm$ 1.93 (2.06 $\pm$ 0.12)	5.13 $\pm$ 1.30 (1.96 $\pm$ 0.01)	0.539	23.13 $\pm$ 2.21 (2.10 $\pm$ 0.14)	4.26 $\pm$ 1.02 (1.97 $\pm$ 0.11)	0.439	17.41 $\pm$ 1.73 (1.83 $\pm$ 0.13)	4.23 $\pm$ 0.86 (2.06 $\pm$ 0.12)	0.745
	N	24.08 $\pm$ 2.70 (2.29 $\pm$ 0.10)	11.29 $\pm$ 1.43 (1.86 $\pm$ 0.08)	0.158	20.00 $\pm$ 2.17 (1.88 $\pm$ 0.12)	10.58 $\pm$ 1.54 (1.93 $\pm$ 0.11)	0.795	17.54 $\pm$ 1.87 (1.82 $\pm$ 0.12)	10.33 $\pm$ 1.31 (2.01 $\pm$ 0.03)	0.245
< 2m	L	4.21 $\pm$ 0.17 (2.13 $\pm$ 0.13)	0.92 $\pm$ 0.21 (1.82 $\pm$ 0.10)	0.088	4.31 $\pm$ 0.17 (2.27 $\pm$ 0.10)	0.85 $\pm$ 0.20 (1.87 $\pm$ 0.12)	0.042	3.11 $\pm$ 0.28 (1.60 $\pm$ 0.11)	1.54 $\pm$ 0.24 (2.31 $\pm$ 0.11)	0.178

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N	$3.84 \pm 0.23$	$2.81 \pm 0.26$	0.123	$3.97 \pm 0.23$	$2.38 \pm 0.27$	0.050	$3.41 \pm 0.25$	$2.29 \pm 0.24$	0.052
	$(1.97 \pm 0.09)$	$(2.20 \pm 0.11)$		$(2.23 \pm 0.10)$	$(1.88 \pm 0.11)$		$(1.80 \pm 0.11)$	$(1.92 \pm 0.12)$	

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Table 17. A comparison of Yellow Warblers' responses to Black-billed Cuckoo, American Robin and Common Grackle models presented at their nests during the laying and nestling stages. Conventions as in Table 6.

Sex	Response	Model					
		Cuckoo		Robin		Grackle	
		Change	P	Change	P	Change	P
Female	Chips	=	ns	=	ns	-	0.025
	Metallic chips	=	ns	=	ns	+	0.039
	Distraction displays	+	0.012	+	0.037	+	0.000
	Bill wipe	+	0.014	+	0.015	+	0.024
	Perch change	=	ns	=	ns	+	ns
	< 2m	=	ns	=	ns	+	ns
Male	Chips	+	0.025	+	0.044	+	0.037
	Metallic chips	=	ns	=	ns	=	ns
	Songs	+	0.000	+	0.014	+	0.000
	Distraction displays	=	ns	+	0.020	+	0.001
	Bill wipe	=	ns	=	ns	=	ns
	Perch change	+	0.000	+	0.000	+	0.000
	< 2m	-	0.000	+	0.000	+	0.022



#### BLACK-BILLED CUCKOO

Females performed significantly more distraction displays and bill wipes in response to the cuckoo during the nestling stage than during laying. Males uttered significantly more chips and songs, changed perches significantly more and spent significantly more time within 2 m of the cuckoo during the nestling stage.

#### COMMON GRACKLE

Females uttered significantly more metallic chips, performed significantly more distraction displays and wiped their bills significantly more in response to the grackle at the nestling stage. Females uttered significantly fewer chips in response to the grackle at the nestling stage. Males uttered significantly more songs, chips and made significantly more perch changes, spent significantly more time within 2 m, and performed significantly more distraction displays at the nestling stage.

#### AMERICAN ROBIN

Females wiped their bills significantly more and performed significantly more distraction displays in response to the robin at the nestling stage. Males also performed significantly more distraction displays plus uttered significantly more chips, songs, made significantly more perch changes and spent significantly more time within 2 m of the robin at the nestling stage.

*Number of individuals responding to models*

At laying, Yellow Warblers responded singly to the cuckoo and robin more often than they did to the grackle (Table 18). There was no significant difference among models in the number of individuals responding at the nestling stage.

## DISCUSSION

Red-winged Blackbirds and Yellow Warblers responded to the Black-billed Cuckoo at laying but not as strongly as they did to the grackle and their responses to the cuckoo increased or remained the same between nesting stages. If Red-winged Blackbirds and Yellow Warblers had recognized the Black-billed Cuckoo as a brood parasite then one would have expected them to respond as strongly, if not more strongly, to the cuckoo in comparison with the grackle at laying and for the intensity of their response to decrease between stages. Furthermore, Yellow Warblers did not see call or perform any nest protection behaviours which would have suggested that they recognized the Black-billed Cuckoo as a parasitic threat. Thus, the results are inconsistent with the hypothesis that Red-winged Blackbirds and Yellow Warblers recognized the Black-billed Cuckoo as a brood parasite.

Since cuckoos can act as egg (Sealy 1994) and nestling predators (Bent 1940), and because the intensity of the Red-winged Blackbirds' response to the cuckoo increased (i.e. became more aggressive) between the laying and nestling stage, Red-winged Blackbirds may have recognized to the cuckoo as a nest predator. However, Red-winged Blackbird reactions to the cuckoo, particularly their aggressive and high-risk

Table 18. Number of trials in which one or both members of Yellow Warbler nesting pairs responded to Black-billed Cuckoo, American Robin and Common Grackle models placed at their nests during the laying and nestling stages in May-June 2001.

Stage	Model						X <sup>2</sup>	P
	Cuckoo		Robin		Grackle			
	one	both	one	both	one	both		
Laying	22	17	23	16	13	26	6.22	0.045
Nestling	3	45	9	39	4	44	4.36	0.113

Grackle may have elicited a more aggressive response from Red-winged Blackbirds than the Black-billed Cuckoo because it is the more common predator and Red-winged Blackbirds are thus more likely to have had previous experience with the grackle and/or the selection pressure to recognize the grackle may be stronger than the selection pressure to recognize the cuckoo. Alternatively, although Red-winged Blackbirds could assess the threat that the grackle and robin imposed, if they were unfamiliar with the cuckoo they may not have been able to fully assess the threat posed by the cuckoo causing them to respond more cautiously (Montgomerie and Weatherhead 1988), or as they would to any novel nest intruder. Bazin and Sealy (1993) found that although Eastern Kingbirds, a rejector of cowbird eggs, responded to both a Brown-headed Cowbird and Common Grackle with increased intensity over the nesting cycle, the kingbirds' response to the grackle was stronger at both stages. Because cowbird parasitism and predation on kingbirds is low, there was no selective pressure on kingbirds to recognize the cowbird as a specific threat and they likely gave a generalized nest defence response to the cowbird (Bazin and Sealy 1993). Red-winged Blackbirds may have similarly given a generalized nest defence response to the Black-billed Cuckoo.

Red-winged Blackbirds' reaction to the Eurasian Blackbird demonstrated that Red-winged Blackbirds are fairly aggressive towards unfamiliar species at their nests. The similarity in intensity in their responses to the Black-billed Cuckoo and the Eurasian Blackbird, as well as the fact that the intensity of their responses to both species did not change over the course of the nesting cycle, indicate that Red-winged Blackbirds are also likely unfamiliar with the Black-billed Cuckoo. This generalized nest defence response

to unknown intruders is likely adaptive, given that many different bird species have been observed depredate other birds' nests (Sealy 1994, Braden et al. 1997). For example, Gray Catbirds, Baltimore Orioles (*Icterus galbula*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Red-winged Blackbirds have all been observed destroying and/or consuming eggs from other passerines' nests, despite that none of these species are typically considered to be egg predators (Sealy 1994). Not only are some of these depredation events probably opportunistic but it is unlikely that any one nest owner will have had the necessary experience to recognize each of these egg and nestling predators specifically, nor would it be adaptive given that the threat posed by each is similar (McLean and Rhodes 1991).

Although Yellow Warblers responded to the Black-billed Cuckoo and Common Grackle with similar behaviours (chips and distraction displays), there were few differences in the intensity of their response between the cuckoo and the robin. Hobson et al. (1988) and Gill et al. (1997) also found that Yellow Warblers responded to unfamiliar intruders and predators similarly. Furthermore, Hobson et al. (1988) found that Yellow Warblers' responses to unfamiliar intruders varied little over the nesting cycle. However, neither of these studies used a predator model as a positive control and thus, they could not compare Yellow Warblers' responses to a novel species and a predator directly. Because Yellow Warblers responded to the cuckoo much less strongly than they did to the grackle, and because the intensity of their response to the cuckoo was similar to the intensity of their response to the robin, Yellow Warblers did not seem to recognize the cuckoo specifically. Nevertheless, Yellow Warblers responded to the

cuckoo and robin with some distraction displays and chips, which suggests that Yellow Warblers may have perceived both species as potential threats. Interestingly, Yellow Warblers responded more strongly to a large control, the American Robin, in comparison with previously reported responses to a smaller control species like the Fox Sparrow (*Passerella iliaca*; e.g., Briskie et al. 1992, Gill and Sealy 1996). Although a few researchers have suggested that the intensity of host aggression is not influenced by the size of the enemy relative to the host (Robertson and Norman 1976, Neudorf and Sealy 1992), these results suggest that Yellow Warblers may respond somewhat more intensely to larger intruders at their nest, probably because if birds sometimes act as opportunistic egg or nestling predators, e.g., Sealy (1994) observed Red-winged Blackbirds depredating Yellow Warbler nests, larger species are more likely to be potential threats.

Although the results found here do not support the suggestion that Black-billed and Yellow-billed cuckoos parasitized Red-winged Blackbirds and Yellow Warblers more frequently in the past, they do not necessarily negate the possibility. Four reasons why Red-winged Blackbirds and Yellow Warblers may not have recognized the Black-billed Cuckoo as a brood parasite are: (1) Red-winged Blackbirds and Yellow Warblers were previously parasitized but have subsequently lost their specific enemy recognition of the Black-billed Cuckoo, (2) they were previously parasitized by the Black-billed Cuckoo but did not develop specific enemy recognition either because selection pressures for specific enemy recognition were weak and/or they responded to the cuckoo with other anti-parasite defences, (3) they were previously parasitized and previously recognized the Black-billed Cuckoo as a brood parasite but this recognition was primarily learned and

thus, was not a suitable candidate for retention, or (4) they were not previously parasitized by the Black-billed Cuckoo.

Even if one or both Red-winged Blackbirds and Yellow Warblers were cuckoo hosts, over time, they may have lost their ability to recognize the cuckoo as a parasitic threat. For example, California ground squirrels (*Spermophilus beecheyi*) that are sympatric, or recently allopatric, with snakes discriminate between rattlesnakes (*Crotalus viridis oregonos*) and gopher snakes (*Pituophis melanoleucus catenifer*; Towers and Coss 1991). Other squirrel populations that have been allopatric with snakes for up to 300 000 years cannot discriminate between rattlesnakes and gopher snakes, but still exhibit defensive behaviours unique to squirrel-snake encounters (Coss 1993). Thus, allopatric populations have lost the higher behavioural organization associated with specific snake recognition (Coss 1999). Furthermore, Arctic ground squirrels that have been separated from snakes for more than 3 million years have lost their anti-snake behaviour entirely (Coss and Goldthwaite 1995). Coss (1999) suggested that if recognition traits have a low heritability or depend on too few recognition cues specific enemy recognition may be lost over time. If Black-billed Cuckoos previously parasitized Red-winged Blackbirds and Yellow Warblers, over time, these hosts may have also lost their ability to discriminate between the Black-billed Cuckoo and other nest intruders.

Additionally, if the retention of a trait is costly, e.g., leads to a host rejecting their own eggs or abandoning an unparasitized nest (Marchetti 1992, Peer and Bollinger 1997), hosts may vary their defence levels in relation to perceived parasitism pressure (Davies et al. 1996, Brooke et al. 1998, Robert and Sorci 1999). African populations of Village

Weavers (*Ploceus cucullatus*), which are heavily parasitized by the Dideric Cuckoo (*Chrysococcyx caprius*) in Africa, reject non-mimetic eggs from their nests (Victoria 1972). However, Village Weavers introduced into Hispaniola in the 18<sup>th</sup> century, which was free of any brood parasitic species until the 1970s, accepted non-mimetic eggs (Cruz and Wiley 1989). Cruz and Wiley (1989) suggested that Village Weavers decreased their egg-rejection behaviour in the absence of the selective pressure from brood parasitism. Their hypothesis was further supported by recent work that demonstrated that Hispanola Village Weavers' rejection rates of non-mimetic eggs have increased substantially in response to increased parasitism by the Shiny Cowbird (*Molothrus bonariensis*), since the time of Cruz and Wiley's study (Robert and Sorci 1999).

Similarly, if nest defence in response to the Black-billed Cuckoo is costly, then one would expect Red-winged Blackbirds and Yellow Warblers' nest defence to be reduced in the absence of selection pressure or under low levels of parasitism. Robertson and Norman (1977) suggested that nest defence in response to the threat of brood parasitism could have several opposing selection pressures. For example, high levels of aggression may be energetically expensive and could potentially cause injury or the death of the defending nest owner (Curio and Regelman 1985, Brunton 1986). Furthermore, aggressive or distraction displays, vocalizations and nest protection behaviours could potentially expose the nest to predators and/or to brood parasites themselves which in turn could increase parasitism frequencies (Smith et al. 1984, Uyehara and Narins 1995). Thus, under low parasitism frequencies birds may not defend their nests specifically against brood parasites.



Alternatively, if brood parasite recognition involves learning (Smith et al. 1984, Hobson and Sealy 1989, Briskie et al. 1992, Lindholm and Thomas 2000) then parasite recognition may be an unsuitable candidate for retention. Hobson and Sealy (1989) found that yearling female Yellow Warblers responded with fewer parasite-specific responses to Brown-headed Cowbirds than older females or, previously parasitized females, which suggests that learning may play an important role in their responses to brood parasites. Furthermore, Yellow Warblers in an allopatric population rarely uttered seat calls and did not perform nest-protection behaviours in response to the cowbird (Briskie et al. 1992). If Yellow Warblers' brood parasite recognition is contingent on individuals' past experiences then it is not surprising that Yellow Warblers would not recognize the Black-billed Cuckoo as a specific threat since they are not currently parasitized and there are no recent records of parasitism. On the other hand, if a generalized nest defence response was sufficient to deter a parasite, hosts may successfully prevent a parasite from laying in their nests by mounting a defensive response regardless of whether the response is specific to the threat.

Finally, Red-winged Blackbirds and Yellow Warblers may not recognize the Black-billed Cuckoo because they were not previously frequent hosts of the Black-billed Cuckoo. There are only two and one records of parasitism for these Red-winged Blackbirds and Yellow Warblers respectively (in the case of the Red-winged Blackbird, they were parasitized by the Yellow-billed Cuckoo), and these records could be cases of intraspecific egg dumping by the cuckoo. Furthermore, Yellow Warblers lay eggs that are much smaller than the cuckoo and if Yellow Warblers are too small to have been

suitable hosts then there would not have been any selection pressure for them to recognize the Black-billed Cuckoo as a threat. Alternatively, Yellow Warblers may have been too small to effectively defend their nests from the larger parasite (Rothstein and O'Loughlen unpublished), and thus they may have used alternative defence mechanisms like egg rejection. These hypotheses are discussed further in Chapter 2.

Red-winged Blackbird response to the Black-billed Cuckoo at the laying stage was somewhat more aggressive (i.e., numbers of passes and hovers directed at the cuckoo) in 2001 than in 2002. Although the order in which models were presented was randomized, by chance, Black-billed Cuckoos were presented first in 19/47 (40%) of the trials at laying in 2001. Models that are presented first, may elicit a somewhat stronger response from nest owners (Sealy et al. 1998). However, a regression analysis revealed that there was no relationship between the intensity of the Red-winged Blackbirds' more aggressive behaviours and the order in which the cuckoo was presented (pass:  $r = 0.19$ ,  $t = -1.3$ ,  $n = 47$ ,  $P = 0.19$ ; hover:  $r = 0.01$ ,  $t = -0.1$ ,  $n = 47$ ,  $P = 0.92$ , hit:  $r = 0.20$ ,  $t = -1.4$ ,  $n = 47$ ,  $P = 0.18$ ). Alternatively, stronger responses to the cuckoo in 2001 could have been the result of carry-over aggression from the grackle model but since cuckoos were often presented before the grackle, this seems unlikely.

Another possible reason for the somewhat less aggressive responses seen in 2002 is that the nesting population of Red-winged Blackbirds decreased at Delta Marsh in 2002 and many harems were unusually large (3 to 5 females per male vs. 2 to 3 females per male the year previous). Also there appeared to be large numbers of unmated second-year Red-winged Blackbird males in the area. These males often came in during

trials and were chased away by one of the nest owners (usually the male) thus distracting them from the model presentation. If increased territory sizes and floater populations led to increased intruders at Red-winged Blackbird nests, nest owners may have become somewhat habituated to intrusions and their levels of aggression towards intruders at their nests may have been diminished. However, these observations are anecdotal and the number of females per harem, changes in harem size, and the number of unmated second-year males were not quantified. Regardless, the differences in the Red-winged Blackbirds' reaction to the cuckoo between the years were few and did not appear to bias the general trends seen in the data.

## CONCLUSION

Red-winged Blackbirds and Yellow Warblers responded to the Black-billed Cuckoo in a manner that suggested that they did not recognize the Black-billed Cuckoo as a specific threat, as either a brood parasite or predator. Instead their responses were consistent with the hypothesis that the Black-billed Cuckoo is an unfamiliar species. These results do not negate the possibility that Red-winged Blackbirds and Yellow Warblers were once hosts to the Black-billed Cuckoo. Their recognition of the Black-billed Cuckoo as a brood parasite may have been lost in the absence of parasitism or specific recognition of the Black-billed Cuckoo may not have been selected for, either because a generalized nest defence response was sufficient to deter parasitism or because selection for specific recognition was weak.

## CHAPTER 2

### YELLOW WARBLERS ACCEPT MOST MODEL CUCKOO EGGS AND CAN INCUBATE CUCKOO-SIZED EGGS UNTIL HATCHING

#### INTRODUCTION

When Hughes (1997) designated Black-billed and Yellow-billed cuckoo eggs as a “match” or “non-match” for their hosts’ eggs she did not take size into account.

However, other brood parasites like the Common Cuckoo and Brown-headed Cowbird lay eggs that are small relative to their body size, it is believed, because (1) hosts discriminate against large eggs (Davies and Brooke 1988, Moksnes and Røskaft 1992, 1995, Marchetti 2000) and, (2) because small hosts cannot incubate eggs that are substantially larger than their own (Davies and Brooke 1988, 1989). Five of the 17 putative Black-billed and Yellow-billed hosts (Yellow Warbler, Chipping Sparrow, Black-throated Sparrow, Eastern Wood Pewee, House Finch) lay eggs that are less than 35% of the volume of Black-billed Cuckoo eggs and less than 24% of the volume of Yellow-billed Cuckoo eggs (see Table 1, General Introduction). These size differences are greater than those seen between the Common Cuckoo and Brown-headed Cowbird eggs and those of their smallest respective common host species (Johnsgard 1997). Thus, small birds like the Yellow Warbler may not be suitable Black-billed Cuckoo hosts.

Two often-listed characteristics of a suitable host are that they accept and can incubate parasitic eggs (Davies and Brooke 1988, Sealy et al. 2002). Brood parasites

have adopted several different strategies to ensure that their eggs are accepted by potential hosts, including rapid egg-laying (Davies and Brooke 1988, Sealy et al. 1995, Burhans 2000) and host egg mimicry (Brooke and Davies 1988, Davies and Brooke 1988, 1989; Moksnes and Roskaft 1995). Parasitic birds have shorter laying bouts in comparison with non-parasitic species—some last less than 10 seconds (Sealy et al. 1995)—to reduce their detection by hosts (Davies and Brooke 1988, Moksnes and Røskaft 1989, Moksnes et al. 1993). Also, the Common Cuckoo lays polymorphic eggs that can be used to divide it into several races or “gentes” (“gens” singular) based on their egg morphs (Davies and Brooke 1988, Moksnes and Roskaft 1995, Gibbs et al. 2000). Each gens lays eggs of similar size, maculation and/or ground colour to their preferred host species and each specializes on one host (Brooke and Davies 1988, Davies and Brooke 1989, Moksnes and Røskaft 1995). Thus, Common Cuckoos that parasitize Redstarts (*Phoenicurus phoenicurus*) lay pale blue eggs that are nearly identical to those of the Redstart (Moksnes et al. 1995) and Common Cuckoos that parasitize Meadow Pipits (*Anthus pratensis*) lay brownish grey eggs mottled with dark brown that match the pipit’s brown egg (Brooke and Davies 1988, Davies and Brooke 1988). This type of host egg mimicry results from a long-term co-evolutionary relationship where the host’s ability to discriminate between and reject non-matching eggs selects for brood parasites that lay more mimetic eggs (Davies 1999). North American cowbirds do not appear to have evolved a mimetic egg and their hosts are typically less discriminating (Rothstein 1975, Graham 1988, Sealy and Bazin 1995, Peer et al. 2000) and many accept cowbird

eggs in their nests despite sometimes great differences in egg ground colour and maculation (Rothstein 1975, Graham 1988, Sealy and Lorenzana 1998).

However, although cuckoo and cowbird eggs may vary in the degree to which their colour and spotting patterns match those of their hosts' eggs, a common feature of both brood parasites is that they lay small eggs relative to those laid by similarly sized nesting cuckoos (Payne 1974, Rahn et al. 1975, Johnsgard 1997). There are three exceptions to this general rule: the Great Spotted Cuckoo (*Clamator glandarius*), the Koel (*Eudynamis scolopacea*) and the Channel-billed Cuckoo (*Scythrops novaehollandiae*) lay relatively large eggs in comparison with other parasitic cuckoos (Payne 1974). However, all three species parasitize hosts of similar body size and thus smaller eggs may not have been selected for in these parasites (Soler 1990, Johnsgard 1997). Moksnes and Røskaft (1995) found that egg volumes of different cuckoo genets' were positively correlated with the volume of their main host's eggs and argued that the relationship between brood parasite and host egg size supports the view that host behaviour is the selective agent responsible for the cuckoo's small eggs. Furthermore, some rare Common Cuckoo hosts, like the Willow Warbler (*Phylloscopus trochilus*), discriminate against mimetic model cuckoo eggs (mimetic in terms of colour and pattern) because of size differences between their own egg and the parasite's (a Willow Warbler egg is 38% the volume of a Common Cuckoo egg; Moksnes and Røskaft 1992). Because no gens currently specializes on Willow Warblers, Moksnes and Røskaft (1995) postulated that the Willow Warbler gens likely became extinct because of the Willow Warbler's strong discriminative abilities and because the cuckoo was likely constrained

from evolving a smaller egg. The Yellow-browed Leaf Warbler (*Phylloscopus humei*), another presumed former cuckoo host, also discriminates against model eggs on the basis of size (Marchetti 2000). Thus, size can be a strong cue for rejection, perhaps particularly for smaller hosts whose eggs are much smaller than the brood parasite's egg.

Several authors have also suggested that there is a lower limit to host size because small hosts are likely unable to incubate eggs that are substantially larger than their own (Davies and Brooke 1988, 1989, Thomas 1995, Sealy et al. 2002). In compiling a list of potentially suitable hosts for Australian cuckoos, Brooker and Brooker (1989) arbitrarily set the lower limit of suitable host size at hosts whose eggs were only one-third the volume of their parasite's. Because the amount of heat a female can produce and transfer to her clutch is limited (Tøien 1989) and because incubating females need more energy to incubate larger clutches (Biebach 1981, Moreno et al. 1991), the addition of a large parasitic egg could impede incubation of both the host's and the parasite's egg (s) by reducing the amount of heat transferred to each egg thus causing extended cooling and subsequent embryonic mortality (see also Webb 1987). It is believed that Common Cuckoos and Brown-headed Cowbirds remove a host egg (prior to, at or after a parasitic laying) to reduce a parasitized nest's clutch volume to a size the host can incubate efficiently thus ensuring that the parasitic egg will hatch (Davies and Brooke 1988, McMaster and Sealy 1997, Peer and Bollinger 2000). However, Brown-headed Cowbirds do not always remove a host egg and several common cowbird hosts lay eggs that are less than one-third the volume of the Brown-headed Cowbird egg (e.g., Blue-gray Gnatcatcher; Goguen and Mathews 1996). A large parasitic egg may sit higher in

the nest relative to the host eggs and thus is unlikely to have reduced contact with the female's brood patch. Along these same lines, Peer and Bollinger (2000) suggested that the removal of a host egg by the brood parasite is probably more important when the parasite parasitizes a host species with eggs of similar size and is probably less important for smaller hosts (McMaster and Sealy 1997). Thus, the host's potential to incubate the parasite's egg efficiently is not necessarily limited by egg size and/or increased clutch volume.

If Black-billed and Yellow-billed cuckoos were once obligate brood parasites that parasitized smaller host species, it should be expected that, like the other parasitic cuckoos and cowbirds that use small species as hosts, they would lay a smaller egg relative to their body size to better match the egg size of their hosts. However, Black-billed and Yellow-billed cuckoos lay large eggs relative to their body size in comparison with other parasitic cuckoos and their egg volume-to-body size ratio is more typical of non-parasitic cuckoo species. Thus, some of the species that have been reported as Black-billed Cuckoo hosts may be unsuitable hosts if they do not accept Black-billed Cuckoo eggs and/or if they cannot incubate the eggs. My objective was to test whether the Yellow Warbler, a reported Black-billed Cuckoo host whose eggs are considerably smaller than the cuckoo's, is a suitable Black-billed Cuckoo host. If so, they should accept and incubate Black-billed Cuckoo eggs. If Yellow Warblers are an unsuitable cuckoo host then they should either reject Black-billed Cuckoo eggs or be unable to incubate them. Another important aspect of host suitability is that the host can fledge a cuckoo nestling but, because Black-billed Cuckoos and their eggs and nestlings were not



available, the Yellow Warbler's ability to fledge a Black-billed Cuckoo could not be tested.

## METHODS

### **Study species**

The Yellow Warbler, which weighs 9-11 g (Lowther et al. 1999), is the smallest reported Black-billed Cuckoo host (Hughes 2001). Yellow Warbler eggs are  $17 \times 13$  mm, weigh about 1.4 g (Sealy 1992) and are grayish white with brown spots or blotches that form a wreath around the blunt end (Lowther et al. 1999). Black-billed Cuckoo eggs are  $27 \times 21$  mm, weigh about 6.3 g (Schönwetter 1967) and are an immaculate light blue to light green colour. Thus, Yellow Warbler and Black-billed Cuckoo eggs differ greatly in size, colour and maculation. Despite being considered an acceptor of Brown-headed Cowbird eggs (an acceptor continues to lay or incubate its eggs after a parasitic egg is laid in its nest, i.e., it does not reject the parasite's egg; Rothstein 1975), Yellow Warblers frequently reject naturally laid Brown-headed Cowbird eggs through nest desertion or egg burial (Sealy 1995, Hosoi and Rothstein 2000). Yellow Warblers exhibit "true burial", in which they build an entirely new nest on top of the old nest and its contents (Mico 1998). Different Yellow Warbler populations show different rejection frequencies in response to cowbird parasitism depending on the timing of parasitism during nesting cycle (Burgham and Picman 1989, Clark and Robertson 1981, Sealy 1995), the length of sympatry with cowbirds (Briskie et al. 1992, Hosoi and Rothstein 2000), or the frequency with which the population is parasitized (Burhans et al. 2001). Their responses also vary

depending on whether their nest is naturally parasitized (Clark and Robertson 1981) or experimentally parasitized (Sealy 1995)—in the case of the latter they rarely desert or bury the cowbird egg.

### **Study site**

The study was done at the Delta Marsh Field Station (described in Chapter 1) during May and June 2001 and 2002. Nest searching and numbering techniques were identical to those described in Chapter 1.

### **Nests artificially parasitized with model Black-billed Cuckoo eggs**

To determine whether Yellow Warblers accept Black-billed Cuckoo eggs, single model plaster-of-Paris cuckoo eggs were added to Yellow Warbler nests on the warblers' second day of laying (laying day two or LD2). Model cuckoo eggs were used instead of real eggs because Black-billed Cuckoos generally nest in low densities (Hughes 2001) and their presence at Delta Marsh is inconsistent between years (Sealy 1978, Sealy in press). Model Black-billed Cuckoo eggs were cast from two silicone molds made from real Black-billed Cuckoo eggs (molds made by J. Lorenzana, see Lorenzana and Sealy 2002). Model eggs ( $n = 42$ ) were  $28 \times 20$  mm and had a mean weight of  $6.6 \text{ g} \pm 0.1 \text{ SE}$ , which was slightly heavier than real Black-billed Cuckoo eggs (Schönwetter 1967). Model eggs were painted with Liquitex™ acrylic paint (a mixture of 3 parts unbleached titanium #1045-434, 1 part light blue #1045-128 and  $\frac{1}{2}$  part burnt umber #1045-128) to match the light blue-green colour of the real Black-billed Cuckoo eggs and were finished

with an acrylic matte medium to waterproof the eggs as well as to give them a sheen typical of real eggs. To the naked eye, model cuckoo egg colour was nearly identical to the colour of the real cuckoo eggs from which they were made.

Most Yellow Warbler nests were found prior to clutch initiation or on LD1. A few nests were found with two eggs. At these nests the eggs were candled. Candling is a technique where an egg is held at the end of a short dark tube (in this case a black, 15-cm piece of foam pipe insulation) and ambient light allows one to see through the semi-translucent eggshell to determine the age of the embryo (Fig. 1; after Lokeman and Koford 1996). If the Yellow Warbler eggs had not been incubated (small air cell and no separation within the egg), I assumed that it was LD2. No Yellow Warbler eggs were removed at the time of parasitism because there is no evidence that Black-billed Cuckoos remove an egg when they parasitize a nest (although it has been suggested by Hughes 2000). Furthermore, egg removal does not influence Yellow Warblers' responses to parasitic cowbird eggs (Sealy 1992) nor, does the removal of small host eggs usually affect parasite egg incubation (McMaster and Sealy 1997).

Following the addition of a model Black-billed Cuckoo egg to a Yellow Warbler nest, artificially parasitized nests were visited for at least six days (typically incubation day four) after the addition of the model egg to determine if warblers accepted or rejected the model egg. Many studies have used a six-day acceptance criterion (e.g., Davies and Brooke 1988, Braa et al. 1992, Lotem et al. 1995, Lorenzana and Sealy 2001). The six-day acceptance criterion is a trade-off between including delayed rejections of parasitism

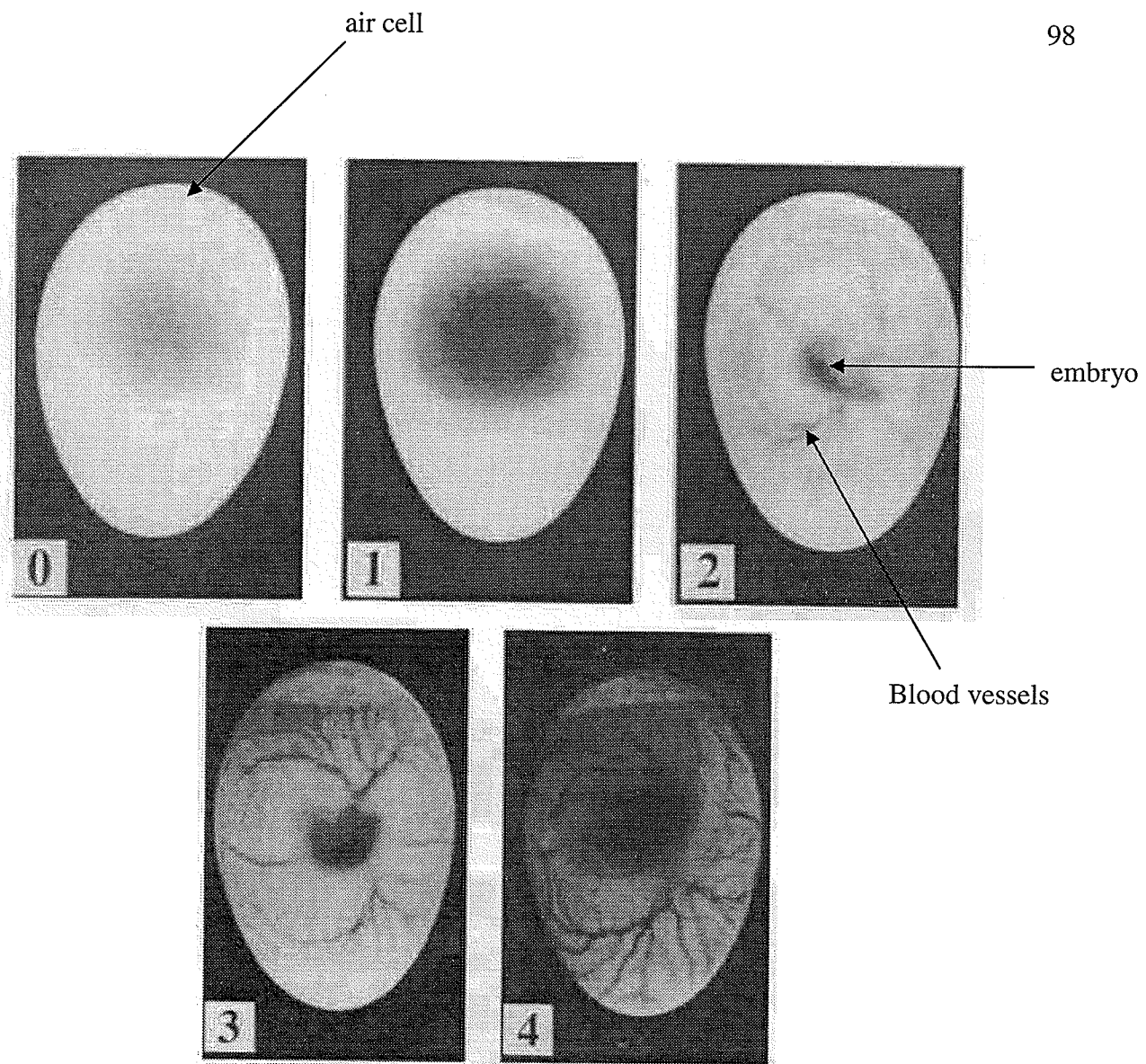


Fig. 1. Passerine egg development sequence for days zero through five (from Lokeman and Koford 1996). The embryo in the centre of the egg first becomes visible on day two of incubation.

and excluding rejections that are related to external factors other than parasitism— Rothstein (1982) found that less than 1% of rejections occur after 5 days and Lotem et al. (1995) found that 4 -10% of rejections occur after this period. An egg was considered accepted if the female was observed sitting on the clutch and/or if eggs were warm to the touch (i.e., from being incubated) and/or if the female defended her nest (e.g., with distraction displays or chipping). Eggs were considered rejected if they were cold and the female was not in the nest area or if the female buried the model egg, along with her own eggs, under a new nest. If the model egg was accepted, it was removed from the warbler nest after the six-day period. Forty-five more Yellow Warbler nests, to which no model eggs were added, were also inspected for six days to control for the influence that observer nest visitation may have had on acceptance/rejection behaviour.

### **Incubation of large eggs**

To determine whether Yellow Warblers could incubate a Black-billed Cuckoo egg, American Robin eggs, which are similar to Black-billed Cuckoo eggs in size, shape and colour (see Table 1 in General Introduction), were added to Yellow Warbler nests on the warbler's LD2. Other studies have used other species' eggs in lieu of a parasite's egg to examine host responses to parasitic eggs (Moksnes and Røskaft 1992, Davis et al. 2002) and in cross-fostering experiments (e.g., Eastzer et al. 1980). Robin eggs placed in warbler nests were  $28.8 \text{ mm} \pm 0.5 \text{ SE} \times 20.4 \text{ mm} \pm 0.4 \text{ SE}$  and had a mean volume of  $6.1 \pm 0.2 \text{ ml SE}$  ( $n = 40$ ). Yellow Warbler eggs ( $n = 213$ ) were  $16.9 \text{ mm} \pm 0.1 \times 12.9 \text{ mm} \pm 0.1$  and had a mean volume of  $1.4 \text{ ml} \pm 0.1$ . Thus, a robin egg was 4.3 times the volume

of a Yellow Warbler egg (or Yellow Warbler eggs were 23% the volume of American Robin eggs) and the addition of one robin egg to a clutch of four warbler eggs essentially doubled the clutch volume. In 2001, most robin eggs were collected from robin nests on LD2 to minimize the amount of incubation they received prior to being placed in a Yellow Warbler nest (robins begin incubating on LD3; Sallabanks and James 1999). Eggs were collected on LD2 rather than LD1 to prevent robins from deserting what they might have perceived as a depredated clutch. Because not all robin nests were found prior to LD2, some eggs were collected on LD3 or 4. In these instances, the clutch was candled at the time of collection to determine which egg had been freshly laid that day and the freshest egg (i.e., incubated the least) was collected. Freshly laid eggs were distinguished from eggs laid on previous days because they had a small air cell or no air cell (Lokeman and Koford 1996). In 2002, American Robin eggs collected on LD2 were also candled to determine which egg was most recently laid or the first egg was numbered on LD1 to distinguish it from the second-laid egg the following day. Collected robin eggs were wrapped in cotton and placed in sealed containers, and then stored in a water bath at 17 °C to maintain embryonic viability until they could be placed in a Yellow Warbler nest. American Robin eggs were kept in the water bath for one to seven days following collection.

American Robin eggs were added to Yellow Warbler nests on the warbler's LD2. In 2002, Yellow Warbler eggs in nests to which an American Robin egg was added were numbered according to laying date (i.e., number one for the first laid egg and so on) on the day that they were laid, using a non-toxic black felt marker. After clutch completion,

American Robin and Yellow Warbler eggs in parasitized Yellow Warbler clutches were measured to the nearest mm using calipers. Also following clutch completion, American Robin and Yellow Warbler eggs in parasitized Yellow Warbler clutches were candled daily until the embryo and blood vessels first became visible. In most passerines the embryo and blood vessels become visible on the second day of incubation (INC2; Fig. 1). The first day after the laying of the penultimate egg was considered INC1, the second day INC2 and so on. Once the blood vessels and embryo became visible (robin or warbler) the incubation day was recorded and the egg was no longer candled. Once blood vessels and embryos appeared in all eggs in the clutch (both robin and warbler) the nest was left undisturbed until INC8. At INC8 the nest was again visited daily to check for "pipped" eggs (prior to hatching the chick breaks a small hole in the eggshell to allow air exchange) and/or hatchlings. Pipped American Robin eggs, and in one instance an American Robin hatchling, were immediately placed in a robin nest at a similar stage to ensure that nestlings received appropriate parental care (birds do not typically reject parasitic nestlings; Davies and Brooke 1989, Lorenzana and Sealy 2001). Pipped eggs were transported in glass jars surrounded by cotton and the nestling was transported in a cardboard box with a towel. If there was no future foster nest available (i.e., an American Robin nest at the same stage in the nesting cycle to which a pipped egg or hatchling could be later transferred) when blood vessels and embryo became visible in all eggs in a parasitized clutch, the robin egg in the Yellow Warbler nest was removed. Because robins began laying 12 May and warblers 5 June in 2002, 9 of 12 robin eggs were removed once the blood vessels and embryos became visible in both the host and

“parasite” eggs. Three robin eggs were left to develop in Yellow Warbler nests. At the time of removal, robin eggs were candled to ensure that they had developed since the appearance of the blood vessels and embryo (the embryo was larger and could be seen moving, the size of the air cell increased substantially, and many dark vesseled areas that encircled the egg interior had developed). They were then destroyed to prevent further development. In addition, in 2002, nest volume was measured at the time of parasitism for approximately half of the Yellow Warbler nests parasitized. To measure nest volume to the nearest ml, a plastic bag was placed in the warbler nest, filled with rice and then poured into a graduated cylinder.

To compare the incubation abilities of the Yellow Warbler with that of a larger host species, 39 American Robin eggs were collected from robin nests on LD2 and added to 39 conspecific nests on their LD2. To reduce the number of disturbed nests, robin nests that had an egg removed, also had a robin egg added (i.e., conspecific eggs were “switched” between nests). Robin eggs were collected, stored and transferred between different American Robin nests in the same way that robin eggs that were added to Yellow Warbler nests were collected, stored and transferred, to ensure that the transfer of American Robin eggs to Yellow Warbler nests did not affect their subsequent incubation rates. Robin eggs placed in conspecific nests were marked with a letter “P” at the time of parasitism so that the cross-fostered robin egg could be distinguished from the nest owners’ eggs. In 2002, all of the eggs in the parasitized robin clutches were numbered according to laying date. Both the parasitic robin egg and the nest owner’s eggs were measured to the nearest mm using digital or dial callipers. Following clutch completion,



both the “parasitic” robin egg and the nest owner’s eggs were candled daily to determine the day blood vessels and embryo became visible. As in the Yellow Warbler nests that were parasitized with a robin egg, once the blood vessels and embryos were visible in an egg, the egg was no longer candled. Once the blood vessels and embryo had become visible in all eggs in the clutch (both the cross-fostered robin egg and in the nest owner’s eggs) the nest was left undisturbed until INC8. On INC8, nests were checked daily for hatching. Unlike in Yellow Warbler nests, cross-fostered robin hatchlings were not removed because conspecifics could provide appropriate parental care. As an additional control, 40 Yellow Warbler nests were also visited daily and manipulated in the same way as artificially parasitized Yellow Warbler nests (eggs candled daily and measured) but no robin egg was added.

### **Statistical Analyses**

Likelihood ratio Chi-square tests were used to determine whether the fate of artificially parasitized clutches and control clutches differed. The likelihood ratio Chi-square test is similar to the Pearson’s Chi-square test (for large samples this statistic will be the same as the Pearson’s Chi-square statistic) but is more appropriate for smaller samples (Neter et al. 1996). Mann-Whitney U tests were used to compare the number of days for robin eggs to develop visible embryos in experimental and control nests. A Mann-Whitney U test was also used to determine if nests that were rejected had smaller volumes than nests where artificial parasitism was accepted.

## RESULTS

### Acceptance/rejection of model and real eggs

Yellow Warblers accepted 17/27 (63%) model Black-billed Cuckoo eggs and 17/27 (63%) American Robin eggs placed in their nests (Table 19). Only nests that were not depredated or parasitized by a cowbird before acceptance/rejection could be determined were included in the above total nest counts (15 and 13 Yellow Warbler nests parasitized with model cuckoo and robin eggs, respectively, were depredated, parasitized by a Brown-headed Cowbird or disturbed in some other way before the 6-day acceptance period was complete; Table 19). Because there was no difference between the warblers' acceptance/rejection of model cuckoo and robin eggs the data from both experiments were pooled for the subsequent analyses. The fate of artificially parasitized nests differed significantly from control Yellow Warbler nests (likelihood ratio  $X^2 = 47.786$ ,  $df = 5$ ,  $P = 0.000$ ). Yellow Warblers deserted or buried American Robin and model Black-billed Cuckoo eggs at 37% of nests tested (20/54) but neither desertion nor burial behaviours were observed at control Yellow Warbler nests. Eighteen of 82 (22%) of artificially parasitized Yellow Warbler nests were depredated whereas 10/85 (12%) of control Yellow Warbler nests were depredated. Six of the 20 females that deserted or buried did so after they laid their 3rd egg, and 6/20 females deserted or buried parasitized nests after they laid their 4th egg. The rest appeared to desert/bury immediately following parasitism by the day after artificial parasitism. There was a trend for nests where robin eggs were accepted to have larger volumes ( $45.14 \text{ ml} \pm 1.19 \text{ SE}$ ,  $n = 28$ ) than nests that

Table 19. Fate of experimental and control Yellow Warbler and American Robin nests. Percent total for each treatment is in brackets.

Experiment	Fate					n
	Accepted	Desertion	Burial	Depredated	Other <sup>1</sup>	
<u>Cuckoo egg acceptance</u>						
YW + model egg	17 (0.40)	6 (0.14)	4 (0.10)	8(0.19)	7 (0.16)	42
YW no egg added	41 (0.91)	0	0	4 (0.09)	0	45
<u>Robin egg incubation</u>						
YW + AR egg	17 (0.42)	5 (0.12)	5 (0.12)	10 (0.40)	<sup>3</sup> (0.07)	40
AR + AR egg	33 (0.87)	0	0	4 (0.10)	1(0.03)	38
YW no egg added	29 (0.72)	0	0	6 (0.15)	5 (0.12)	40

<sup>1</sup> These nests were blown-out, tipped over or parasitized by a Brown-headed Cowbird before Yellow Warblers' acceptance or rejection could be determined.

females deserted/buried ( $41.63 \text{ ml} \pm 1.19 \text{ SE}$ ,  $n = 6$  deserted plus 2 buried nests) but the difference was not significant (Mann-Whitney U,  $Z = 1.495$ ,  $P = 0.134$ ) and the range in volume between accepted (35 to 56 ml) and deserted nests (39 to 48 ml) overlapped (Fig. 2).

### **Incubation**

Twelve of 17 (70%) robin eggs accepted in warbler nests developed embryos and blood vessels. No significant differences were found between years for the mean number of days between the laying of the penultimate egg and when the embryo and blood vessels became visible in robin eggs in warbler nests (Mann-Whitney U test, mean for 2001 =  $1.33 \pm 0.67 \text{ SE}$ ,  $n = 3$ , mean for 2002 =  $2.22 \pm 0.28 \text{ SE}$ ,  $n = 9$ ,  $Z = 1.210$ ,  $P = 0.226$ ), thus the data for 2001 and 2002 were pooled. All 33 (100%) cross-fostered robin eggs in conspecific nests developed blood vessels and embryos (excluding nests that were depredated before the eggs could be candled). Also, no significant differences were found between years for the mean number of days for the embryo and blood vessels to become visible in robin eggs in conspecific nests (Mann-Whitney U test, mean days for 2001 =  $1.89 \pm 0.20$ ,  $n = 9$ , mean days for 2002 =  $2.21 \pm 0.13 \text{ SE}$ ,  $n = 24$ ,  $Z = 1.235$ ,  $P = 0.217$ ) so the data for 2001 and 2002 were pooled. There was no significant difference in the mean number of days for the embryo and blood vessels to develop in robin eggs in warbler and conspecific nests (Mann-Whitney U test, mean days for warbler nests =  $2.00 \pm 0.28 \text{ SE}$ ,  $n = 12$ , mean days for robin nests =  $2.12 \pm 0.11 \text{ SE}$ ,  $n = 33$ ,  $Z = 0.445$ ,  $P = 0.656$ ).

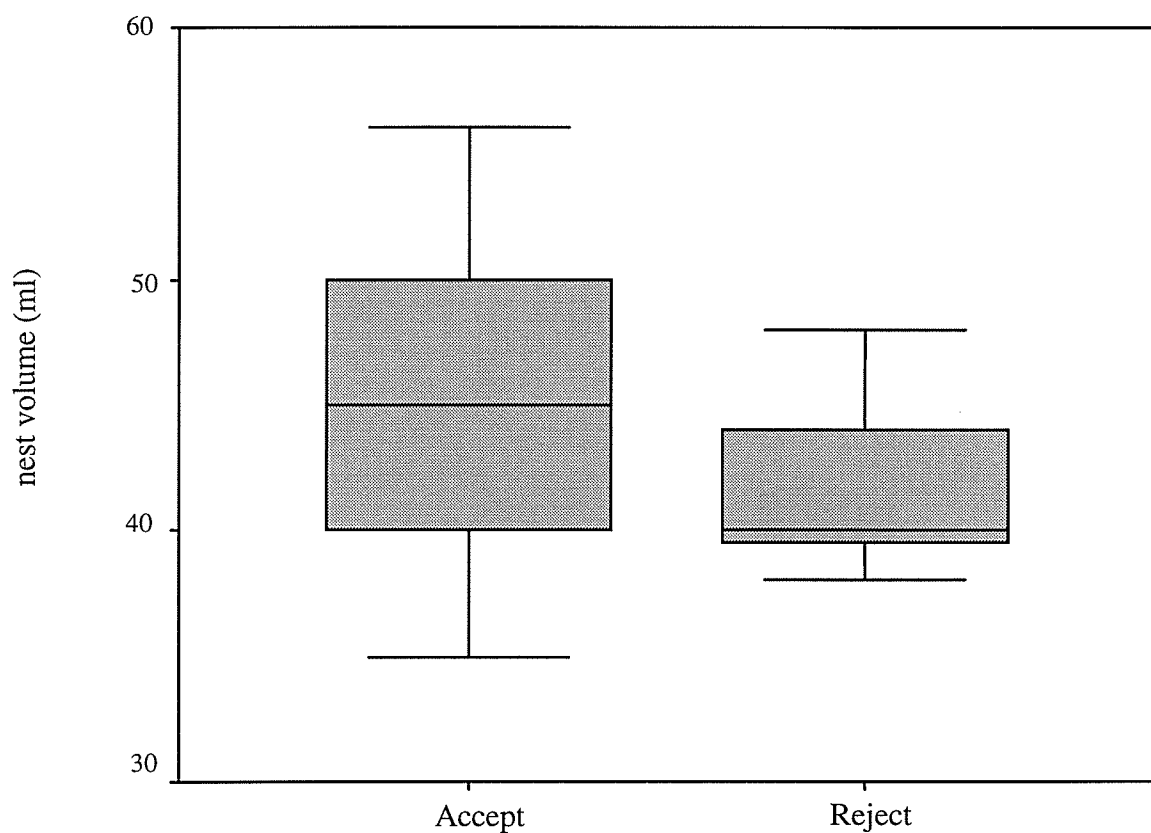


Fig. 2. Nest volumes of artificially parasitized Yellow Warbler nests where females accepted the model cuckoo or robin egg ( $n = 28$ ) and nests that females deserted or buried ( $n = 8$ , or, 6 deserted and 2 buried nests). The middle 50% of the data values for Yellow Warbler nest volumes are contained within the boxes, and the whiskers at the top and the bottom of the boxes run from the 75<sup>th</sup> to the 90<sup>th</sup> percentile and from the 25<sup>th</sup> to the 10<sup>th</sup> percentile, respectively. The line in each box's centre represents the median. There was no significant difference in nest volumes between artificially parasitized nests that were accepted and those that were rejected (Mann-Whitney U,  $Z = 1.495$ ,  $P = 0.134$ ).

Five of the 17 (30%) accepted robin eggs in Yellow Warbler nests did not develop. One of the robin eggs had been collected from a nest that had blown out of a tree. At another Yellow Warbler nest the robin egg was found to have a small hole in it after it was already placed in the Yellow Warbler nest (another egg from the robin nest from which it was collected also had a small hole and did not develop, thus, it does not appear as though the Yellow Warbler caused the damage to the robin egg placed in its nest). Also one of the robin eggs that did not develop was recollected from an experimental Yellow Warbler nest where the female deserted and thus the embryo was not kept at a constant temperature prior to being placed in the experimental nest. At the other two nests, the reason why the robin egg did not develop was not determined.

There was no significant difference in the mean number of days for the embryo and blood vessels to become visible in Yellow Warbler eggs in experimental and control clutches following the laying of the penultimate egg (Mann-Whitney U test, mean number of days for experimental clutches =  $2.66 \pm 0.19$  SE, mean number of days for control clutches =  $2.58 \pm 0.13$  SE,  $n = 17$  experimental,  $n = 29$  control,  $Z = 0.023$ ,  $P = 0.982$ ). In control warbler nests, single warbler eggs in 3/29 (10%) control nests did not develop blood vessels and embryos. In artificially parasitized Yellow Warbler nests, single warbler eggs in 2/17 (12%) experimental nests did not develop blood vessels and embryos.

## Hatching

The nine robin eggs removed from Yellow Warbler nests continued to develop after the blood vessels and embryo became visible. There was no significant difference in the number of days from when the parasitic egg was placed in the nest until hatching for cross-fostered American Robin eggs in Yellow Warbler and conspecific nests (Mann-Whitney U test, mean number of days in Yellow Warbler nests =  $13.33 \pm 0.33$  SE,  $n = 3$ , mean number of days in American Robin nests =  $13.23 \pm 0.11$  SE,  $n = 17$ ,  $Z = 0.352$ ,  $P = 0.725$ ). Although sample size was small, robin eggs in warbler nests apparently developed at the same rate as robin eggs in robin nests.

Host incubation period was determined for four experimental warbler nests (at one nest a robin egg that did not develop was left in the warbler nest until the host eggs hatched). Warbler eggs that developed in experimental nests with robin eggs took significantly longer to hatch (1.6 days) than warbler eggs in control nests (Mann-Whitney U test, mean number of days to mean clutch hatching in experimental nests =  $14.0 \pm 0.1$  SE,  $n = 4$ , mean number of days to mean clutch hatching in control nests =  $12.4 \pm 0.2$  SE,  $n = 15$ ,  $Z = 2.071$ ,  $P = 0.038$ ).

## DISCUSSION

### **Yellow Warblers' responses to Black-billed Cuckoo sized eggs**

Yellow Warblers often accepted both model and real Black-billed Cuckoo-sized eggs. Although some Common Cuckoo hosts discriminate against otherwise mimetic cuckoo eggs on the basis of size alone (Braa et al. 1992, Marchetti 2000), previous

studies have demonstrated that Yellow Warblers do not recognize their own eggs nor do they distinguish between their own eggs and other non-mimetic eggs (Sealy and Lorenzana 1998). Birds will only discriminate against larger eggs if there has been selection for such discrimination (Marchetti 2000). If the Black-billed Cuckoo did not previously parasitize Yellow Warblers, there has not been a selective pressure for them to discriminate against eggs four times larger than their own. However, it is also possible that previous parasitism by the Black-billed Cuckoo selected for cuckoo egg rejection in Yellow Warblers at one time in their evolutionary past but, rejection frequencies have been reduced under relaxed selection pressures. This could explain why only some Yellow Warblers deserted or buried the cuckoo eggs.

Unlike previous studies where researchers found that Yellow Warblers usually accepted artificially placed cowbird eggs in their nests during laying (e.g. Sealy 1995), in the present study a relatively large proportion of Yellow Warblers abandoned or buried artificially parasitized clutches. However, whether the Yellow Warblers' desertion and burial behaviours should be considered a "rejection" of the large parasitic egg is questionable. The results might suggest that some Yellow Warblers are able to recognize that their nest has been parasitized if the parasitic egg is substantially different from their own. Although Yellow Warblers do not distinguish between Brown-headed Cowbird eggs and their own eggs, cowbird eggs are only twice the volume of Yellow Warbler eggs and are somewhat similar in appearance to warbler eggs (white with brown maculation; McMaster and Sealy 1997). On the other hand, robin or model cuckoo eggs are blue-green, four to five times the volume of Yellow Warbler eggs, and sat higher in



the nest than the Yellow Warbler eggs. The combination of a strong tactile stimulus (i.e., the brood patch's contact with a very large smooth surface) and the visual differences in size and colour might have been sufficient for Yellow Warblers to recognize that their clutch had been disturbed regardless of whether they associated that disturbance with a parasitic event (but see Lorenzana and Sealy 1998). A test to determine whether it is the size of the cuckoo egg that elicits this rejection behaviour, would be to place cuckoo-sized model Yellow Warbler eggs (white with brown maculation) in warbler nests to determine if similar rejection frequencies are elicited.

A second possibility is that, because most females that abandoned or deserted did so after laying a third or fourth egg (i.e., not within the first 24 hours after parasitism), their rejection response could have been related to factors other than the presence of the egg alone. Sealy (1995) usually detected burial in Yellow Warbler nests the day after they were parasitized, if not the day of parasitism (however, some rejectors wait until the clutch is complete before ejecting a parasitic egg; Marchetti 2000, Davies and Brooke 1989). The egg's large size affected incubation in some way that caused Yellow Warblers to desert their clutches after they laid additional eggs.

My study may underestimate Yellow Warblers' desertion and/or burial frequencies in response to large eggs. Firstly, twice as many experimental Yellow Warbler nests compared to control Yellow Warbler nests were depredated. Some of these depredated experimental Yellow Warbler nests may have actually been deserted prior to depredation and the host's absence may have provided the predator with easy access to the nest. Additionally, the large blue eggs in the warbler nests may have

attracted predators (Wallace 1889), but Davies and Brooke (1988) found that mimetic model eggs were as likely to be depredated as non-mimetic models in host nests.

Similarly, Mason and Rothstein (1987) found that spotted and immaculate eggs were depredated at similar frequencies in parasitized nests. Secondly, Sealy (1995) found that while Yellow Warblers accepted nearly 100% of artificially added cowbird eggs in their nests during laying, Yellow Warblers rejected substantially more naturally laid cowbird eggs (> 50%). The rejection frequencies recorded here may similarly underestimate the Yellow Warblers' response to naturally laid Black-billed Cuckoo eggs if Yellow Warblers would also respond to additional cues not simulated in the present study.

### **Incubation of cuckoo-sized eggs**

The second often-cited reason for brood parasites laying small eggs relative to their body size is because their smaller host species will not be able to incubate an egg much larger than their own (Davies and Brooke 1988, Sealy et al. 2002). Contrary to this prediction, Yellow Warblers were not only capable of producing sufficient heat to incubate cuckoo-sized eggs, but embryos and blood vessels developed as quickly in robin eggs in Yellow Warbler nests as they did in the nests of conspecifics. Yellow Warblers are likely equally capable of incubating Black-billed Cuckoo eggs and are thus potentially suitable cuckoo hosts. Furthermore, cuckoos might benefit from laying a larger egg than their host because Yellow Warbler eggs in artificially parasitized nests had extended incubation periods (although sample size was small) while robin eggs in warbler nests had incubation periods similar to robin eggs in conspecific nests. However,

the results do not negate the possibility that there is a lower limit to suitable host size and that incubation may in some way be impeded by host size and/or that smaller host species are unsuitable hosts. The fact that hosts with eggs less than one-third the size of a brood parasite's egg are rarely used as hosts (Johnsgard 1997) indicates that individuals parasitizing these smaller hosts are likely less successful (Nolan 1978, Weatherhead 1989).

Incubation by Yellow Warblers may be impeded by factors related to host size other than the amount of heat that a female can produce and transfer to the egg. Small hosts and/or small nests may also impede incubation behaviours, like egg turning (the process whereby the bird moves or rotates the egg within the nest, by reaching beneath the egg with its bill; Deeming 2002). Thus, Yellow Warblers' responses might have been related to the degree of "crowding" in their nest rather than to the large egg itself. During nest visitations robin or model cuckoo eggs typically remained in the centre of the nest and Yellow Warbler eggs were found around the robin or model egg (Fig. 3). Yellow Warblers may have had difficulties adjusting the eggs' locations in the nest. The fact that deserted and buried nests often had smaller volumes than nests where robin or model cuckoo eggs were accepted supports this postulation. However, there was no strict volume limit below which hosts always deserted or above which hosts always accepted. This may be because the volume measurements taken cannot account for nest shape. For example, a shallow but wide nest with a smaller nest volume might have had more "room" for a robin or model cuckoo egg than a narrow but deep nest with a larger volume. Briskie



Fig. 3. American Robin egg in a Yellow Warbler nest.

(1995) reported the mean inside nest diameter for 30 Yellow Warbler nests measured at Delta Marsh to be  $4.7 \text{ cm} \pm 0.43 \text{ SD}$ . The combined mean length of a single American Robin egg and a single Yellow Warbler egg is 4.6 cm. Thus, particularly in Yellow Warbler nests with smaller-than-average inside diameters, females may not have been able to turn the eggs and thus they could not be incubated. This could also explain why robin eggs in two Yellow Warbler nests did not develop because even if females transferred a sufficient amount of heat to the egg, if the egg was not turned then it would not develop. Another possible indication that nests became "overcrowded", is that when one parasitized Yellow Warbler nest was checked on LD5, a Yellow Warbler egg, presumably the female's 5<sup>th</sup> egg, was discovered on the ground below the nest. There may not have been enough room in the nest for the female to lay her egg. Similarly, at another experimental Yellow Warbler nest a Brown-headed Cowbird egg was found on the ground below the nest on LD3. Further work, where eggs are marked to determine egg turning frequencies and nest diameters are measured, is needed to confirm this hypothesis.

Since Yellow Warblers, despite their small size, are apparently suitable Black-billed Cuckoo hosts, their lack of anti-parasite defences in response to the stuffed cuckoo (Chapter 1) and model cuckoo eggs lend support to the hypothesis that Yellow Warblers were not previously parasitized by the Black-billed Cuckoo. Researchers have categorized rarely parasitized Common Cuckoo hosts as rarely used but suitable hosts, or, as unsuitable hosts (Davies and Brooke 1989). These rarely used but suitable hosts reject cuckoo eggs (Davies and Brooke 1989; Braa et al. 1992, Moksnes and Røskaft

1992, Marchetti 2000) and respond strongly to taxidermic mounts of cuckoos placed at their nest (Braa et al. 1992). On the other hand, unsuitable hosts do not reject eggs unlike their own (Davies and Brooke 1989) and do not respond to dummy cuckoos placed at their nests (Moksnes and Røskaft 1988). The fact that unsuitable hosts show no anti-parasite behaviour in response to the cuckoo is generally cited as evidence that rarely used but suitable hosts' rejection behaviours evolved in response to cuckoo parasitism (i.e., these species are presumed to be former hosts that are currently ahead of the cuckoo in the evolutionary arms race; Moksnes and Røskaft 1992, Marchetti 2000), whereas unsuitable hosts are thought to lack defences because they have not been previously parasitized (Davies and Brooke 1989, Braa et al. 1992). Similarly, Brown-headed Cowbirds' host species that are sympatric with the cowbird and are parasitized, exhibit anti-parasite defences (either egg rejection or nest defence behaviours) in response to cowbird models and their eggs, whereas, populations that are allopatric with cowbirds do not, presumably because they have not been previously parasitized (Briskie et al. 1992). If, Yellow Warblers were previously parasitized by the Black-billed Cuckoo, and given the negative effects that such parasitism would have on Yellow Warblers' reproductive success, anti-parasite defence strategies should have evolved. Instead, Yellow Warblers' lack of anti-parasite nest defence strategies in response to the Black-billed Cuckoo supports the hypothesis that Yellow Warblers were not formerly Black-billed Cuckoo hosts. Again, however, the possibility that Yellow Warblers were previously hosts but lost their anti-parasite strategies under relaxed selection pressures cannot be ignored.

## CONCLUSION

Yellow Warblers often accepted and incubated eggs four times larger than their own eggs. Thus, the lower limit to host size is not necessarily determined by acceptance and incubation abilities. Simultaneously, however, some Yellow Warblers deserted artificially parasitized nests. These “rejectors” typically had smaller nests and may have rejected because large eggs “crowded” their nests and possibly impeded incubation. Thus, Yellow Warblers, particularly those individuals that construct larger nests, are potentially suitable cuckoo hosts. Yellow Warblers’ acceptance of model Black-billed Cuckoo eggs and lack of nest defence behaviour in response to the cuckoo supports the hypothesis that Yellow Warblers were not previously Black-billed Cuckoo hosts.

## SUMMARY

1. When presented with Black-billed Cuckoo, Common Grackle and American Robin models at laying, Red-winged Blackbirds responded to the cuckoo with an intermediate level of aggressiveness relative to their response to the grackle (predator/ positive control) and robin (non-threatening species/ negative control).
2. The intensity of the Red-winged Blackbirds' responses to the cuckoo increased or remained the same between the laying and nestling stages, thus, Red-winged Blackbirds did not recognize the cuckoo as a brood parasitic threat.
3. When presented with Black-billed Cuckoo, Eurasian Blackbird and American Robin models at laying, Red-winged Blackbirds responded most strongly to the cuckoo and the Eurasian Blackbird.
4. The Red-winged Blackbirds' responses to the Eurasian Blackbird and Black-billed Cuckoo were similar and the intensity of their response to both models increased from the laying to nestling stage. Red-winged Blackbirds are likely as unfamiliar with the cuckoo as they are with the Eurasian Blackbird and appear to give generalized nest defence response to unfamiliar intruders at their nest.
5. When presented with Black-billed Cuckoo, Common Grackle and American Robin models at the laying and nestling stages, Yellow Warblers responded to all three models



but, spent significantly more time performing distraction displays in response to the grackle at both stages.

6. The intensity of the Yellow Warblers' responses to the cuckoo increased between the laying and nestling stages and Yellow Warblers did not seet call or "rush" to sit on their nests in response to the cuckoo, thus, they did not recognize the cuckoo as a brood parasite. Their response to the cuckoo was consistent with the hypothesis that Yellow Warblers responded to the Black-billed Cuckoos as they would to an uncommon or unfamiliar nest intruder.

7. The results do not negate possibility that either the Red-winged Blackbird or the Yellow Warbler were previously parasitized more frequently by the Black-billed Cuckoo because recognition of the Black-billed Cuckoo as a brood parasite may have been lost or, despite being previously parasitized, there may have been no selection for specific enemy recognition.

8. Yellow Warblers accepted 17/27 (63%) of model Black-billed Cuckoo eggs placed in their nests and 17/27 (63%) of American Robin eggs (used in lieu of real cuckoo eggs) placed in their nests. At the other nests, Yellow Warblers deserted or buried artificially parasitized clutches.

9. Yellow Warbler clutches that were deserted or buried, usually had a smaller nest mean nest volume than accepted clutches, but, this difference was not significant.

10. Twelve of 17 American Robin eggs placed in Yellow Warbler nests developed blood vessels and embryos.

11. There was no difference in the mean number of days it took for the embryo and blood vessels to develop in American Robin eggs in Yellow Warbler nests and American Robin eggs in conspecific nests. This suggests that host size is not limited by the amount of heat a host can produce but by some other factor (e.g., host unable to turn larger egg).

12. Because Yellow Warblers are apparently suitable Black-billed Cuckoo hosts, their lack of anti-parasite defences (i.e., accepted model cuckoo eggs and did not recognize the cuckoo as a brood parasite) indicates that they were likely not previously parasitized by the Black-billed Cuckoo.

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