

How small is too small? Incubation of large eggs by a small host

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Abstract: The Yellow Warbler (*Setophaga petechia* (L., 1766)) is among the putative hosts of the Black-billed Cuckoo (*Coccyzus erythrophthalmus* (Wilson, 1811)), which is hypothesized to have once been an obligate brood parasite. Most parasites lay a small egg relative to their body size, possibly to prevent hosts from discriminating against the larger egg and to facilitate incubation. We tested whether warblers, which lay eggs ~17% of the volume of cuckoo eggs, could have potentially been suitable hosts of *Coccyzus* cuckoos by determining whether they accept and successfully incubate cuckoo-sized eggs. Warblers accepted 63% ($n = 54$) of cuckoo-sized eggs added into their nests and successfully incubated eggs as large as cuckoo eggs (surrogate American Robin (*Turdus migratorius* L., 1766) eggs). This suggests that the lower limit to host size is not just related to egg size. Warblers are not ideal hosts because they rejected a high frequency of experimental eggs (37%). Nests from which eggs were rejected tended to have smaller volumes than nests at which eggs were accepted. The nest cups of warblers are oval, which may promote egg crowding more than round cups. Factors such as nest size, not host size, influence acceptance or rejection of large eggs by Yellow Warblers.

Résumé : La paruline jaune (*Setophaga petechia* (L., 1766)) est un des hôtes putatifs du coucou à bec noir (*Coccyzus erythrophthalmus* (Wilson, 1811)), une espèce qui est supposée avoir été, dans le passé, un parasite obligatoire des nids. La majorité des parasites pondent un œuf petit relativement à leur taille corporelle, possiblement pour prévenir que leurs hôtes puissent défavoriser l'œuf plus gros et pour faciliter l'incubation. Nous avons testé si les parulines, qui pondent des œufs ~17 % du volume des œufs de coucou, auraient pu être des hôtes appropriés en déterminant si elles acceptent et incubent avec succès les œufs plus gros du coucou. Les parulines jaunes ont accepté 63 % ($n = 54$) des œufs de taille coucou ajoutés dans leurs nids et elles ont incubé avec succès des œufs aussi gros que ceux du coucou (des œufs du merle d'Amérique (*Turdus migratorius* L., 1766)). Donc la taille minimale de l'hôte n'est pas uniquement reliée à la taille de l'œuf. Les parulines ne sont pas des hôtes idéaux puisqu'elles ont rejeté les œufs expérimentaux à une haute fréquence (37 %). Les nids desquels les œufs ont été rejetés avaient souvent des volumes plus petits que ceux où les œufs ont été acceptés. L'intérieur des nids des parulines est ovale, ce qui pourrait augmenter l'entassement des œufs par comparaison aux nids ronds. Des facteurs comme la taille du nid, et non la taille de l'hôte, influencent l'acceptation ou le rejet de gros œufs par les parulines jaunes.

Introduction

Brood parasites such as the Common Cuckoo (*Cuculus canorus* L., 1758) and Brown-headed Cowbird (*Molothrus ater* (Boddaert, 1783)) lay small eggs relative to their body size, likely because (i) hosts discriminate against large eggs (Davies and Brooke 1988; Moksnes and Røskaft 1992; Marchetti 2000) and (ii) small hosts cannot incubate eggs substantially larger than their own (Davies and Brooke 1988, 1989). Compiling a list of potentially suitable Australian cuckoo hosts, Brooker and Brooker (1989) set the lower limit of suitable host size at those whose eggs are no less than one-third the volume of the parasite's eggs. This limit seems reasonable given that the amount of heat females can transfer to their clutches is limited (Tøien 1989) and because larger clutches require more energy for incubation (Biebach 1981; Moreno et al. 1991). An additional large egg may impede in-

cubation of both host and parasite eggs by diluting the amount of heat transferred to each egg, thus increasing cooling and subsequent embryonic mortality (Webb 1987; McMaster and Sealy 1997, 1998).

Hughes (1997) hypothesized that cuckoos of the genus *Coccyzus* Vieillot, 1816 were once obligate brood parasites on nests of passerine birds, but they have reverted to caring for their own young. However, unlike most brood parasites, *Coccyzus* cuckoos do not lay eggs that are small relative to their body size, even though several of their recorded putative hosts are smaller and thus lay smaller eggs than the cuckoo. The smallest species recorded parasitized by the Black-billed Cuckoo (*Coccyzus erythrophthalmus* (A. Wilson, 1811)) is the Yellow Warbler (*Setophaga petechia* (L., 1766)), whose eggs are ~17% of the volume of cuckoo eggs (Stewart 2003). This size difference is substantially greater than the difference between the egg of a well-studied obligate

Received 29 October 2010. Accepted 5 May 2011. Published at www.nrcresearchpress.com/cjz on 4 October 2011.

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brood parasite (the Common Cuckoo) and that of its smallest commonly used host (35%; but see Johnsgard 1997; p. 261–262 in Sealy et al. 2002).

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). Of course, the definitive test of a good host is its ability to hatch and fledge parasitic nestlings, but we were not able to test this directly because cuckoo eggs and nestlings were not available. Instead, we used American Robin (*Turdus migratorius* L., 1766) eggs, which are almost equal in volume to Black-billed Cuckoo eggs, and model Black-billed Cuckoo eggs to test whether Yellow Warblers accept and incubate Black-billed Cuckoo eggs.

Materials and methods

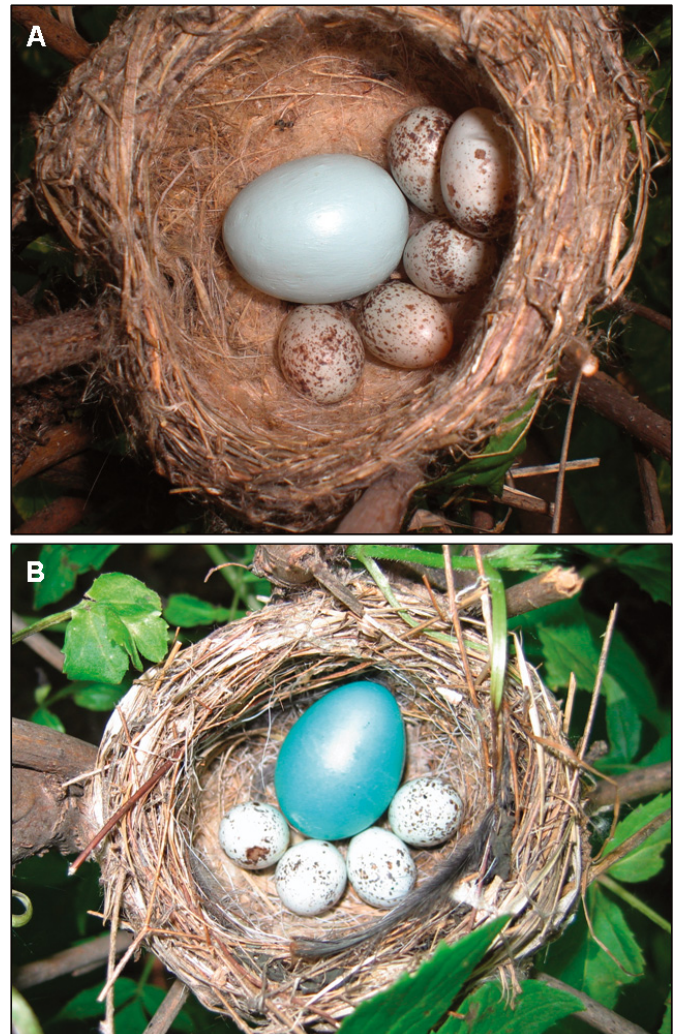
Fieldwork was centred at the Delta Marsh Field Station (University of Manitoba) on Lake Manitoba's south shore (50°11'N, 98°19'W), from May to early July 2001 and 2002; additional nest measurements were taken as part of a study of cues used in decision making by Yellow Warblers in 2008 (Guigueno and Sealy 2011). The site consists of a dune-ridge forest ~80 m wide (MacKenzie 1982) with Lake Manitoba on the north and Delta Marsh on the south side. Yellow Warblers nest densely in this area (Woolfenden et al. 2004). Nests were numbered with flagging tape tied to vegetation 1–2 m from the nests; their contents were inspected every 1–3 days prior to testing.

In a sample of 85 Yellow Warbler eggs measured at Delta Marsh (Sealy 1992), mean length and breadth were 16.80 mm (SE = 0.08 mm) and 12.60 mm (SE = 0.04 mm), respectively; mean mass was 1.43 g (SE = 0.01 g); mean volume was 1.33 mL (SE = 0.11 mL). Eggs are grayish white with brown spots or blotches that often form a wreath around the blunt end (Lowther et al. 1999; Figs. 1A, 1B). In a sample of 102 Black-billed Cuckoo eggs measured in Ontario (Hughes 2001), mean length and mean breadth were 27.55 mm (SE = 0.14 mm) and 20.77 mm (SE = 0.15 mm), respectively; mean mass was 6.3 g (Schönwetter 1967). Cuckoo eggs are light blue to light green (Lorenzana and Sealy 2002). Warbler eggs are ~17% of the size of cuckoo eggs (Sealy 1992; Hughes 2001).

Yellow Warblers at our field site bury naturally laid eggs of a Brown-headed Cowbird at 11%–70% of parasitized nests, depending on which day of the laying cycle parasitism occurred (Sealy 1995; Guigueno and Sealy 2010). Warblers bury by building a new nest on top of the nest and its contents (Mico 1998; Guigueno and Sealy 2010). Different Yellow Warbler populations reject cowbird parasitism at different frequencies depending on the length of sympatry with cowbirds or frequency of parasitism on the population (Briskie et al. 1992; Hosoi and Rothstein 2000; Kuehn 2009). Until about 20 years ago, responses of Yellow Warblers also varied depending on whether their nest was naturally parasitized (Clark and Robertson 1981) or experimentally parasitized—in the case of the latter, they rarely desert or bury the cowbird egg (Sealy 1995). However, warblers at the same field site recently rejected experimentally added cowbird egg models at frequencies similar to naturally parasitized nests, suggesting phenotypic plasticity or a ge-

Fig. 1. (A) An artificial egg of a Black-billed Cuckoo (*Coccyzus erythrophthalmus*) and (B) a real egg of an American Robin (*Turdus migratorius*) in nests of Yellow Warblers (*Setophaga petechia*).

Photographs were taken at Delta Marsh, Manitoba, on 3 June 2010 by A.M. Westphal (A) and on 14 June 2007 by M.F. Guigueno (B).



netic change has occurred in the individuals' recognition of manipulated clutches (Guigueno and Sealy 2011).

Parasitism with model egg

To determine the frequency of acceptance of Black-billed Cuckoo eggs, single model plaster-of-paris cuckoo eggs were added to Yellow Warbler nests on laying day 2 (LD2). Model 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 among years (Sealy 2003). Model eggs were cast from silicone molds made from real Black-billed Cuckoo eggs (Lorenzana and Sealy 2002). Models were painted with Liquitex™ acrylic paint (mixture of 3 parts unbleached titanium #1045-434, 1 part light blue #1045-128, and 1/2 part burnt umber #1045-128) to match the light blue to green color of real Black-billed Cuckoo eggs. They were finished with an acrylic matte medium for waterproofing and to create a sheen typical of real eggs. To the naked eye, models were nearly identical in color to real Black-billed Cuckoo eggs and looked similar

to American Robin eggs (Figs. 1A, 1B). Forty-two model eggs averaged 28 mm × 20 mm and at 6.6 g (SE = 0.1 g) weighed, on average, just 0.3 g more than real Black-billed Cuckoo eggs (Schönwetter 1967; Hughes 2001).

Most Yellow Warbler nests were found before clutch initiation or on laying day 1 (LD1), but a few contained two eggs when found. In these cases, eggs were candled by holding them on the end of a 15 cm piece of foam insulation pipe with ambient light permitting one to see through the semi-translucent eggshell (Lokeman and Koford 1996). We assumed that eggs with a small air cell and no separation within the egg had not been incubated and were on LD2 and not a small and (or) partially depredated clutch (see Hébert 1991).

One model cuckoo egg was added to each of 42 experimental warbler nests on LD2. Nests were then inspected for 6 days, typically incubation day 4 (INC4), to determine whether warblers accepted or rejected the model egg. Many studies have used a 6-day acceptance criterion (e.g., Davies and Brooke 1988; Braa et al. 1992; Lotem et al. 1995; Lorenzana and Sealy 2001; Guigueno and Sealy 2011), which is a trade-off between including delayed rejections of parasitism and excluding rejections related to factors other than parasitism (Rothstein 1982; Lotem et al. 1995). We considered an egg accepted if the female was observed sitting on the clutch and (or) the eggs were warm to the touch and (or) the female behaved defensively. Eggs were considered rejected if cold and the female warbler was not near the nest or the model and warbler eggs had been buried. Accepted model eggs were removed after the 6-day period. An additional 45 Yellow Warbler nests, to which no model eggs were added, were inspected for 6 days to control for the influence visits may have had on responses to the models.

Incubation of large eggs

To determine whether Yellow Warblers can incubate a Black-billed Cuckoo egg, an American Robin egg (which is similar to Black-billed Cuckoo eggs in size, shape, and colour) was added to Yellow Warbler nests on LD2. Other studies have also used other species' eggs in lieu of a parasite's egg to examine host responses (Rothstein 1975; Moksnes and Røskaft 1992), as well as in cross-fostering experiments (e.g., Eastzer et al. 1980). In 2001, most robin eggs were collected from nests on LD2 to minimize the amount of incubation that they received prior to being placed in a Yellow Warbler nest (robins usually initiate incubation on laying day 3 (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 laying day 4 (LD4). In these cases, all eggs in the clutch were candled and the least-incubated egg was collected. Freshly laid eggs were distinguished from eggs laid earlier because the air cell was small or not visible (Lokeman and Koford 1996). In 2002, robin eggs collected on LD2 were also candled to determine which egg was most recently laid or the first egg was numbered on LD1, using a nontoxic marker, to distinguish it from the second-laid egg the following day. Robin eggs were then stored in a water bath at 17 °C for 1–7 days to maintain embryonic viability, while preventing embryonic develop-

ment (R.A. MacArthur, personal communication), until they could be placed in a warbler's nest.

After clutch completion, robin and warbler eggs in 40 "parasitized" warbler clutches were measured to the nearest millimetre using calipers and are reported as mean ± SE unless otherwise indicated. Forty robin eggs placed in warbler nests measured 28.8 ± 0.5 mm × 20.4 ± 0.4 mm and had a volume of 6.1 ± 0.2 mL. Yellow Warbler eggs ($n = 213$) were 16.9 ± 0.1 mm × 12.9 ± 0.1 mm and had a volume of 1.4 ± 0.1 mL. A robin egg was 4.3 times the volume of a Yellow Warbler egg (or a warbler egg was 23% the volume of a robin egg), thus the addition of one robin egg to a clutch of four warbler eggs essentially doubled the clutch volume.

Also following clutch completion, robin and warbler eggs 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; Lokeman and Koford 1996). The first day after laying of the penultimate egg was considered INC1, the second day INC2, and so on. Once blood vessels and embryo became visible (robin or warbler), the incubation day was recorded and the egg was no longer candled and robin eggs were either removed from the nest to prevent further development or, in instances where it was determined a foster nest would be available at hatching (i.e., a robin nest at the same stage in the nesting cycle), left to develop in the host nest. Because robins began laying on 12 May and warblers on 5 June in 2002, 9 out of 12 robin eggs were removed. At the time of removal, robin eggs were candled to ensure that they had continued to develop since the initial appearance of the blood vessels and embryo. In all cases, the embryo was larger, the size of the air cell increased substantially, and many dark areas with vessels that encircled the egg's interior had developed. For the remaining three warbler nests in which robin eggs were left to develop, daily nest inspections resumed on the eighth day of incubation (INC8) to check for "pipped" eggs and (or) hatchlings. Pipped eggs and, in one case, a hatchling were immediately removed and placed in a foster conspecific nest to ensure proper parental care (birds do not typically reject parasitic nestlings; Davies and Brooke 1989; Lorenzana and Sealy 2001).

In 2002, nest volume (nearest millilitre) was also measured at the time of parasitism for approximately half of the Yellow Warbler nests parasitized by placing a plastic bag in the warbler nest, filling it with rice, then pouring the rice into a graduated cylinder. This measurement allowed us to determine whether nests where rejection occurred had smaller volumes than nests where parasitism was accepted. In addition, interior depth and minimum and maximum widths were measured at 158 Yellow Warbler nests in May and June 2008 as part of a related study (Guigueno and Sealy 2011). We used these data in the present study to determine whether nest measurements varied among nests during the same breeding season and whether minimum and maximum widths at the same nests differed significantly. This would demonstrate whether nest cups are spherical and whether width could potentially affect rejection of large cuckoo-sized eggs.

To compare the incubation ability of Yellow Warblers 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 robin nests in the same way that robin eggs that were added to warbler nests were collected, stored, and transferred to ensure that the transfer of robin eggs to warbler nests did not affect the subsequent progression of incubation. Robin eggs placed in conspecific nests were marked so that the cross-fostered robin egg could be distinguished from the other eggs. In 2002, all eggs in the parasitized robin clutches were numbered according to laying date. Following clutch completion, the parasitic robin egg and the nest owner’s eggs were measured and candled following the same protocol as previously described for parasitized warbler nests. As in Yellow Warbler nests parasitized with a robin egg, 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 when daily nest checks resumed to determine hatching date. Cross-fostered robin hatchlings were not removed because conspecifics provided 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 χ^2 tests were used to determine whether there was a difference in the fates of artificially parasitized clutches and control clutches. This test is similar to Pearson’s χ^2 test but more appropriate for smaller samples (Neter et al. 1996). Mann–Whitney U tests were used to compare the number of days before parasitic robin eggs developed visible embryos in warbler and robin nests, as well as to compare nest volume between warbler host nests where artificial parasitism was accepted or rejected. A Wilcoxon’s signed rank test was used to analyze differences between minimum and maximum widths at the same nests.

Results

Responses to model and real eggs

Yellow Warblers accepted 17 out of 27 (63%) model cuckoo eggs and 17 out of 27 (63%) robin eggs placed in their nests (Table 1). Nests depredated or parasitized by cowbirds before acceptance or rejection could be determined were not tallied. Fifteen and 13 warbler nests that received model cuckoo or robin eggs, respectively, were depredated, parasitized by cowbirds, or otherwise disturbed before the end of the 6-day acceptance period. Because there was no difference between acceptance or rejection of model cuckoo and robin eggs, the data from both experiments were pooled for subsequent analyses. Fates of experimental and control nests differed significantly (likelihood ratio $\chi^2_{[5]} = 47.786$, $P < 0.001$). At parasitized nests, warblers rejected 20 cuckoo-sized eggs through desertion ($n = 11$) or burial ($n = 9$), whereas no rejection occurred at control nests. Eighteen out of 82 (22%) experimental nests were depredated, whereas 10 out of 85 (12%) of control nests were depredated. At nests where rejection occurred, 8 out of 20 females deserted or buried by day 1 following artificial parasitism, 6 deserted or

buried after LD3, and the remaining 6 females deserted or buried after LD4. Nests where large eggs were accepted tended to have larger volumes (45.14 ± 1.19 mL, $n = 28$) than nests where desertion or burial occurred (41.63 ± 1.19 mL, $n = 6$ deserted plus 2 buried nests), but this difference was not significant (Mann–Whitney U test, $Z = 1.495$, $P = 0.134$).

Interior depths of Yellow Warbler nests ranged from 23 to 44 mm (34.77 ± 0.34 mm, $n = 158$). Minimum widths ranged from 32 to 56 mm (45.17 ± 0.29 mm, $n = 158$) and maximum widths ranged from 39 to 83 mm (49.14 ± 0.42 mm, $n = 158$). Minimum and maximum widths differed significantly ($S = 4257.5$, $P < 0.0001$), therefore nest cups were more oval than round.

Incubation

Twelve out of 14 (85%) robin eggs accepted by warblers developed embryos and blood vessels. An additional three warbler nests were experimentally parasitized with robin eggs. These eggs did not develop, but this was expected because the collection was opportunistic and thus diverged from the protocol. One robin egg was collected from a downed nest, another had a small hole in it, and another was collected from a previously deserted nest. We opted to use these eggs to increase sample size in determining whether Yellow Warblers would accept the cuckoo-sized egg ($n = 17$) but did not include data from these nests in the analyses of incubation.

No significant differences were found between years for the mean number of days between laying of the penultimate egg and when the embryo and blood vessels became visible in robin eggs in warbler nests (year 2001 = 1.33 ± 0.67 days, $n = 3$; year 2002 = 2.22 ± 0.28 days, $n = 9$; Mann–Whitney U test, $Z = 210$, $P = 0.226$), thus the data for 2001 and 2002 were pooled. All 33 robin eggs cross-fostered in robin nests developed blood vessels and embryos, excluding four nests depredated before the eggs could be candled (Table 1). Also, there were no significant differences between years for the mean number of days for the embryo and blood vessels to become visible in robin eggs in conspecific nests (year 2001 = 1.89 ± 0.20 days, $n = 9$; year 2002 = 2.21 ± 0.13 days, $n = 24$; Mann–Whitney U test, $Z = 1.235$, $P = 0.217$), hence the data for 2001 and 2002 were pooled. There was no significant difference in the mean number of days for development of the embryo and blood vessels in robin eggs in warbler and conspecific nests (warbler nests = 2.00 ± 0.28 days, $n = 12$; robin nests = 2.12 ± 0.11 days, $n = 33$; Mann–Whitney U test, $Z = 0.445$, $P = 0.656$).

In addition, in the three warbler nests where the robin egg was left until hatching, there was no difference in the number of days from when the parasitic egg was placed in the nest until hatching for cross-fostered robin eggs in Yellow Warbler and conspecific nests (Yellow Warbler nests = 13.33 ± 0.33 days, $n = 3$; robin nests = 13.23 ± 0.11 days, $n = 17$; Mann–Whitney U test, $Z = 0.352$, $P = 0.725$). The sample size was small but robin eggs in warbler nests developed at the same rate as robin eggs in conspecific nests.

There was no difference in the mean number of days for the embryo and blood vessels to become visible following laying of the penultimate egg in host eggs in experimental and control clutches (experimental clutches = $2.66 \pm$

Table 1. Fate of experimental and control nests of Yellow Warbler (*Setophaga petechia*; YW) and American Robin (*Turdus migratorius*; AR).

Experiment	Fate					<i>n</i>
	Accepted	Desertion	Burial	Depredated	Other*	
Acceptance of a Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>) model egg						
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
Incubation of an American Robin (AR) egg						
YW + AR egg	17 (0.42)	5 (0.12)	5 (0.12)	10 (0.40)	3 (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

Note: Percentage of total for each treatment is in parentheses.

*Nests were blown-out, tipped over, or parasitized by a Brown-headed Cowbird (*Molothrus ater*) before acceptance or rejection could be determined.

0.19 days, $n = 17$; control clutches = 2.58 ± 0.13 days, $n = 29$; Mann–Whitney U test, $Z = 0.023$, $P = 0.982$). However, in nests where warbler eggs were incubated alongside robin eggs, the total incubation period for warbler eggs was significantly longer than that for warbler eggs in control nests (number of days to clutch hatching of last warbler egg of the clutch in experimental nests = 14.0 ± 0.1 days, $n = 4$; number of days to clutch hatching in control nests = 12.4 ± 0.2 days, $n = 15$; Mann–Whitney U test, $Z = 2.071$, $P = 0.038$). A small number of single warbler eggs in experimental (2 out of 17) and control (3 out of 29) nests did not develop.

Discussion

Despite their small size, many Yellow Warblers accepted and incubated eggs four times larger than their own eggs and thus, in this regard, qualify as suitable Black-billed Cuckoo hosts. In addition, not only did Yellow Warblers produce sufficient heat to incubate cuckoo-sized eggs, the embryos and blood vessels of “parasitic” eggs developed as quickly in warbler nests as they did in conspecific nests. Yellow Warblers are likely equally capable of incubating Black-billed Cuckoo eggs and, so long as they fed cuckoo nestlings appropriate food, could be suitable cuckoo hosts. However, these results do not negate the possibility that there is a lower limit to suitable host size or that incubation may in some way be impeded by host size. The fact that smaller 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 smaller hosts are likely less successful (Nolan 1978; Weatherhead 1989).

If Black-billed Cuckoos and Yellow-billed Cuckoos (*Coccyzus americanus* (L., 1758)) regularly parasitized nests of smaller species in the past, their eggs should be smaller relative to their body mass, thus matching more closely the size of host eggs, as in parasitic cuckoos and cowbirds that parasitize small species (Briskie and Sealy 1990; Brooker and Brooker 1990; Sealy et al. 2002). However, the eggs of *Coccyzus* cuckoos are relatively large and their egg volume to body size ratio (Black-billed Cuckoo = 0.11; Yellow-billed Cuckoo = 0.13) is larger than the ratio for Brown-headed Cowbirds (0.08) (Hoyt 1979; Lowther 1993; Hughes 1999, 2001). On the other hand, parasites could potentially benefit

by laying a larger egg than their host. Here incubation periods for warbler eggs in artificially parasitized nests were extended (although sample size was small), whereas incubation periods for robin eggs were not. Similarly, cowbird eggs hatch before warbler eggs because the larger cowbird egg disrupts incubation of the smaller host eggs (McMaster and Sealy 1998). A similar disruption of incubation also presumably occurred in warbler nests with artificial cuckoo eggs and robin eggs.

Although Yellow Warblers accepted most model and real cuckoo-sized eggs, more interestingly, they rejected 37% of each of them. Yellow Warblers have shown a similar rejection frequency (~40%) of naturally laid Brown-headed Cowbird eggs and varying rejection frequencies (8%–24%) at nests where Brown-headed Cowbird eggs were experimentally added (Sealy 1995; Guigueno and Sealy 2011). Although larger experimentally added cuckoo eggs were rejected more frequently than experimentally added cowbird eggs to clearly demonstrate that size alone increases the probability of rejection in Yellow Warblers, we would need to experimentally parasitize warblers with eggs of increasing size within the same breeding season. Thus, although our results suggest that rejection by Yellow Warblers is influenced by egg size, the varying rejection frequencies observed also suggest that the rejection behaviour is plastic and is influenced by additional factors that may or may not be related to egg size.

Sealy and Lorenzana (1998) suggested that Yellow Warblers do not recognize their own eggs or distinguish between them and other nonmimetic eggs. However, results of an experiment involving a larger sample size and video recordings of warblers before and after clutch manipulation demonstrated that they do recognize changes in their clutches and possibly distinguish between their own eggs and a blue cowbird-sized egg (Guigueno 2010). In the present study, warblers responded to model cuckoo and robin eggs because burial and desertion were recorded significantly more frequently at nests that received an egg than those that did not. Although Yellow Warblers may not distinguish between Brown-headed Cowbird eggs and their own eggs, cowbird eggs are only twice the volume of Yellow Warbler eggs and are similar in appearance to warbler eggs (McMaster and Sealy 1997). Cuckoo and robin eggs are blue–green and four-to-five times the volume of warbler eggs. These results

suggest that some Yellow Warblers recognize that their nest has been parasitized when the parasitic egg differs substantially from their own.

Previous parasitism by Black-billed Cuckoo may have selected for cuckoo egg rejection in Yellow Warblers in their evolutionary past and rejection frequencies may have been reduced under relaxed selection pressures. Parasitism by the Brown-headed Cowbird, however, may maintain the expression of desertion and burial as rejection responses to any larger foreign egg. This would explain why only some Yellow Warblers deserted or buried cuckoo eggs. However, the Yellow Warbler's lack of nest defence response to the mounted cuckoo (Stewart 2003) support the hypothesis that Yellow Warblers were not previously parasitized by the Black-billed Cuckoo regularly. Unsuitable hosts of old world cuckoos are thought to lack defences because they have not been previously parasitized (Davies and Brooke 1989; Braa et al. 1992). It seems more likely in our study that the combination of a strong tactile stimulus (i.e., contact of the brood patch with a very large smooth surface) and the visual differences in size and colour were sufficient for Yellow Warblers to recognize their disturbed clutch regardless of whether they associated that disturbance with a parasitic event (but see Sealy and Lorenzana 1998).

Shape also increases rejection by Yellow Warblers (Guigueno and Sealy 2009). Cowbird egg-sized stars added to 32 warbler nests were rejected at 44% of nests (stars represented debris-like objects that could fall into the nest; Guigueno and Sealy 2009), which is similar to the rejection frequency of Black-billed Cuckoo eggs in this study. Thus, nest sanitation behaviour is likely an important evolutionary stage toward rejection of parasitic eggs by Yellow Warblers (Guigueno and Sealy 2009).

Incubation by Yellow Warblers may be impeded by factors related to size other than the amount of heat that a host female can transfer to the egg. Small hosts and (or) small nests may also impede incubation behaviour, such as egg turning (Deeming 2002). Sixty percent of females that deserted or buried did so after laying a third or fourth egg and thus their rejection response could have been related to factors other than the presence of the egg alone. Responses of Yellow Warblers may have been related to the degree of "crowding" in their nest rather than to the mere presence of the large egg. Overcrowding may also explain why robin eggs in two Yellow Warbler nests did not develop. If the eggs were not turned, then they would not develop, even if females transferred a sufficient amount of heat to them. During nest visits, we noted that robin or model cuckoo eggs typically remained in the centre of the nest with the warbler eggs surrounding it (Figs. 1A, 1B). Debris-shaped objects (stars) added to warbler nests also remained in the centre of the nest (Guigueno and Sealy 2009; M.F. Guigueno, personal observation). Nest sanitation or impediments to incubation may be a preadaptation for egg burial and may be stimulated by disturbances such as crowding (Guigueno and Sealy 2009).

The fact that the cups of 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 below which hosts always deserted or above which hosts always accepted, possibly because the volumetric measurements taken do not account for nest

shape. For example, a shallow but wide nest with less volume may have had more "room" for a robin or model cuckoo egg than a narrow but deeper, more voluminous nest. Maximum and minimum widths differ significantly, therefore, nest cups are not perfectly round and a more oval shape probably promotes even more crowding. The mean minimum width was 45 mm and mean maximum width was 49 mm and the combined mean length of a single American Robin egg and a single Yellow Warbler egg is 46 mm. Thus, particularly in Yellow Warbler nests with smaller-than-average inside diameters and more oval nest cups, females may not have been able to turn the eggs appropriately and thus they were not incubated.

Another indication that nests became "overcrowded" was that when one parasitized Yellow Warbler nest was checked on laying day 5 (LD5), a Yellow Warbler egg, presumably the female's 5th egg, was discovered on the ground below the nest. At another experimental Yellow Warbler nest, a cowbird egg was found on the ground below the nest on LD3. There may not have been enough room in the nest for the cowbird to lay her egg. Furthermore, the timing of Yellow Warbler desertion in response to the cuckoo-sized egg was somewhat different than previously observed rejection behaviour. 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). In the current study, most females that abandoned or deserted did so after laying a third or fourth egg (i.e., not within the first 24 h after parasitism); thus, their rejection response could have been related to factors other than the presence of the egg alone. In Eurasian Reed Warblers (*Acrocephalus scirpaceus* (Hermann, 1804)), larger parasitic eggs were rejected sooner, primarily by desertion, than smaller parasitic eggs that were ejected (Stokke et al. 2010). The large egg possibly influenced incubation in some way that caused Yellow Warblers to desert their clutches after they laid additional eggs.

Further work, where eggs are marked to determine egg-turning frequencies and nest diameters are measured, is needed to support the above hypothesis. Regardless, the persistence of rejection of large cuckoo-sized eggs in this study is likely due to factors that are not mutually exclusive, but are unrelated to previous parasitism by Black-billed Cuckoos, such as crowding, nest sanitation, and parasitism by cowbirds (Deeming 2002; Guigueno and Sealy 2009).

Acknowledgements

We thank T. MacEachen, E. Progoda, R.J. Bisson, A.J.-A. Garroni, V.A.N. Grandmaison, J.L. Rasmussen, and D.M. Tétrault for assistance in the field; Delta Marsh Field Station (University of Manitoba) for accommodation; and the officers of the Portage Country Club and Delta Waterfowl Foundation for allowing us to conduct some of this work on their properties. We also thank R.A. MacArthur for constructing the water bath used to store robin eggs and T.J. Underwood who suggested putting a large egg into a small bird's nest in the first place. This research was funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to S.G.S. and a NSERC Canada Graduate Scholarship to M.F.G.

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