The Condor 112(2):399–406
© The Cooper Ornithological Society 2010

CLUTCH ABANDONMENT BY PARASITIZED YELLOW WARBLERS: EGG BURIAL OR NEST DESERTION?

Mélanie F. Guigueno[1] and Spencer G. Sealy

Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

Abstract. In response to brood parasitism by the Brown-headed Cowbird (*Molothrus ater*), some female Yellow Warblers (*Dendroica petechia*) bury cowbird eggs and sometimes their own eggs, whereas other females desert parasitized nests and renest at new sites. We identified circumstances that elicit burial or desertion by analyzing the histories of 132 naturally parasitized nests inspected over 13 breeding seasons in Manitoba. Damaged nests and clutches reduced to zero, one, or two host eggs were deserted, whereas the clutch was buried when zero, one, or two host eggs were present the morning cowbirds laid and the probability of hatching was high. Response times for burial (2.3 ± 0.1 [SE] days) and desertion (2.5 ± 0.3 days) were similar, but the variance differed significantly (1.29 days^2 for burial versus 2.58 days^2 for desertion). Burial is the Yellow Warbler's more frequent method of rejection, though desertion is used about one-third of the time, and it may be elicited by factors unrelated to brood parasitism, such as interference by predators and inclement weather.

Key words: brood parasitism, clutch abandonment, Dendroica petechia, *egg burial, nest desertion, Yellow Warbler.*

Abandono de Nidadas Parasitadas de *Dendroica petechia*: ¿Entierro de Huevos o Deserción del Nido?

Resumen. En respuesta al parasitismo del nido por parte de *Molothrus ater*, algunas hembras de *Dendroica petechia* entierran los huevos del parásito y a veces sus propios huevos, mientras que otras hembras abandonan el nido parasitado y vuelven a anidar en sitios nuevos. Identificamos las circunstancias que desencadenan el entierro o la deserción mediante el análisis de las historias de 132 nidos parasitados naturalmente que fueron inspeccionados a lo largo de 13 épocas reproductivas en Manitoba. Los nidos dañados y con puestas reducidas a cero, uno o dos huevos del hospedero fueron desertados, mientras que los huevos fueron enterrados cuando el nido contenía cero, uno o dos huevos del hospedero la mañana en que *M. ater* puso sus huevos y en que la probabilidad de eclosión era alta. El tiempo de respuesta para el entierro (2.3 ± 0.1 [EE] días) y la deserción (2.5 ± 0.3 días) fueron similares, pero la varianza fluctuó significativamente (1.29 días^2 para la cobertura versus 2.58 días^2 para la deserción). El entierro es el método más frecuente de rechazo en *D. petechia*, aunque la deserción es usada en un tercio de los casos y puede ser desencadenada por factores que no están relacionados al parasitismo de los nidos, como la interferencia por depredadores y las condiciones climáticas adversas.

INTRODUCTION

Parasitism by the Brown-headed Cowbird (*Molothrus ater*) has exerted pressure on many species to evolve behaviors that minimize or eliminate the costs of parasitism (Davies 2000). Some of these hosts eject cowbird eggs from their nests (Sealy 1996, Hosoi and Rothstein 2000, Peer and Sealy 2004). When ejection involves grasping the cowbird egg, it requires a bill of which the minimal length of the tomium must be from 14.91 to 17.08 mm (Rasmussen 2008). Yellow Warblers (*Dendroica petechia*) apparently cannot grasp-eject cowbird eggs because with a tomial length of 13.4 ± 1.1 mm (Rohwer and Spaw 1988) their bills are too short; also, they are not known to puncture-eject cowbird eggs. Yellow Warblers apparently do not recognize their own eggs (Sealy and Lorenzana 1998), as is necessary for ejection. Yellow Warblers nevertheless reject cowbird eggs by a unique form of clutch abandonment: they construct part of a new nest (embedded burial) or an entirely new one (true burial) over the parasitized clutch (Sealy 1995, Mico 1998). Both forms of burial have been reported occasionally in other passerines, but these behaviors generally occurred when cowbirds laid in unfinished nests and the "hosts" incorporated the cowbird eggs into the structure of the nests as they completed them (Mico 1998). Only the Yellow Warbler buries cowbird eggs and often its own eggs under a new nest (Sealy 1995, Mico 1998), but, like other species, parasitized or not, Yellow Warblers desert their nests in response to other stimuli and renest at different sites (Clark and Robertson 1981, Graham 1988, Burgham and Picman 1989, Hill and Sealy 1994, Hosoi and Rothstein 2000).

Manuscript received 9 July 2009; accepted 3 December 2009.
[1]E-mail: melguigueno@mts.net

The Condor, Vol. 112, Number 2, pages 399–406. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2010.090135

The stimulus that elicits clutch abandonment continues to interest researchers, who have attempted to determine whether nest abandonment by hosts is an adaptive response to cowbird parasitism (Clark and Robertson 1981, Graham 1988, Burgham and Picman 1989, Hobson and Sealy 1989, Sealy 1992, 1995, Hill and Sealy 1994, Hosoi and Rothstein 2000, Kosciuch et al. 2006). Brood parasitism may select for a high frequency of desertion in passerines, as nonforest species, which are more likely to encounter cowbirds, desert more frequently than forest-inhabiting species (Hosoi and Rothstein 2000). Furthermore, Yellow Warblers desert naturally parasitized nests more frequently than control nests (Sealy 1995). Partial clutch loss associated with parasitism, and the concomitant reduction in clutch volume, not parasitism per se, elicits desertion in some other parasitized species (Hill and Sealy 1994, Kosciuch et al. 2006) but not all (Peer et al. 2005).

The cue or cues to which Yellow Warblers respond when deciding whether to bury or to desert parasitized clutches have not been identified, but if they are different, each decision nevertheless leads to a new clutch, though slightly sooner when the decision is burial (Clark and Robertson 1981). Is the decision to bury, rather than to desert and renest, made at a certain point during the warbler's cycle of laying? This seems to be the case with the decision to reject parasitism in the first place, whether by burial or by desertion, as opposed to accepting the cowbird egg (Clark and Robertson 1981, Burgham and Picman 1989, Sealy 1995). But why does one female bury a parasitized clutch, whereas another may desert and renest at another site? Is burial elicited when the female warbler intercepts the laying cowbird, as she might with a potential nest predator, though in the first scenario the nest may be left with a cowbird egg and a reduced chance of success? In the latter, the warblers may be left with nothing. Cowbirds lay about 45 to 25 min before sunrise, followed by the warblers a few minutes later, on average 13 min after sunrise (Neudorf and Sealy 1994, McMaster et al. 2004). The laying cowbird may interfere with the warbler's laying, despite the former laying within only seconds (Sealy et al. 1995). Here, we describe the circumstances prior to burial and desertion by parasitized Yellow Warblers.

HYPOTHESIS

We hypothesized that burial is maintained primarily by selection from brood parasitism, although under some circumstances it also may occur in the context of nest sanitation (Guigueno and Sealy 2009); nest desertion, however, may be maintained by multiple sources of selection (Clark and Robertson 1981, Goossen and Sealy 1982) such as disturbances by predators (Rothstein 1975). To tease apart the circumstances under which warblers buried or deserted parasitized clutches, we analyzed the daily chronology of laying at 132 naturally parasitized nests of the Yellow Warbler over 13 years at Delta Marsh, Manitoba (50° 11′ N, 98° 19′ W). We made five predictions before compiling and analyzing the data to eliminate the effects of post-hoc testing. The proximate mechanisms we describe below also may be interpreted in terms of their ultimate cause, i.e., brood parasitism (see below).

1. The interval between laying of the cowbird egg and initiation of burial or nest desertion should be different. If burial is elicited by brood parasitism, it should begin sooner after the appearance of the cowbird's egg, and this interval should be less variable than that at nests that are deserted, if desertion is a response to other disturbances in addition to brood parasitism (Rothstein 1975, Hosoi and Rothstein 2000).

2. Most rejections later in the clutch-initiation period should be by burial, if warblers renest after desertion, because the new clutches are laid 3 to 6 days sooner after burial (Clark and Robertson 1981). We therefore expected that birds able to bury continue to do so for slightly longer than those constrained to desertion only.

3. Burial should occur more frequently than desertion when the likelihood that the cowbird will hatch is greatest (i.e., zero, one, or two host eggs in nest at the time of parasitism). Yellow Warblers are more likely to bury cowbird eggs up to the day they lay their second egg, usually sacrificing their own egg(s) (Clark and Robertson 1981, Sealy 1995). Cowbird eggs laid later in the warbler's laying cycle are less likely to hatch and, hence, they pose less risk to the host (Clark and Robertson 1981, Briskie and Sealy 1990, Sealy 1995). This evidence led Sealy (1995) to conclude that burial by Yellow Warblers is an anti-parasite adaptation.

4. Deserted nests are more likely to have been damaged than those in which the eggs have been buried (Clark and Robertson 1981, Burgham and Picman 1989). Clark and Robertson (1981) considered nest desertion an alternate rejection option for the Yellow Warbler when burial was impossible because the damaged nest could not support construction of a superimposed nest. They did not test this hypothesis statistically.

5. Desertion should be recorded more frequently than burial at parasitized nests reduced to two, one, or zero host eggs, as clutch reduction this substantial probably was caused by a predator. Hosts should desert their current nesting attempt and relocate to a different site to reduce risk of subsequent depredation. In many birds, clutch reduction elicits desertion of the current nesting attempt (Armstrong and Robertson 1988, Sealy 1992, Hill and Sealy 1994, McLaren and Sealy 2000, Ackerman et al 2003, Kosciuch et al. 2006). Clutch reduction usually results from depredation, but sometimes it is perpetrated by a cowbird (Clark and Robertson 1981, Sealy 1992, McLaren and Sealy 2000) or by another predator (Armstrong and Robertson 1988, Ackerman et al. 2003). At Delta Marsh, however, about one-third of parasitized Yellow Warbler nests lose one egg, rarely more, to female cowbirds (Sealy 1992). When complete clutches of 4 or 5 eggs are reduced to 2 or fewer, Yellow Warblers typically desert them and the nest site,

though reductions of this magnitude at Delta Marsh generally resulted from depredation by predators other than a cowbird (Sealy 1992, McLaren and Sealy 2000). The warbler's response (burial or desertion) to clutch reduction in combination with brood parasitism has not been examined.

METHODS

We analyzed data collected at Delta Marsh from late May to mid-July by J. P. Goossen (1974–1976), G. C. Biermann (1978–1979), and S. G. Sealy (1980–1987) in conjunction with other studies (Goossen 1978, Biermann 1980, Biermann and Sealy 1982, Goossen and Sealy 1982, Sealy 1992, 1995). Nests were located in dune-ridge forest that separates Lake Manitoba and Delta Marsh on the properties of the Delta Marsh Field Station and Portage Country Club (MacKenzie 1982) and the village of Delta. Most nests were discovered during construction or laying (those found at the nestling stage were not used). Nests were inspected daily throughout laying, but in some years they were visited only every 2–3 days during the incubation and nestling stages. From 1974 to 1976 warbler and cowbird eggs were numbered with waterproof markers in the order they were laid. We extracted data from all parasitized nests at which clutches were buried or nest sites were deserted, and we used the day-to-day history of each nest to sort the remaining nests into subgroups to test our predictions. "Clutch abandonment" includes burial and nest desertion (i.e., rejection): burial is the construction of a new nest over the previous nest or re-lining of the original nest (Mico 1998), whereas nest desertion refers to a nest and its site abandoned with adults starting over at a new location. To better explain the costs of burial and desertion at our field site, we calculated the number of days between burial or nest building at a new site and initiation of the second clutch. The latter gives the approximate time for warblers to initiate a new clutch after desertion, and only data from nests that were monitored from the day nest building was initiated to the day the first egg was laid were included. Clark and Robertson (1981) reported that it takes 3 to 6 days longer for a new clutch to be initiated after desertion than when the eggs are buried; we determined whether this interval was similar to differences between burial and desertion at our field site.

1. We recorded the number of days between parasitism and the first indication of clutch abandonment. However, burial may take about 1 to 3 days to complete (M. F. Guigueno and S. G. Sealy, unpubl. data), so we considered a nest deserted if the parents were not seen for 3 consecutive days and the eggs were cold (Sealy 1992, 1995, Guigueno and Sealy 2009). We recorded the clutch as abandoned on the first day when strands of nest material were strewn in the cup or the eggs felt cold; this response was confirmed over the next couple of days.

2. We divided the number of days burial or desertion occurred after the clutch-initiation period started by the number of days in that period in that year. This result expressed the timing of rejection relative to the progress of the clutch-initiation period as a percentage. For example, a burial that occurred on the 17th day of a 30-day clutch initiation period was given a percentage of 57% $[(17/30) \times 100]$.

3. Nests parasitized at the zero- (nest completed), one-, or two-egg stage were grouped as having a higher risk of parasitism, whereas nests parasitized later were grouped as lower risk of parasitism (Sealy 1995). We compared the frequency of higher-risk parasitism at nests that were buried or deserted.

4. We sorted data from all nests to extract records of nests that had been damaged but not completely destroyed. For comparison, we included in the analysis another group of nests at which clutch abandonment without damage was recorded. We compared the frequency of damage recorded at nests that had been buried or deserted. Damage included nests tilted so eggs could roll out, nests with loosened nest material, and water-logged nests. We compared rates of desertion of damaged nests, parasitized versus unparasitized, to determine whether desertion at damaged nests was related to brood parasitism. Data from unparasitized nests came from a representative sample studied in 1974, 1975, and 1976.

5. We categorized abandoned clutches as containing two, one or zero warbler eggs when abandoned (clutches reduced by half or more) or as containing three or more warbler eggs (clutches reduced by one egg or not at all). We assumed that reduction of a clutch of four or five eggs, the typical size of a Yellow Warbler clutch at Delta Marsh (Sealy 1992), to two or fewer host eggs resulted from depredation by a predator other than a cowbird. We compared the frequency of burials and desertions of nests whose clutches were reduced by half or more. We compared frequencies of desertions of clutch-reduced nests, parasitized versus unparasitized, to determine whether desertion of nests whose clutches were severely reduced was related to brood parasitism. Data from unparasitized nests came from a representative sample studied from 1974 to 1976.

STATISTICAL ANALYSES

We tested for differences in the average response time (prediction 1) and progression in the clutch-initiation period (prediction 2) between burial and desertion by using Wilcoxon two-sample tests in SAS (PROC NPAR1WAY; SAS Institute 1990), as the data were not normally distributed and the data used to test the first prediction had unequal variances. Because there was one degree of freedom for each test, we used chi-squared tests with continuity corrections to test for differences in the frequency of burial versus desertion of nests that were parasitized at the zero-, one-, or two-egg stage (prediction 3), of damaged nests (prediction 4), and of nests whose clutches were reduced to zero, one, or two host eggs (prediction 5). We did not use the same dataset to test each hypothesis, as information pertinent to each hypothesis was not available from every nest, so Bonferroni corrections were not required.

To determine whether the time (in days) between parasitism and nest desertion varied more than the time between parasitism and burial (prediction 1), we used Levene's test because our data were not normally distributed and this test is less sensitive to departures from normality than Barlett's test (Zar 1999). We report means ± SE. We used chi-squared tests with continuity corrections to compare the desertion rates of parasitized and unparasitized nests where the clutch was reduced and the nest was damaged. For all tests, we considered results of $P \leq 0.05$ significant.

RESULTS

We analyzed 132 naturally parasitized nests at which rejection was recorded. Eighty-nine (67%) rejections were by burial and 43 (33%) were by desertion. In each analysis, sample sizes differed (Table 1) because information for all five predictions was not available from every nest. Five to 10 days elapsed between the first day of nest construction and clutch initiation at nests built at new sites (average 7.29 ± 0.75 days, $n = 7$) versus 0 to 4 days for initiation of new clutches at nests that were buried (average 2.65 ± 0.19 days, $n = 40$). At some "buried" nests, only the cowbird egg was buried and the warbler's laying was uninterrupted, thus the warbler took zero days to initiate a "new" clutch.

Nests that were buried and those that were deserted did not differ significantly in progression within the clutch-initiation period or time between parasitism and response (Table 1). The variance of the response time, however, did differ significantly (burial: 1.29 days^2, 95% CI 0.93–1.93; desertion: 2.58 days^2, 95% CI 1.66–4.56; Levene's test, $F = 4.5$, $P = 0.04$). Buried and deserted nests differed significantly in damage to nests, clutch reduction, and number of eggs at the time of parasitism (Table 1). Frequencies of nest damage and clutch loss were less at nests in which eggs were buried (Table 1). Frequency of desertion at parasitized and unparasitized nests was similar for damaged nests (52.0% for parasitized [$n = 25$] versus 80.8% for unparasitized [$n = 26$], $\chi^2 = 3.54$, df = 1, $P = 0.06$) and for clutch-reduced nests (62.5% for parasitized [$n = 24$] versus 81.6% for unparasitized [$n = 38$], $\chi^2 = 1.89$, df = 1, $P = 0.17$). Burial also was more frequent when nests were parasitized when they contained zero, one, or two host eggs at the time of parasitism (Table 1).

DISCUSSION

Whether Yellow Warblers buried or deserted parasitized clutches did not differ significantly through the season, though desertion was more frequent later in the clutch-initiation period. We had predicted the opposite. New clutches are typically initiated sooner after burial, though desertion may be adaptive if the warblers renest. But as the breeding season wanes warblers generally accept parasitism, presumably because the time for renesting is diminishing (Clark and Robertson 1981, Burgham and Picman 1989). We predicted that if warblers rejected later in the season, they would bury rather than desert and renest at another site. Clark and Robertson (1981) suggested that Yellow Warblers that desert nests late in the season favor self-preservation and should not renest. We did not track individual warblers and thus could not determine whether this expectation was met.

BURIAL AND DESERTION AS ANTI-PARASITE DEFENSES

Warblers whose nests contained zero (nest complete but empty), one, or two eggs when parasitized tended to bury, but those whose nests contained three or more eggs were more likely to desert, if they responded with rejection at all. Consistent with our findings, Clark and Robertson (1981) reported that burial typically occurs when there are no eggs or one Yellow Warbler egg at the time of parasitism, but with a larger sample of parasitized nests, Sealy (1995) concluded burial occurs until the day the second warbler egg is laid. Clark and Robertson (1981) considered nest desertion an alternative rejection response, used when burial is not an option, as when the nest structure is not likely to support a superimposed nest. Burial usually progresses with fewer delays because the same nest site is used (Burgham and Picman 1989, Clark and Robertson 1981, Sealy 1995), though sacrificing a complete clutch is costly and is likely similar to the cost incurred by deserting

TABLE 1. Statistics of nests rejected by Yellow Warblers in response to natural cowbird parasitism, leading to burial or nest desertion.

	Burial (n)	Desertion (n)	Statistic	P
1. Average response time (days)	2.3 ± 0.1 (59)	2.5 ± 0.3 (32)	$z = 0.1$	0.91[a]
2. Average clutch-initiation progression (%)	27.7 ± 2.2 (74)	31.0 ± 3.0 (35)	$z = 1.2$	0.24[a]
3. Nests parasitized when they contained 0, 1, or 2 host eggs (%)	94 (48)	21 (19)	$\chi^2_1 = 33.0$	<0.001[b]
4. Nests damaged (%)	13 (61)	42 (31)	$\chi^2_1 = 8.1$	0.004[b]
5. Nests with clutches reduced to 0, 1, or 2 host eggs (%)	8 (53)	54 (28)	$\chi^2_1 = 19.1$	<0.001[b]

[a] Wilcoxon two-sample test.
[b] Continuity adjusted chi-squared test.

a nest (Clark and Robertson 1981). During incubation, Yellow Warblers seldom bury foreign objects in the nest (Sealy 1995, Guigueno and Sealy 2009). If nest desertion were solely an anti-parasite adaptation, it should be most frequent when the potential cost of parasitism to the host is greatest. Parasitism during incubation is less costly because cowbird eggs are less likely to hatch; however, cowbird eggs laid early in the warbler's laying are more likely to hatch before or at the same time as the hosts' (Clark and Robertson 1981, Sealy 1995). In the latter situation, host fledglings would have to compete with the larger cowbird.

Egg burial also may be more frequent early in laying because it increases the probability that the female can use at least some of her eggs already in development for the new clutch in the superimposed nest. In passerines, initiating a replacement after depredation usually takes 5 to 8 days because females must reabsorb their developing ova and their hormones must reinitiate laying of the second clutch (Johnson 2000, Winkler 2004). In the Yellow Warbler, these physiological changes likely occur after desertion of a parasitized clutch because at our study site it takes from 5 to 10 days for a clutch to be initiated at a new site. However, it takes from 0 to 4 days for a new clutch to be initiated over a buried parasitized clutch. Yellow Warblers that bury a parasitized clutch may be able to use eggs already developing, thus spending less energy than deserting a parasitized clutch and renesting require.

Time between parasitism and rejection was nearly the same for both types of clutch abandonment; however, time between parasitism and desertion varied more. Burial was initiated more consistently about 2 days after parasitism than was nest desertion. Yellow Warbler nests were inspected for 6 days after the cowbird egg was laid, and this criterion is a tradeoff between excluding rejections related to factors other than parasitism and including delayed rejections due to experimental parasitism; fewer than 1% of rejections were delayed by more than 5 days (Rothstein 1982). Therefore, rejection later is less likely to be related to parasitism than when it occurs the day after parasitism. Responses elicited by parasitism should also be recorded consistently sooner (i.e., within 2 days) after parasitism.

Nest desertion is an alternative method of rejection. Hosoi and Rothstein (2000) showed that the frequency of nest desertion is higher in nonforest host species, which have been exposed to cowbird parasitism longer than have forest species that seldom interact with adult cowbirds. This difference suggests that high frequencies of nest desertion evolved in response to cowbird parasitism (Hosoi and Rothstein 2000). Desertion may be a first step toward rejection, with ejection evolving in hosts that have learned to recognize their own eggs (Hosoi and Rothstein 2000), thus in the Yellow Warbler burial may be considered more advanced than desertion. Experienced individuals may bury their parasitized clutch, whereas less experienced individuals desert their nest (Langmore et al. 2009); individuals with little or no breeding experience should respond more variably and be less consistent in the timing of their decision to reject parasitism. Langmore et al. (2009) reported that experienced female Superb Fairy-Wrens (*Malurus cyaneus*) abandoned cuckoo chicks and accepted their own chicks more frequently than did inexperienced females. Sealy (1995) determined that second-year and after-second-year adult Yellow Warblers are equally likely to abandon parasitized clutches by burial or by desertion; however, age is not a good measure of experience (Nol and Smith 1987, Stokke et al. 2004). Some individuals may be parasitized again in the same year (McLaren and Sealy 2000; M. F. Guigueno and S. G. Sealy, unpublished data), whereas others may escape parasitism. Of 85 naturally parasitized nests studied by McLaren and Sealy (2000), eight received more than one parasitic egg; however, this frequency of multiple parasitism is lower than that of other hosts, such as the Song Sparrow (*Melospiza melodia*), on our field site (McLaren et al. 2003).

Burial not only requires less time and energy, our data suggest the likelihood of buried clutches being parasitized again is less than that of replacement nests. Five (6%) of 89 nests at which burial was recorded were reparasitized, and from 1974 to 1987 the frequency of parasitism of all nests varied annually from 14 to 31% (Sealy 1995). However, we cannot compare the frequency of parasitism of nests at which burial occurred with that of new nests built after desertion of a parasitized clutch because identities of renesting warblers were unknown. Burial may be more adaptive than desertion because it takes ~4 days longer (Clark and Robertson 1981) to initiate a new clutch after desertion than after burial and reproductive success of many species of songbirds decreases as the breeding season progresses (Perrins 1970, Verhulst et al. 1995, Mermoz and Reboreda 1998). Burial, in addition to eliminating costs related to parasitism, may be more adaptive than acceptance because "buried" nests are depredated less than "accepted" nests (McLaren and Sealy 2000). Burial seems to be an alternative, yet unique, rejection strategy of the Yellow Warbler because it is not known to eject cowbird eggs and its productivity is reduced by cowbird parasitism (Lorenzana and Sealy 1999). Burial may evolve in more species as they are parasitized, especially in small hosts that are physically unable to grasp-eject parasitic eggs.

DESERTION UNRELATED TO BROOD PARASITISM

Most damaged and a few undamaged nests were deserted. Clark and Robertson (1981) and Burgham and Picman (1989) suggested that desertion should be favored over burial when the nest is damaged because it is difficult to superimpose a new nest on a nest that now lacks a solid base. Damage may result from exposure to wind and rain; disturbance by a predator may elicit desertion even at unparasitized nests, as in the Blue-gray Gnatcatcher (*Polioptila caerulea*; Goguen and

Mathews 1996) and dabbling ducks (*Anas* spp.; Ackerman et al. 2003). Therefore, the Yellow Warbler's desertion of parasitized and damaged nests is likely not related to brood parasitism only, though in both cases (i.e., inclement weather and cowbird parasitism), renesting at a different site should be adaptive. Damaged parasitized nests are not likely deserted because of parasitism, as we found that the frequencies of desertion of damaged parasitized and damaged unparasitized nests are similar.

Clutches reduced at parasitized nests are rarely buried. In a series of clutch reductions by Sealy (1992), 79% (n = 14) of parasitized clutches reduced to a single cowbird egg were deserted, whereas parasitized clutches reduced to one warbler egg and one cowbird egg were deserted 31% (n = 13) of the time. No burials were recorded. In a study of Bell's Vireo (*Vireo bellii*), Kosciuch et al. (2006) reported that nearly all desertions were due to clutch reduction. Cowbirds remove one warbler egg from about one-third of nests parasitized at Delta Marsh; removal of half of the clutch or more likely would be the work of a predator (Sealy 1992). Desertion of severely reduced clutches is likely not related to parasitism, as frequencies of desertion of clutch-reduced parasitized and unparasitized nests are similar. Predictably, parasitized clutches reduced by predators are deserted (Hill and Sealy 1994), although desertion also may be influenced by pressure from brood parasitism (Hosoi and Rothstein 2000).

PROXIMATE VERSUS ULTIMATE CAUSES

The proximate causes alluded to above suggest ultimate selection pressures underly the observed behaviors (Fig. 1). In several passerines, reproductive success tends to decrease as the breeding season progresses (Perrins 1970, Verhulst et al. 1995, Mermoz and Reboreda 1998), and Fig. 1 assumes a shape similar to that provided by Verhulst et al. (1995) for the Great Tit (*Parus major*). If post-fledging survival were included, the decline would likely be even more dramatic (Verhulst et al. 1995), but the cost of acceptance also would likely be higher because of competition between host and cowbird fledglings (Rasmussen and Sealy 2006). Although the relationships and costs shown in Fig. 1 are approximations, Fig. 1 shows that desertion (and subsequent renesting) and burial are adaptive early in the season, but acceptance and burial are adaptive later, although burial later in the season is less advantageous over acceptance than it is early in the season. Furthermore, the costs indicated in Fig. 1 depend on the date a nest is parasitized: if early in laying, the cowbird is more likely to hatch and exact a higher cost, so the "acceptance" arrow should be longer relative to nests parasitized in incubation, and burial or desertion is more likely to be favored (prediction 3). Therefore, the interaction between seasonal effects and brood parasitism provide the ultimate selection pressures that underlie the proximate mechanisms for burial we present. For desertion, which is elicited by several other factors, the costs will reflect those factors as well: the "acceptance" arrow in

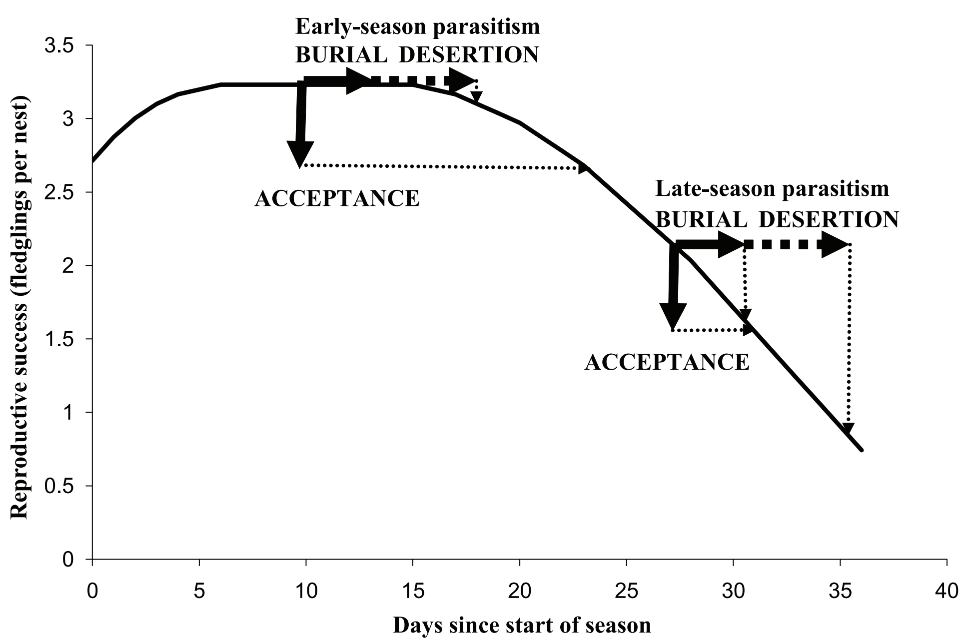

FIGURE 1. The fitness cost of burial, desertion, and acceptance throughout the Yellow Warbler's breeding season. The curve for reproductive success versus date is modified from Verhulst et al. (1995) to result in a mean reproductive success of 3.23 fledglings (Lorenzana and Sealy 1999), whereas the cost of acceptance (0.6 fledglings; Lorenzana and Sealy 1999), time for the initiation of a new clutch after burial (2.65 days, this study), and time for initiation of a new clutch at a new site (approximate time for desertion 7.29 days, this study) are based on the actual costs measured at Delta Marsh, Manitoba.

Fig. 1 would be replaced by other costs, such as the possibility of egg loss through nest damage (prediction 4) or more predation (prediction 5), if the warblers do not desert.

EVOLUTION OF BURIAL AND FUTURE RESEARCH

Yellow Warblers do not bury cowbird eggs only (Guigueno and Sealy 2009). Non-egg-shaped objects the same volume and mass as cowbird eggs are more likely to be buried at the pre-incubation stage when the cost of burial is low. Acceptance prevails during incubation when the female must sacrifice the entire clutch (Guigueno and Sealy 2009). Great Reed Warblers (*Acrocephalus hirundinacea*), which eject, bury, or desert nests containing cuckoo eggs, also bury disk-shaped objects (Moskát et al. 2003). A foreign object in the nest, whether a parasitic egg or an artificial non-egg-shaped object, seems to elicit burial, although in nature burial of objects other than eggs has rarely been recorded. Nest sanitation may be a pre-adaptation for egg rejection in these host species (Moskát et al. 2003, Guigueno and Sealy 2009). Future research will involve tracking the reproductive history of individual female Yellow Warblers over multiple breeding seasons to determine whether more experienced individuals are more likely to bury parasitized clutches and whether females that desert later in the season renest at different locations.

ACKNOWLEDGMENTS

We thank Roxanne J. Bisson and Cole M. Robson-Hyska for assistance in compiling the data and Gloria C. (Biermann) Pohjadak and J. Paul Goossen for use of their data. We thank Michael J. Kuehn and Brian D. Peer for their constructive comments on the manuscript. This work was funded by grants from the Natural Sciences and Engineering Research Council of Canada to SGS and a Natural Sciences and Engineering Research Council of Canada graduate scholarship to MFG.

LITERATURE CITED

Ackerman, J. T., J. M. Eadie, G. S. Yarris, D. L. Loughman, and M. R. McLandress. 2003. Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks. Animal Behaviour 66:871–883.

Armstrong, T., and R. J. Robertson. 1988. Parental investment based on clutch value: nest desertion in response to partial clutch loss in dabbling ducks. Animal Behaviour 36: 941–943.

Biermann, G. C. 1980. Parental care, growth rates and pre-fledgling condition of Yellow Warbler nestlings in different brood sizes. M.Sc. thesis, University of Manitoba, Winnipeg, MB.

Biermann, G. C., and S. G. Sealy. 1982. Parental feeding of nestling Yellow Warblers in relation to brood size and prey availability. Auk 99:332–341.

Briskie, J. V., and S. G. Sealy. 1990. Evolution of short incubation periods in the parasitic cowbirds, *Molothrus* spp. Auk 104:789–794.

Burgham, M. C. J., and J. Picman. 1989. Effect of Brown-headed Cowbirds on the evolution of Yellow Warbler anti-parasite strategies. Animal Behaviour 38:298–308.

Clark, K. L., and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. Wilson Journal of Ornithology 93:249–258.

Davies, N. B. 2000. Cuckoos, cowbirds and other cheats. T. & A. D. Poyser, London.

Goguen, C. B., and N. E. Mathews. 1996. Nest desertion by Blue-gray Gnatcatchers in association with Brown-headed Cowbird parasitism. Animal Behaviour 52:613–619.

Goossen, J. P. 1978. Breeding biology and reproductive success of the Yellow Warbler on the Delta Beach Ridge, Manitoba. M.Sc. thesis, University of Manitoba, Winnipeg, MB.

Goossen, J. P., and S. G. Sealy. 1982. Production of young in a dense nesting population of Yellow Warblers, *Dendroica petechia*, in Manitoba. Canadian Field-Naturalist 96:189–199.

Graham, D. S. 1988. Response of five host species to cowbird parasitism. Condor 90:588–591.

Guigueno, M. F., and S. G. Sealy. 2009. Nest sanitation plays a role in egg burial by Yellow Warblers. Ethology 115:247–256.

Hill, D. P., and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have Clay-coloured Sparrows evolved an anti-parasite defense? Animal Behaviour 48:1063–1070.

Hobson, K. A., and S. G. Sealy. 1989. Responses of Yellow Warblers to the threat of cowbird parasitism. Animal Behaviour 38:510–519.

Hosoi, S. A., and S. I. Rothstein. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. Animal Behaviour 59:823–840.

Johnson, A. L. 2000. Reproduction in the female, p. 569–596. *In* G. C. Whittow [ed.], Sturkie's avian physiology. Academic Press, San Diego.

Kosciuch, K. L., T. H. Parker, and B. K. Sandercock. 2006. Nest desertion by a cowbird host: an anti-parasite behaviour or a response to egg loss? Behavioral Ecology 17:917–924.

Langmore, N. E., A. Cockburn, A. F. Russell, and R. M. Kilner. 2009. Flexible cuckoo chick-rejection rules in the Superb Fairy-Wren. Behavioral Ecology 20:978–984.

Lorenzana, J. C., and S. G. Sealy. 1999. A meta-analysis of the impact of parasitism by the Brown-headed Cowbird on its hosts. Studies in Avian Biology 18:241–253.

MacKenzie, D. I. 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. Canadian Field-Naturalist 96:61–68.

McLaren, C. M., and S. G. Sealy. 2000. Are nest predation and brood parasitism correlated in Yellow Warblers? A test of the cowbird predation hypothesis. Auk 117:1056–1060.

McLaren, C. M., B. E. Woolfenden, H. L. Gibbs, and S. G. Sealy. 2003. Genetic and temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Song Sparrows (*Melospiza melodia*). Canadian Journal of Zoology 81: 281–286.

McMaster, D. G., D. L. H. Neudorf, S. G. Sealy, and T. E. Pitcher. 2004. A comparative analysis of laying times in passerine birds. Journal of Field Ornithology 75:113–122.

Mermoz, M. E., and J. C. Reboreda. 1998. Nesting success in Brown-and-yellow Marshbirds: effects of timing, nest site, and brood parasitism. Auk 115:871–878.

Mico, M. A. 1998. Yellow Warbler nests: structure, building materials and cowbird parasitism. M.Sc. thesis, University of Manitoba, Winnipeg, MB.

Moskát, C., T. Székely, T. Kisbenedek, Z. Karcza, and I. Bártol. 2003. The importance of nest cleaning in egg ejection behaviour of Great Reed Warblers *Acrocephalus arundinaceus.* Journal of Avian Biology 34:16–19.

Neudorf, D. L., and S. G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. Condor 96:162–169.

Nol, E., and J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. Journal of Animal Ecology 56:301–313.

PEER, B. D., AND S. G. SEALY. 2004. Correlates of egg rejection in hosts of the Brown-headed Cowbird. Condor 106:580–599.

PEER, B. D., S. I. ROTHSTEIN, M. J. KUEHN, AND R. C. FLEISCHER. 2005. Host defenses against cowbird (*Molothrus* spp.) parasitism: implication for cowbird management, p. 84–97. *In* C. P. Ortega, J. F. Chace, and B. D. Peer [EDS.]. Management of cowbirds and their hosts: balancing science, ethics, and mandates. Ornithological Monographs 57.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

RASMUSSEN, J. L. 2008. Limits of grasp-ejection in hosts of the parasitic Brown-headed Cowbird: implications for the evolutionary equilibrium and evolutionary lag hypotheses. M. Sc. thesis, University of Manitoba, Winnipeg, MB.

RASMUSSEN, J. L., AND S. G. SEALY. 2006. Hosts feeding only Brown-headed Cowbird fledglings: where are the host fledglings? Journal of Field Ornithology 77:269–279.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.

ROTHSTEIN, S. I. 1982. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejector species? Behavioral Ecology and Sociobiology 11:229–239.

ROWHER, S., AND C. D. SPAW. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evolutionary Ecology 2:27–36.

SAS Institute. 1990. SAS/STAT 6.0, user's guide, 4th ed. SAS Institute, Cary, NC.

SEALY, S. G. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor 94:40–54.

SEALY, S. G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. Animal Behaviour 49:877–889.

SEALY, S. G. 1996. Evolution of host defenses against brood parasitism: implications of puncture-ejection by a small passerine. Auk 113:346–355.

SEALY, S. G., AND J. C. LORENZANA. 1998. Yellow Warblers (*Dendroica petechia*) do not recognize their own eggs. Bird Behavior 12:57–66.

SEALY, S. G., D. L. NEUDORF, AND D. P. HILL. 1995. Rapid laying by Brown-headed Cowbirds *Molothrus ater* and other parasitic birds. Ibis 137:76–84.

SPAW, C. D., AND S. ROHWER. 1987. A comparative study of eggshell thickness in cowbirds and other passerines. Condor 89:307–318.

STOKKE, B. G., G. RUDOLFSEN, A. MOKSNES, AND E. RØSKAFT. 2004. Rejection of conspecific eggs in Chaffinches: the effect of age and clutch characteristics. Ethology 110:459–470.

VERHULST, S., J. H. VAN BALEN, AND J. M. TINBERGEN. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? Ecology 76:2392–2403.

WINKLER, D. W. 2004. Nests, eggs, and young: breeding biology of birds, p. 8.1–8.152. *In* S. Podulka, R. W. Rohrbaugh, Jr., and R. Bonney [EDS.], Handbook of bird biology. Cornell Lab of Ornithology, Ithaca, NY.

ZAR, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.