

**YELLOW WARBLER NESTS:
STRUCTURE, BUILDING MATERIALS AND COWBIRD PARASITISM**

BY

MICHELLE A. MICO

**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**

© Copyright by Michelle A. Mico, 1998



National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-32191-6

**THE UNIVERSITY OF MANITOBA
FACULTY OF GRADUATE STUDIES

COPYRIGHT PERMISSION PAGE**

**YELLOW WARBLER NESTS: STRUCTURE, BUILDING MATERIALS
AND COWBIRD PARASITISM**

BY

MICHELLE MICO

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

of

MASTER OF SCIENCE

Michelle Mico ©1998

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

**The author reserves other publication rights, and neither this thesis/practicum nor
extensive extracts from it may be printed or otherwise reproduced without the author's
written permission.**

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

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

Michelle A. Mico

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

Michelle A. Mico

The University of Manitoba requires the signatures of all persons using or photocopying this thesis. Please sign below, and give address and date.

ABSTRACT

Egg burial in Yellow Warblers is a behaviour that has been frequently observed and recorded in the ornithological literature. According to the literature, burial in North America is rarely observed in passerine species other than the Yellow Warbler. One hundred and twenty-five records of burial were found for 56 species, 89% of these records were in the context of cowbird parasitism. Most of these cases (93%) involved burial of cowbird egg(s) only. Due to the lack of host eggs being buried along with the cowbirds suggests that the majority of these burials is a result of premature egg laying by the female cowbird and the host simply buried the cowbird egg while finishing its nest.

To explain the high frequency of burial observed in Yellow Warblers, Rothstein (1975) suggested that Yellow Warblers build nests with similar lining and frames. Thus, female cowbirds may not be able to determine when the nest is finished and possibly parasitize the nest too soon. The prematurely laid egg would simply be covered over by lining as the Yellow Warbler completes its nest. A total of 113 Yellow Warbler nests were dissected and it was found that Yellow Warblers usually built nests with three distinct layers, although 24% of the time two-layered nests were also built. All three-layered nests consisted of a base, frame and liner. Nettles/hops, deer hair, fruits, grass, feathers and “other” materials were found in all three layers, however, the proportion of the materials differed significantly, resulting in a colour and textural difference between the layers. To test whether the layer below the buried egg is the same in colour and

material as the layer above, 27 Yellow Warbler nests were dissected. Most of the burial nests had six layers, three layers below the buried egg and three layers above.

Recognition of the layers, by materials and colour, reveal that each burial nest had two bases, two frames and two liners. Cononical Variates Analysis confirmed that the burial layer was a three-layered structure, similar to the original nest, consisting of a liner, frame and base. Thus burial is a building of the nest at the same nest site, the original nest is deserted, but not the nest site (as in typical nest desertion). There are two types of burials, true burials and embedded eggs. True burials are the type of burial observed most frequently in Yellow Warblers. Conversely, embedded eggs seem to explain most of the burial records in other species, although, it may also explain a few cases of burials in Yellow Warblers.

ACKNOWLEDGEMENTS

Thanks to Ron Duerkson, Barb Dyck, Kim Caldwell, Sharon Gill, Karim Haddad, Claire Herbert, Janice Lorenzana, Glen McMaster, Cori Schuster and Joanne Tuckwell who provided their assistance, support, ideas, comments and friendship. I also thank the staff of the University of Manitoba Field Station (Delta Marsh) for providing support, accommodation, weather data and chocolate chip cookies.

Challenging questions and statistical advice from Dr. N. Kenkel was invaluable and greatly appreciated. I would like to thank Dr J. Gee for his ideas and suggestions. Thanks are extended to Dr. P.N. Hébert who kindly joined the committee late in my tenure and provided invaluable advice and suggestions. A round of applause to Dr. D. Gillies for his knowledge, humour and use of computer equipment. A special thanks to S.A. Gill, J. Lorenzana, D.G. McMaster for providing suggestions that improved the quality of the thesis. To my supervisor, Dr. S.G. Sealy, I wish to thank him for providing the opportunity to study this interesting topic and for his advice and guidance throughout.

I can not express enough gratitude towards my family (Mom, Dad, Kathleen and Grandma) who have supported me throughout my whole life and helped me immensely to get through my degrees. Finally, kudos to Brent Horton for introducing me to that word (as well as for personal support and well spent holiday time).

This research was supported by a University of Manitoba Students Union Bursary to me and a Natural Sciences and Engineering Research Council research grant to Dr. S.G. Sealy.

TABLE OF CONTENTS

	page
ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	v
TABLE OF CONTENTS.....	vi
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
GENERAL INTRODUCTION.....	1
Cowbird Parasitism.....	1
Nest Building by Yellow Warblers.....	4
Study Area.....	5
 CHAPTER 1.....	 7
EGG BURIAL IN PASSERINE BIRDS OF NORTH AMERICA:	
A LITERATURE REVIEW.....	7
INTRODUCTION.....	7
TREATMENT OF RECORDS.....	9
RESULTS.....	11
Burial in the Context of Cowbird Parasitism.....	11
Burial in the Absence of Cowbird Parasitism.....	11
DISCUSSION.....	22
Frequency of Burial.....	22
Burial in the Context of Cowbird Parasitism.....	22
Burial in the Absence of Cowbird Parasitism.....	27
 CHAPTER 2.....	 28
STRUCTURE OF YELLOW WARBLER NESTS.....	28
INTRODUCTION.....	28
METHODS.....	32
Field Work.....	32
Nest Dissections.....	32
Statistical Analysis.....	40
T^2 Statistic.....	40
Canonical Variate Analysis.....	41
Students <i>t</i> -tests.....	42
RESULTS.....	43
Yearly Differences:.....	43
Nest Structure: Two- versus Three-layered Nests.....	43
Three-layered Nests.....	46
Burial Nests.....	52
DISCUSSION.....	60
Nest Structure: Two- versus Three-layered Nests.....	60

Three-layered and Burial Nests.....	61
SUMMARY.....	69
LITERATURE CITED.....	71
APPENDIX 1. Daily mean temperature and total precipitation for the 23-year mean (1967-1990), 1994, 1995 and 1996; from Environment Canada 1993). Weather data from 1994 was included because the majority of the plant material used to build 1995 nests grew in 1994.....	81
APPENDIX 2. Proportion of nesting materials found in the 1995 (n = 51) and 1996 (n = 36) three-layered Yellow Warbler nests.....	82
APPENDIX 3. Proportion of nesting materials found in the 1995 (n = 14) and 1996 (n = 12) two-layered Yellow Warbler nests.....	83
APPENDIX 4. Proportion of nesting materials found in the 27 Yellow Warbler burial nests.....	84
APPENDIX 5. Results and Discussion of yearly differences between nests built in 1995 and 1996.....	85

LIST OF TABLES

	page
TABLE 1. Materials used by Yellow Warblers in nest construction.....	6
TABLE 2. List of species that have been recorded burying in the context of cowbird parasitism.....	12
TABLE 3. List of species that have been recorded burying in the absence of cowbird parasitism.....	20
TABLE 4. Canonical Variate Analysis: eigenvalue (E.V.), canonical coorelation (C.C) and Chi-square values of the first two axes for 51 three-layered Yellow Warbler nests collected in 1995 with six variables (nest groupings) and three groups (nest layers).....	49
TABLE 5. Canonical Variate Analysis: eigenvalue (E.V.), canonical coorelation (C.C.) and Chi-square values of the first two axes for 36 three-layered Yellow Warbler nests collected in 1996 with six variables (nest groupings) and three groups (nest layers).....	50
TABLE 6. Mass and size of three-layered 1995 nests (n=51) (see Figure 4 for definition of measurements).....	53
TABLE 7. Features of the 27 burial nests. Sample size are in parentheses.....	54
TABLE 8. Mean (\pm SD) of the mass (g) and size of 27 Yellow Warbler burial nests with six layers. Sample size in parenthesis.....	56
TABLE 9. Canonical Variate Analysis: eigenvalue (E.V.), canonical coorelation (C.C.) and Chi-square values of the first two axes for 27 burial Yellow Warbler with six variables (nest groupings) and six groups (nest layers).....	58

LIST OF FIGURES

	page
FIGURE 1. Photograph of one-half of a Yellow Warbler nest showing three layers (see Figure 4A for the separation of the layers).....	33
FIGURE 2. Photograph of one-half of a Yellow Warbler nest showing two layers (see Figure 4B for the separation of the layers).....	34
FIGURE 3. Photograph of a buried cowbird egg between the original and top nest (see Figure 5 for separation of layers).....	35
FIGURE 4. Line drawing indicating the layers of a three-layered nest from Figure 1 (A) and the two-layered nest from Figure 2 (B).....	36
FIGURE 5. Line drawing of a Yellow Warbler burial nest showing the buried cowbird egg (CB egg) and the separation of the layers (from Figure 3).....	38
FIGURE 6. Dimensions of a Yellow Warbler nest.....	39
FIGURE 7. Comparison of the proportion of nesting materials in 1995 (A) between three- (n=51) and two-layered (n=14) nests and in 1996 (B) between three- (n=36) and two-layered (n=12) nests. Note that the left and right axes are of different scale. Boxplot represents median, 25 th and 75 th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*)......	44
FIGURE 8. Comparison of nest size in 1995 (A) between three- (n=51) and two-layered (n=14) nests and in 1996 (B) between three- (n=36) and two-layered (n=12) nests. See Figure 7 for definition of measurements. Boxplot represents median, 25 th and 75 th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*)......	45
FIGURE 9. Comparison of nest mass in two- (n=14) and three-layered (n=51) nests built in 1995 and two- (n=12) and three-layered (n=36) nests built in 1996. Note that nest mass is based on one-half nests. Boxplot represents median, 25 th and 75 th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*)......	47

FIGURE 10. Canonical Variate Analysis of 1995 (A; n=51) and 1996 (B; n=36) three-layered Yellow Warbler nests displaying the separation of the nest layers (base, frame and liner) attributable to the six different nesting materials (represented by arrows). Circles represent 95% confidence intervals around the mean of each layer. Sample point symbols represent the liner (o), frame (*) and base (•).....48

FIGURE 11. Colour values (Smithe 1974) for each layer of the 87 three-layered Yellow Warbler Nests (1995 and 1996 data combined).....51

FIGURE 12. Canonical Variate Analysis of 27 Yellow Warbler burial nests exhibiting the separation of the six nest layers attributable to the six nesting materials (represented by arrows). Circles represent 95% confidence intervals around the mean of each layer. Sample point symbols represent the liner (o), frame (*), base (^), top-liner (+), top frame (-) and top base (•).....57

FIGURE 13. Colour values (Smithe 1974) for the six layers of the 27 Yellow Warbler burial nests.....59

FIGURE 14. Comparison of the proportion of nesting materials in nests built in 1995 (n=65) and 1996 (n=48). Note that the left and right axes are of different scale. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*)86

FIGURE 15. Comparison of nest size (A) and mass (B) between nests collected in 1995 (n = 65) and (n = 48). Note that nest mass is based on one-half nest. See Figure 6 for explanation of the measurements. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*)..... 87

GENERAL INTRODUCTION

Cowbird Parasitism

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite that parasitizes the nests of many species, including the Yellow Warbler (*Dendroica petechia*) (Bent 1953, Friedmann 1963). Cowbird parasitism usually reduces host nesting success by one or more fledgling per nest (Weatherhead 1989, Payne 1977). Nesting success in parasitized nests is reduced by the parasitic young outcompeting the smaller host chicks in addition to the removal of one or more host eggs by the female cowbird (Rothstein 1990). Due to the high costs associated with cowbird parasitism, there is assumed to be intense selection pressure on cowbird hosts to reduce or avoid parasitism. This selection pressure has led to the evolution of several host strategies to reduce the costs associated with cowbird parasitism.

One host strategy is the removal of the parasitic egg. At least 15 host species are known to reject cowbird eggs, thus avoiding the costs of raising a parasitic nestling (Rothstein 1975). Known as rejectors (Rothstein 1975), these species physically remove the cowbird egg from their nest either by grasping it with their bill or by puncturing it and lifting it from the nest.

Species that do not reject the cowbird egg through physical removal from the nest are termed acceptors (Rothstein 1975). Although some acceptor species have been observed rejecting nests containing cowbird eggs, via nest desertion and egg burial, it is not known whether this is a response to cowbird parasitism or nest disturbance (Hill and Sealy 1994). Although the Yellow Warbler is considered to be an acceptor species (Rothstein 1975), they do reject (via burial or nest desertion) at a rate higher

(approximately 50%) than most acceptor species (Rothstein 1975, Clark and Robertson 1981, Sealy 1995).

When parasitized, Yellow Warblers display one of three behaviours. First, they may accept the parasitic egg. Acceptance is more likely (66% of the time) when the cowbird parasitizes the nest after the second host egg is laid (laying day two or LD2) or later in the breeding season (Clark and Robertson 1981, Burgham and Picman 1989, Sealy 1995). Alternately, Yellow Warblers may reject the parasitized nest by either deserting it and building elsewhere, or by burying the nest contents. Nest desertion occurs at 13% of all parasitized nests irrespective of the timing of parasitism during laying (Sealy 1995). Egg burial, unlike nest desertion, occurs up to 48% of parasitized nests (Clark and Robertson 1981, Sealy 1995). Burial is usually defined as the female Yellow Warbler building a new nest floor over the parasitic egg(s) as well as any of her own eggs present at the time (Clark and Robertson 1981, Sealy 1995). Unlike egg acceptance, burial is most frequently observed when the nest is parasitized with a small number of host eggs (prior to LD2) and/or early in the breeding season (Clark and Robertson 1981, Burgham and Picman 1989, Sealy 1995).

Egg burial is believed to be a less costly than nest desertion because 1) no time and effort are spent finding a new nest site; 2) the frequency of re-parasitism is lower at the original site than at new sites (9% and 21%, respectively, Sealy 1995); and 3) the new clutch is initiated 3-6 days earlier than in nest desertion (Clark and Robertson 1981). Therefore, the breeding pair continues to be synchronous with the nesting community. Nests out of synchrony with the rest of the Yellow Warbler breeding population may be exposed to a higher depredation rate (Clark and Robertson 1981). Despite the benefits

of burial, desertion may be favoured if the nest becomes unstable with additional layers (Clark and Robertson 1981) or if the nest is damaged (Burgham and Picman 1989).

At Delta Marsh, Manitoba, it has been assumed that Yellow Warblers have been parasitized by the Brown-headed Cowbird for hundreds of years (Thompson 1891, Mayfield 1965, Briskie *et al.* 1992). Over the last 20 years, an average of 21% of Yellow Warbler nests were parasitized (Sealy 1995). Thus, selection should consistently act on Yellow Warblers to avoid or minimize the effects of parasitism.

Burial is known to effectively eliminates the threat of the parasitic egg and reduces the risk of re-parasitism, yet it is believed to be a behaviour unique to Yellow Warblers. To determine whether egg burial is unique to Yellow Warblers, the first chapter is a literature review that summarizes the published records of burial by North American passerine birds and the conditions under which burial was observed, that is, whether burial occurred within the context of cowbird parasitism.

Why only Yellow Warblers frequently bury cowbird eggs is not understood. Rothstein (1975) speculated that Yellow Warblers build homogeneous nests, that is, nest liner and frame are indistinguishable from one another to fool the cowbird into laying early in an unfinished nest. Subsequently, Yellow Warblers simply continue building, embedding the cowbird egg within the upper most portion of the nest. In the second chapter, I test this hypothesis two ways by examining the internal nest structure (layer colour and texture) of Yellow Warbler nests. First, non-burial Yellow Warbler nests were dissected to determine if little structure existed in the nest (i.e., nest frame and liner were identical). Then burial nests were then dissected to determine if the burial layer was the same in materials and colour than the layer prior to burial.

Nest Building by Yellow Warblers

The preferred breeding habitat of Yellow Warblers is dense willows (*Salix* spp.) near open water (Harrison 1979, Mackenzie *et al.* 1982). Males arrive first at the breeding site and set up territories that can be as small as 0.16 hectares (Harrison 1979). The females arrive after the males have established territories and proceed to choose a suitable mate or territory. Once a mate/territory has been chosen, nest building is initiated by the female, although many factors may delay its onset. For example, high temperatures stimulate nest building, whereas low temperatures inhibit it (Nice 1937). The delayed development of vegetation may also influence the beginning of nest building (Pettingill 1985).

The female Yellow Warbler builds the nest in an upright fork of a bush, sapling or tree. Although the nest is usually one to three meters from the ground, nests have been observed as low as 0.25 m and as high as 14 m (Chapman 1968, Briskie *et al.* 1990). The Yellow Warbler nest is a strong, compact, symmetrical, well-woven cup, and is mainly supported from below with its rims standing firmly upright (Chapman 1968, Pettingill 1985). Nest building takes approximately four days (Chapman 1968, Harrison 1979), but this varies depending on the time of building in the breeding season, i.e., longer to build early in the season and shorter later in the season (Sealy pers. comm.). Table 1 summarizes the common nesting materials found in Yellow Warbler nests. Materials used for nest building are usually gathered from the vicinity of the nest, although suitable materials used to line may be sought from great distances (Collias and Collias 1984, Pettingill 1985).

Table 1. Materials used by Yellow Warblers in nest construction.

Materials Used	Reference
Plant fibre	Childs 1905, Schrantz 1943, Chapman 1968, Strauss 1993
Fine grasses	Schrantz 1943, Chapman 1968, Strauss 1993
Plant down and pappus (aspen, willows, cattails, cottonwood, thimbleweed)	Childs 1905, Schrantz 1943, Nickell 1965, Chapman 1968, Strauss 1993
Animal hair (sheep, cattle, horses, dogs, deer)	Child 1905, Schrantz 1943, Nickell 1965, Chapman 1968
Feathers	Nickell 1965, Chapman 1968
Flower inflorescence	Nickell 1965
Fern fronds (fiddlehead stage)	Childs 1905, Nickell 1965
Man-made materials (waste from cleaning steam engines, paper, twine, thread, cotton)	Childs 1905, Nickell 1965
Insect material (webs, spider cocoons)	Nickell 1965

STUDY AREA

The study was conducted on the properties of the University of Manitoba Field Station (Delta Marsh), Portage Country Club, and along the south ridge within the village of Delta (50°11 N, 98°19 W). The study site is located on a forested dune-ridge (average 80 m wide, MacKenzie 1982) that separates Lake Manitoba to the north and Delta Marsh to the south. The Delta Marsh ridge lies in the Aspen-Oak Section of the Boreal Forest Region (Rowe 1972).

The summers (June to September) are warm (23-year mean temperature around 20°C; Environment Canada 1993) with increased precipitation in June and July (total precipitation averages around 78 mm per month) (see Appendix 1).

CHAPTER 1

EGG BURIAL IN PASSERINE BIRDS OF NORTH AMERICA: A LITERATURE REVIEW

INTRODUCTION

The Yellow Warbler is well known among ornithologists for burying eggs laid by the parasitic Brown-headed Cowbird (Friedmann 1929, 1963; Rothstein 1975; Sealy 1995). Burial is a form of nest desertion behaviour in which the nest owner adds additional material to cover eggs in the nest. In Yellow Warblers, the frequency of burial behaviour has been reported at 49% of parasitized nests in Ontario (Clark and Robertson 1981) and 36% in Manitoba (Sealy 1995). Although many other passerine birds are parasitized by the Brown-headed Cowbird (Friedmann 1929, 1963), burial has been recorded in these other species only rarely, with anecdotal records scattered throughout the ornithological literature.

Due to the high selection pressure on Yellow Warblers to reduce the costs of parasitism by the Brown-headed Cowbird, egg burial is believed to be an anti-parasite strategy (Friedmann 1929, Schrantz 1943, Clark and Robertson 1981, Burgham and Picman 1989). Burial is been believed to be an effective adaptation because both burial nests (nests that have the parasitic egg covered) and unparasitized nests fledge a comparable number of young (Clark and Robertson 1981).

However, interpreting burial as an anti-parasite adaptation may not be warranted. Some evidence suggests that burial may not be a response to cowbird parasitism. For example, burial has been reported in the absence of parasitism. Sealy (1995) reported six instances out of about 1800 nests of Yellow Warblers burying their own eggs in apparently unparasitized nests. Also, burial has not been elicited experimentally at the same level as in nature. Even the interaction of adult Yellow Warblers with a model female Brown-headed Cowbird at the nest followed by the addition of a cowbird egg generally does not elicit burial (Sealy 1995). Finally, Rothstein (1975) noted that unlike egg ejection, egg burial is a rejection of the whole nest. This indicates that other influences may have selected for the behaviour, such as weather and visits to the nest by predators. Although burial reduces the cost of parasitism, it may simply be a generalized behaviour induced by a variety of influences (Rothstein 1975) rather than a specialized anti-parasite behaviour.

Egg burial has been recorded, albeit infrequently and generally anecdotally, in many species other than the Yellow Warbler, but these records have never been compiled. In this chapter, I collate records of burial in other North American passerine species to determine whether the belief that egg burial behaviour is unique to Yellow Warblers is warranted.

TREATMENT OF RECORDS

Records of burial were obtained only from the literature. The search was restricted to North American passerine species, including actual and potential hosts of the Brown-headed Cowbird listed by Friedmann (1963), Freidmann *et al.* (1977), and Friedmann and Kiff (1985).

Many terms have been ascribed to the burial of eggs. For example “embedded” (Coues 1878), “covering over” (Parshall 1884), “double nest” (Bendire 1892), “re-lining” (Greene 1892), “flooring-over” (Herrick 1910), “false bottom” (Bailey 1925), “covered by new floor” (Friedmann 1929), and others have been used. Because of this variability, the term burial will be used here exclusively to describe the condition whereby the individual(s) that constructed the original nest adds new materials to partially or fully cover the nest and any eggs within. The following criteria were used to define burial: 1) The partial covering of the nest contents with nesting materials that leaves part of the buried egg exposed were considered burials. Some authors mentioned that the nest must have been incomplete when the eggs were laid, hence, the builder simply finished the nest, embedding the eggs within the lining. These records were included because it was impossible to differentiate between partially and fully covered eggs in many of the records. Nevertheless, a partially covered egg meets the same fate as a fully covered egg, that is, it would not be properly incubated. 2) Ideally, all records required the builder of the nest also to be the one who buries its contents. This eliminates records of species building over active or old nests of other individuals, and infanticide, such as in the Purple Martin (*Progne subis*), in which a male buried a deceased mate’s clutch so that another female could initiate a new clutch (Brown 1983). Because most of the records

did not involve banded individuals, it is assumed that the builder carried out the burial.

3) The time between building the nest to covering the egg(s) is within the same breeding season and, ideally, if the information is adequate, within the same breeding attempt.

Thus, records of old nests used as a base for a new nest for a second clutch within the same breeding season (i.e., double brooding) were not considered. The latter may appear to be burials, especially if not all the eggs hatched in the first breeding attempt, and then were buried under a second nest. However, these nests could usually be distinguished by the presence of egg shells or a dead chick. 4) All records of burial considered required the covering over of an egg with nesting material. The term “double nests” was commonly used in the literature to describe nests with a buried egg(s), however, on occasion, it also referred to nests in which no eggs were buried (i.e., one nest on top of another or two nests built side by side with a shared rim). The former were easily distinguished from egg burials due to their description (or picture) and, hence, were excluded from this review.

Records of burials were separated into whether or not burial occurred in the context of cowbird parasitism. Burial in the context of cowbird parasitism required a Brown-headed Cowbird egg to be found within the nest (buried or not). Burials that occurred in the apparent absence of cowbird parasitism involved the burial of an egg(s) of a species other than the Brown-headed Cowbird. Order of species and nomenclature follow the American Ornithologists' Union (1983), and supplements.

RESULTS

Burial in the Context of Cowbird Parasitism

Egg burial in the context of cowbird parasitism was recorded in 45 species from seven passerine families (Table 2). The Bell's Vireo had the highest number of records (10 records); the Alder Flycatcher, Eastern Phoebe, and American Goldfinch had seven records each. The remaining 41 species had five or fewer records (Table 2).

Most burials (98% of 111 records) were of only Brown-headed Cowbird eggs buried within the nest. Eighteen of these (16%) included the burial of more than one egg (Table 2). These records included: 1) nests that had more than one cowbird egg buried but no host eggs (six records); 2) nests with host egg(s) buried along with a cowbird egg(s) (seven records); 3) one record with three host eggs buried with one cowbird egg found in the upper nest; 4) nests that were covered over twice (double burial) in which two of these records involved host egg(s) buried along with the cowbird(s) (three records); 4) one nest was covered over three times (triple burial), burying single cowbird eggs in each nest cup. In only two of the 111 records, burial involved the covering of host egg(s) only. However in each case, a cowbird egg was found in the upper nest (Burtch 1898, Ashworth 1930).

Egg Burial in the Absence of Cowbird Parasitism.

Burials that occur in the absence of cowbird parasitism have been recorded four times less frequently than burials that occur in the context of cowbird parasitism. In the absence of cowbird parasitism, there were 24 records involving 20 species from seven

TABLE 2. List of species that have been recorded burying in the context of cowbird parasitism.

Species	No. of records	Year	Location	Nest Contents	Source
Eastern Wood-Pewee (<i>Contopus virens</i>)	1	1969	New York	3H,2C/1C ^a	Kedney (1869)
	1	prior 1892	Illinois	3H/1C	Bendire (1892)
Acadian Flycatcher (<i>Empidonax virescens</i>)	1	prior 1894	Illinois	na ^b /1C	Loucks (1894)
	1	1922	Kansas	3H/1C	Linsdale (1928)
	2	prior 1961	Michigan	na/1C	Walkinshaw (1961)
	1	prior 1898	na	na/1C	Anderson (1898)
Alder Flycatcher (<i>E. alnorum</i>)	1	prior 1894	Iowa	na/1C	Savage (1894)
	1	1951	Ohio	3H/1C, 1H	Berger and Parmelee (1952)
	1	prior 1961	Michigan	na/1C	Walkinshaw (1961)
	1	1947	Illinois	3H/1H/1C	Friedmann (1963)
	1	1958	Michigan	na/1C, 1H	Berger (1967)
	1	1963-67	Nebraska	3H, 1C/1C	Holcomb (1972)
	1	1963-67	Nebraska	na/1C	Holcomb (1972)

TABLE 2 continued

Willow Flycatcher (<i>E. traillii</i>)	1	1982-87	Arizona	naH, 1C/1C, 1H	Brown (1988)
	2	1985-86	Colorado	na/1C	Sedgewick and Knopf (1988)
Western Flycatcher (<i>E. difficillii</i>)	2	prior 1887	na	na/1C	Davison (1887)
	2	prior 1892	na	na/1C	Bendire (1892)
Eastern Phoebe (<i>Sayornis phoebe</i>)	1	1888	New York	na/2C, 1H	Burtch (1898)
	1	1888	New York	1H, 1C/3H	Burtch (1898)
	1	prior 1929	na	2H,1C/1C	Friedmann (1929)
	1	1957	Quebec	na/1C	Terrill (1961)
	1	prior 1961	Quebec	na/2C	Terrill (1961)
	1	prior 1975	na	na/1C	Rothstein (1975)
	1	1970	Kansas	na/1C	Rothstein (1986)
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	1	1878	Montana	2H/1C	Coues (1878)
Common Bushy-tit (<i>Psaltriparus minimus</i>)	1	1926	California	2H/1C	Bradford (1928)
	1	1926	California	na/1C, 2H	Bradford (1928)
	1	1929	California	6H, 1C/1H	Ashworth (1930)

TABLE 2 continued

Blue-grey Gnatcatcher (<i>Poliopitila caerulea</i>)	1	1886	Michigan	na/1C	Spicker (1887)
	1	prior 1963	na	na/1C	Friedmann (1963)
Hermit Thrush (<i>Catharus guttatus</i>)	1	1952	Quebec	2C,1H/1C	Terrill (1961)
Wood Thrush (<i>Hylocichla mustelina</i>)	1	na	na	na/1C	Weaver (1949)
Gray Catbird (<i>Dumetella carolinensis</i>)	1	prior 1958	Michigan	na/1C	Detroit Audobon Society (1953)
	4	prior 1958	Michigan	na/1C	Nickell (1958)
Brown Thrasher (<i>Toxostoma rufum</i>)	1	prior 1965	Louisiana	na/1C	Taylor & Goertz (1965)
White-eyed Vireo (<i>Vireo griseus</i>)	1	na	na	na/1C	Hopp, Kirby and Boone (1995)
Bell's Vireo (<i>V. bellii</i>)	1	1926	Arizona	na/1C	Morse (1927)
	1	prior 1929	na	na/2C	Nice (1929)
	1	1939	Illinois	3H/1C	Pitelka & Koestner (1942)
	3	1939	Texas	na/1C	Nyc (1940)
	1	1951	Indiana	1C/1C	Mumford (1952)
	1	1960	Kansas	na/1C	Barlow (1962)
	1	1980	Arizona	na/1C	Clark (1988)

TABLE 2 continued

1	prior 1993	na	na/1C	Brown (1993)
Solitary Vireo (<i>V. solitarius</i>)				
1	1890	Massachusetts	4H,1C/1C	Greene (1892)
1	1912	New York	4H,2C/1C	Allen (1913)
1	prior 1929	na	3H,2C/1C	Friedmann (1929)
1	1909	West Virginia	na/1C	Dickey (1941)
Yellow-throated Vireo (<i>V. flavifrons</i>)				
1	1898	na	na/1C	Jacobs (1903)
1	prior 1963	na	na/1C	Friedmann (1963)
Warbling Vireo (<i>V. gilvius</i>)				
1	1915	na	na/1C	Schlegel (1916)
Red-eyed Vireo (<i>V. olivaceus</i>)				
1	1955-1957	Michigan	na/1C	Southern (1958)
1	prior 1963	na	na/1C	Friedmann (1963)
Northern Parula (<i>Parula americana</i>)				
1	1947	Kansas	3H/1C, 1H	Schwilling (1951)
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)				
1	prior 1911	New York	3H/1C	Mercer (1911)
2	prior 1913	Connecticut	4H/1C	Sage & Bishop (1913)
1	1950	Quebec	1H/1C	Terrill (1961)
1	prior 1970	na	na/1C	Tate (1970)

TABLE 2 continued

Magnolia Warbler (<i>D. magna</i>)	1	1942	Quebec	na/1C	Terrill (1961)
Yellow-rumped Warbler (<i>D. coronata</i>)	3	prior 1953	Ontario	na/1C	Bent (1953)
	1	prior 1953	Ontario	1H,1C/1C	Bent (1953)
Black-throated Green Warbler (<i>D. virens</i>)	1	1907	New York	4H/1C	Burtch (1910)
Kirtland's Warbler (<i>D. kirtlandii</i>)	2	prior 1960	Michigan	na/1C	Mayfield (1960)
	1	1971	Michigan	na/1C	Walkinshaw (1983)
Prairie Warbler (<i>D. discolor</i>)	1		Florida	na/1C	Bailey (1925)
	3	1952-1965	Indiana	na/1C	Nolan (1978)
American Redstart (<i>Setophaga ruticilla</i>)	1	prior 1953	na	na/1C	Bent (1953)
Prothonotary Warbler (<i>Protonotaria citrea</i>)	1	prior 1894	Illinois	na/1C	Loucks (1894)
Louisiana Waterthrush (<i>Seiurus motacilla</i>)	1	1989	Illinois	na/1C	Robinson (1995)
Kentucky Warbler (<i>Oporornis formosus</i>)	1	prior 1963	na	na/1C	Friedmann (1963)
Common Yellowthroat (<i>Geothlypis trichas</i>)	1	prior 1903	na	na/1C/1C	Lippencoth (1903)
Scarlet Tanager (<i>Piranga olivacea</i>)	1	prior 1884	Iowa	3H/1C	Keyes (1884)
	1	prior 1884	Iowa	na/1C	Keyes (1884)

TABLE 2 continued

Northern Cardinal (<i>Cardinalis cardinalis</i>)	1	prior 1929	na	na/2C	Friedmann (1929)
Blue Grosbeak (<i>Guiraca caerulea</i>)	1	prior 1992	na	1/1C	Manry (1992)
Indigo Bunting (<i>Passerina cyanea</i>)	1	prior 1929	na	na/1C	Friedmann (1929)
Dickcissel (<i>Spiza americana</i>)	1	1983	Iowa	3H,1C/1H/1H,3C	Lowther (1983)
Clay-colored Sparrow (<i>Spizella pallida</i>)	1	prior 1929	na	na/1C	Friedmann (1929)
	1	1960	Manitoba	na/1C	Lane (<i>in Bent</i> 1968)
Song Sparrow (<i>Melospiza melodia</i>)	1	1915	na	na/1C	Schlegel (1916)
	1	prior 1929	na	na/1C	Friedmann (1929)
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	1	1968	New York	3H,2C/1C	Kedney (1869)
	1	prior 1884	Maine	3H/2C	W. (1884)
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	1	prior 1899	Nebraska	4H/1C	Wolcott (1899)
Eastern Meadowlark (<i>Sturnella magna</i>)	1	prior 1892	na	na/1C	Bendire (1892)
Western Meadowlark (<i>S. neglecta</i>)	1	prior 1888	Iowa	1H/1C	Akers (1888)
Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)	1	1968	Saskatchewan	na/1C,1H	Paton (1968)

TABLE 2 continued

Baltimore Oriole (<i>Icterus galbula</i>)	1	1883	New York	3H,3C/3C	Parshall (1884)
	1	1985	Manitoba	na/1C	Hobson & Sealy (1987)
American Goldfinch (<i>Carduelis tristis</i>)	1	prior 1867	New England	na/1C	Samuals (1867)
	1	prior 1887	New York	na/1C	Davison (1887)
	1	prior 1891	Nebraska	4H/1C	A. (1891)
	1	1958	Michigan	na/2C	Berger (1960)
	2	1947	Michigan	3H/1C	Berger (1948)
	1	1947	Michigan	4H/1C/1C/1C	Berger (1948)

^a3H,2C/1C = One cowbird egg buried within nest and three host eggs along with two cowbird eggs present in upper nest (not buried).

^bna = Data not available

passerine families (Table 3). Most of the records (88%) are conspecific burials in which the same species' egg was buried. The remaining three records were burials of an egg(s) of another species (Western Flycatcher burying three Black Phoebe eggs, Eastern Phoebe burying an American Robin egg, and Savannah Sparrow burying a Grasshopper Sparrow egg, Table 3). Most species (85%) had one record of burial each. The Eastern Bluebird, Western Flycatcher, and Least Flycatcher were the only species that had more than one record (3 records, 2 and 2, respectively). Nine species have been recorded burying both in the presence and absence of cowbird parasitism (Alder Flycatcher, Western Flycatcher, Common Bushtit, Brown Thrasher, Prothonotary Warbler, Indigo Bunting, Red-winged Blackbird, Western Meadowlark, and Baltimore Oriole). Only two records involving egg burial are questionable because the eggs were not laid in the nest; the Seaside Sparrow (Howell 1928) and Bobolink (Pelton 1912) laid eggs in the dirt and then built nests on top.

TABLE 3. List of species that have been recorded burying eggs in the absence of cowbird parasitism.

Species	Year	Location	Nest Contents	Source
Alder flycatcher	1891	Oregon	4/4 ^a	Bendire (1892)
Western Flycatcher	1937	California	3/3BP ^b	Stoner (1938)
	prior 1887	na ^c	na/1AR ^d	Davison (1887)
Least Flycatcher (<i>Empidonax minimus</i>)	1889	Michigan	na/4	Hanaford (1890)
	1984	Manitoba	2/4	Briskie & Sealy (1988)
American Crow (<i>Corvus brachyrhynchos</i>)	prior 1926	Wisconsin	4/4	Richter (1926)
Black-capped Chickadee (<i>Parus atricapillus</i>)	prior 1898	Ontario	1/1/1/1/1/1	Anderson (1898)
Common Bushtit	prior 1939	Washington	7/1	Maltby (1939)
Ruby-crowned Kinglet (<i>Regulus calendula</i>)	1928	Quebec	na/4	Terrill (1961)
Eastern Bluebird (<i>Sialis sialis</i>)	prior 1884	Virginia	5/2	S. (1884)
	1928	Florida	3/3 ^e	Howell (1928)
	prior 1928	na	3/3	Howell (1928)
Western Bluebird (<i>S. mexicana</i>)	prior 1926	Ohio	4/4	Wharram (1926)

TABLE 3 continued

Brown Thrasher	1914	Connecticut	1/1	Kochler (1914)
Prothonotary Warbler	prior 1893	Illinois	5/7	Loucks (1893)
Indigo Bunting	prior 1908	Kentucky	3/3	Griffin (1908)
Painted Bunting (<i>Passerina ciris</i>)	1883	Georgia	3/2	Perry (1884)
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	1965	Wisconsin	5, GS ^f /GS	Weins (1971)
Seaside Sparrow (<i>Ammodramus maritimus</i>)	prior 1928	Florida	2/2	Howell (1928)
Bobolink (<i>Dolichonyx oryzivorus</i>)	prior 1912	Wisconsin	5/2	Pelton (1912)
Red-winged Blackbird	prior 1928	Florida	3/na	Howell (1928)
Western Meadowlark	1886	Iowa	na/4	Akers (1888)
Common Grackle (<i>Quiscalus quiscula</i>)	prior 1926	Minnesota	^g	Peabody (1926)
Baltimore Oriole	prior 1926	Wisconsin	2/3	Ritcher (1926)

^a 4/4 = Four Alder Flycatcher eggs buried and four Alder Flycatcher eggs found in upper nest.

^bBP = Black Phoebe (*Sayornis nigricans*) eggs.

^c* = unknown dirty blue egg.

^ena = Data not available.

^fGS = Grasshopper Sparrow (*Ammodramus savannarum*) egg.

^dAR = American Robin (*Turdus migratorius*) egg.

^g/ = nest noted to be double, no further information given.

DISCUSSION

Frequency of Burial

The frequency of egg burial in species other than the Yellow Warbler is low. Although burial has been recorded in 56 passerine species, only four species were reported burying more than five times. As many of these burials were detected by early oologists and are anecdotal, there is no way to calculate burial frequency in any of these species because the authors did not include total numbers of nests of the species inspected in which burial was not recorded. However, presumably because of the rarity of finding a nest with a buried egg(s), especially in species other than Yellow Warblers, it was considered to be noteworthy and was generally reported in the early oological and ornithological journals. Today, few anecdotal references to egg burial are published, but, nesting studies can give us some idea of the rarity of burial. For example, a study of 3000 Gray Catbird nests by Nickell (1958) reported only four burials. Nolan (1978) recorded three burials of cowbird eggs out of 800 Prairie Warbler (*Dendroica discolor*) nests despite a 27% parasitism frequency. Of 796 American Goldfinch nests examined by Berger (1960), three of the 11 parasitized nests showed burial. Conversely, Yellow Warblers are known to bury as many as 48% of parasitized nests (Clark and Robertson 1981). This large difference in burial rate between Yellow Warblers and other species indicate that burial is a behaviour unique to Yellow Warblers.

Burial in the Context of Cowbird Parasitism.

In Yellow Warblers, egg burial occurs most frequently when nests are parasitized

by the Brown-headed Cowbird. This trend was also observed for other species in this review. Eighty-two percent of the records involving burials by other passerine species were observed in the context of cowbird parasitism. This may be explained by Partial Clutch Reduction (PCR) as induced by the brood parasite or by the premature laying of the cowbird egg.

Partial clutch reduction (PCR) is the removal of one or more eggs from a clutch, resulting in at least one egg remaining in the nest. Predators, as well as cowbirds, could elicit PCR by removing one or more eggs. PCR has been suggested to elicit egg burial in Eastern Phoebes (Rothstein 1986) and nest desertion in Clay-colored Sparrows (Hill and Sealy 1994). However, studies of Yellow Warblers do not support this hypothesis. Goossen and Sealy (1982) found that unparasitized clutches are deserted infrequently despite PCR, but may be deserted due to weather and depredation. Experiments by Sealy (1992) showed that none of the 13 five-egg clutches that were reduced to as few as two eggs were deserted. Inadequate information in the records (Table 2) make it impossible to determine whether burial was elicited by PCR.

In this study, premature laying is defined as the egg being laid prior to the nest being completed. The end of nest building is sometimes difficult to determine because some nest materials may be added to the nest after the clutch is initiated (Sealy pers. comm.), whereas some species wait a few days after building a nest before starting their clutch (Norris 1947). Thus, for simplification, the day of clutch initiation by the host is considered the same day as nest completion.

The timing of laying is important to the Brown-headed Cowbird (McMaster and Sealy 1998). To parasitize a Yellow Warbler successfully, a female cowbird must lay her

eggs late enough in the laying cycle to ensure the eggs will not be rejected (Clark and Robertson 1981, Sealy 1995), but early enough to enable her offspring to gain a competitive advantage over the host chicks (Mayfield 1960, McMaster and Sealy 1998). If the cowbird lays too early (before host nest building is completed) the egg may simply be buried during the completion of the nest. Yellow Warblers are occasionally reported to bury eggs (and an acorn, Weeks 1922) while completing their nests (Sealy *et al.* 1989, Sealy 1995). Furthermore, Emlen (1941) placed conspecific eggs and young into unfinished Tri-colored Blackbird (*Agelaius tricolor*) nests and found normal nest building was not interrupted.

Since 89% of these records involved the burial of cowbird egg(s) only (such that, no host eggs were buried), indicates that most of these burials involved premature laying by the cowbird. Many authors (e.g., Keyes 1884, Maltby 1939, Friedmann 1963, Mayfield 1960) support this conclusion, stating that premature laying resulted in burial of the cowbird egg. Records of the Bobolink (Pelton 1912) and Seaside Sparrow (Howell 1928) laying their eggs in the dirt and building their nests over the eggs are probably extreme examples of premature laying.

Premature laying may also explain the 10 records of burials by rejector species. Ejection apparently is the most efficient means of eliminating cowbird eggs because it requires little time and energy, and frees the host's reproductive effort from parasitism (Rothstein 1975). Rejector species, therefore, do not need to bury cowbird eggs. However, five of the 45 species recorded burying in the context of cowbird parasitism are known rejectors: Baltimore Oriole, Brown Thrasher, Warbling Vireo, Gray Catbird, and Eastern Kingbird (Rothstein 1975, Sealy 1996). Nine of the 10 records involved the

burial of only one cowbird egg, whereas one record was of the burial of three cowbird eggs (Table 2). As no host eggs were buried in any of these cases, these records suggest that the cowbird eggs were laid before the nests were completed. However, burial can occur in these species as indicated by the records of a Brown Thrasher burying one of its own eggs and a record of a Baltimore Oriole burying three of its own eggs in the apparent absence of cowbird parasitism (Table 3).

Nevertheless, premature egg laying may not account for all the burials observed. For example, the Red-eyed Vireo takes several days to complete its nest and then waits several more before laying its eggs (Norris 1947). Thus, the assumption that nest building is terminated when egg laying is initiated may not always be accurate. Furthermore, the apparent lack of host eggs at the time of burial may be because the female cowbird has returned to the nest after parasitizing it and removed a host egg. Sealy (1992) found that cowbirds remove host eggs from one in every three parasitized Yellow Warbler nests. As these removals occurred most frequently (46%) on the same or subsequent days after parasitism, burial may have precluded some removals. There is no evidence of egg removal in Table 2 (nests were usually not monitored for laying schedules) such that egg removal by the cowbird could account for some of the records of burials without a host egg (Goossen 1985). Finally, some authors have stated that burial was a rebuilding of a nest over a parasitic egg (for example Akers 1888, Bendire 1892). Despite a few exceptions, premature egg laying may explain the majority of the burial records.

Burial is not restricted to either North America or passerine species. The Upland Sandpiper (*Bartramia longicauda*) has been observed burying a Brown-headed Cowbird

egg (Friedmann 1963). In South America, Friedmann (1929) reports frequent burial of Shiny Cowbird (*Molothrus bonariensis*) eggs by the Yellow-browed Tyrant (*Sisopygus icterophrys*). In Europe, hosts are occasionally reported to bury Common Cuckoo (*Cuculus canorus*) eggs (e.g., Ticehurst 1927, Hall 1927, Charteris 1927). Brooker and Brooker (1989) report that five of the nine cuckoos in Australia have hosts that have been recorded as burying eggs.

Burial in the Absence of Cowbird Parasitism

Burial in the absence of cowbird parasitism has also been observed, although it is much less frequent. Similar to burials within the context of cowbird parasitism, these records may be explained by PCR or premature laying of the builder.

Burial has been observed in many contexts, such as the example above of the Purple Martin (Brown 1983). The Zebra Finch (*Poephila guttata*) is well known for burying its own eggs in captivity when nesting materials are not removed from cages after nest building is complete (Martin 1984). In other species, the burial and uncovering of eggs is believed to reduce predation or to aid in the thermoregulation of the eggs (e.g. Welty 1975, Keller 1989, Hohn 1993). In Europe, female Penduline Tits (*Remiz pendulinus*) sometimes bury their eggs to hide their fertile period from their mate and uncover them after the mate deserts or during the late egg-laying period (Valera *et al.* 1997). Intraspecific burials have also been recorded in the Red-headed Woodpecker (*Melanerpes erythrocephalus*; Nicholson 1927), Great-horned Owl (*Bubo virginianus*; Goelitz 1921), and American Coot (*Fulica americana*; Richter 1926). The occurrence of

intraspecific burial in American Coots is interesting because this species is known to parasitize conspecifics (Lyon 1992).

Overall, the frequency of egg burial by North American passerine species is low, compared to that in the Yellow Warbler, and is observed more frequently in the context of cowbird parasitism (82% of records). To explain the majority of these burials, eggs may have simply been laid too early (by the cowbird and perhaps also of the builder such as in the absence of a cowbird egg), and nest building was continued, burying the premature egg(s) in the nest.

CHAPTER 2

STRUCTURE OF YELLOW WARBLER NESTS

INTRODUCTION

As defined in the last chapter, burial is the addition of nesting material to cover, fully or partially, the entire nest and its contents. There has been much debate whether burial is an antiparasitic adaptation (Friedmann 1929; Rothstein 1975, Clark and Robertson 1981; Burgham and Picman 1989; Sealy 1995, see Chapter 1). There have, however, been few attempts to explain why this behaviour occurs most frequently in Yellow Warblers.

In 1910, Herrick proposed that burial occurs when the normal cycle of nest building has been disturbed. Friedmann (1929:242) summarized Herrick:

“[Herrick] found that if the cycle was disturbed at any point, the birds would go back one stage in the cycle and start from that point. Thus, if the egg-laying stage was disturbed by some cause, the birds would go back one stage, i.e., to nest-building. They would build a new nest and then resume egg-laying. In the case of yellow warblers, the egg-laying is disturbed by the introduction of a Cowbird’s egg, and, according to the above idea, the Warbler should desert (as many birds do), and build another nest. However, reasons Herrick, the yellow warbler is so attached to its nesting site that it does not want to leave. At the same time instinct prompts it to build another nest. There is a struggle between two instinctive forces, the one tending to hold the bird to the nesting-site, the other trying to drag it away and build a

new nest. The contest is a fairly even one, and the outcome not predictable in any one case. The presence of eggs of its own in the nest strengthens the attachment of the bird to the nest site and nest, and it is this instinct that wins in the majority of the cases. The new floor, covering the parasitic eggs, is to be interpreted as comparable to a new nest, such as the consequence of the cyclical instinct would demand, but placed directly in or on the old one, due to the strong site attachment.”

The phenomenon described above, commonly observed in the nest building of social insects, is termed stigmergy (Downing and Jeanne 1988). Stigmergy is the ongoing construction of nests that is regulated by previous construction. Thus, nest building is a series of steps with transitions between each step that depend on the builder perceiving cues from previous construction. The characteristics of the nest dictate how construction proceeds, and the cues regulating construction come from the present or immediately preceding step (Downing and Jeanne 1988). The main difference in the stigmergy and Herrick’s hypothesis is that the stages of nest building are not dissected into steps and repeated (such as building a nest base then a cup, etc.), but are rather described as whole reproductive behaviours (stages), such as nest building, egg laying, and incubation. Herrick referred, therefore, to the reproductive cycle as a whole rather than to one behaviour, in this case, nest building. Nevertheless, the ideas are similar. Following Herrick’s explanation, burial in Yellow Warblers may be described as the disruption of the nest-building stage, by a perturbation such as brood parasitism. This disturbance causes the female Yellow Warbler to redo the last step in the reproductive cycle, which according to Herrick, is building a new nest at the original nest site.

More recently, Rothstein (1975) hypothesized that the Yellow Warbler's burial behaviour is a result of the use of similar materials throughout all parts of the nest and is not a behaviour specifically elicited by the presence of a cowbird egg. He wrote (1975:256):

"Possibly some hosts use nesting materials that make it difficult for cowbirds to determine when a nest is nearly completed and this, rather than a direct response to cowbird eggs, may represent an actual antiparasitic adaptation. It may be no coincidence that the yellow warbler, the species most noted for burying cowbird eggs, often builds an unusual nest with similar material used for both the nest frame and the nest lining."

According to Rothstein (1975), burial is not a rejection behaviour (i.e., like ejection and nest desertion), because it is not directed towards the presence of a cowbird egg but to the whole nest. However, it would function as an antiparasitic adaptation if the female cowbird is tricked into laying prematurely and the Yellow Warbler finishes nest building resulting in an egg being embedded (buried) within the liner.

Nest structure has been described for many species. For example, in captivity, the Canary (*Serinus canaria*) builds nests of two discrete layers, an outer layer of grass and an inner feather-rich layer (Kern and Bushra 1980). The Goldcrest (*Regulus regulus*) also builds a two-layered nest with a thick base of mosses and lichens, and a solid inner lining of feathers (Haftorn 1978). Willow Flycatchers and Prairie Warblers each build nests with three layers (Nolan 1978, McCabe 1991). The three-layered nest consists of an outer shell, or nest base, a nest body (or padding, Nolan 1978), and finally a liner. Each layer is distinct and formed with different materials.

Although the nesting materials used by Yellow Warblers are well documented (see Table 1), their nest structure has been poorly described. Bigglestone (1913) and Harrison (1979) reported that Yellow Warbler nests are two layered, with the foundation consisting of interwoven plant fibres, and the lining of soft plant down mixed with hair. Rothstein (1975) and Clark and Robertson (1981) did not note the total number of layers, however, they mentioned a frame and lining, and lining and cup, respectively.

As Rothstein (1975) suggests, the lack of differentiation between nest liner and frame in Yellow Warblers nests may indicate that its nest is unusual and may have evolved under the pressures of cowbird parasitism. I dissected a sample of nests to determine the number of layers within. Following Rothstein's (1975) hypothesis, I tested that female Yellow Warblers create visual homogeneity throughout the nest so that a cowbird cannot correctly determine when the nest is complete and, hence, may parasitize the nest prematurely. Thus, female Yellow Warblers are predicted to select similar materials for the nest liner and frame to achieve visual homogeneity throughout the nest. Furthermore, as burial would result in the female warbler finishing her nest and burying the parasitic egg within the liner, the burial layer is predicted to be visually and structurally the same (materials and color) as the layer prior to burial. This second prediction is examined by dissecting and determining the structure of Yellow Warbler nests with buried cowbird eggs.

METHODS

Field Work

Field work was conducted in 1995 and 1996 at the University of Manitoba Field Station at Delta Marsh, Manitoba. Yellow Warbler nests were sought daily on the forested dune ridge. Nests were checked every second day to ensure that the nest was promptly collected after use (deserted, depredated, young fledged). All nests (n = 116) collected in the 1995 and 1996 were located in the willow community (south side of ridge) to ensure that the vegetation available to building females was similar. Three nests with buried eggs were collected during 1995 while no burial nests were found in 1996. To augment the sample size, 24 nests with buried eggs were collected from Delta Marsh from 1978 to 1994 by K. A. Hobson, D. G. McMaster, and S.G. Sealy. All nests were stored in plastic or paper bags until examined.

Nest Dissection

All nests (n=140) were dried at 80^o C in brown paper bags until no change in mass occurred after two consecutive measurements separated by 24 hours. The dried nests were carefully cut in half with scissors. Stratification of layers was visible by colour, texture, and position (see Figures 1-5). I determined layer colour by using Smithe (1974) colour charts which has a designated name and arbitrary value for each colour. Most non-burial nests had three layers, which were termed base, frame and liner (Figures 1 and 4A), whereas some nests were distinctly two-layered (base and liner; Figures 2 and 4B). Burial nests were more complex with as many as six layers (three layers above the buried egg and three below). The layers above the buried egg were

FIGURE 1. Photograph of one-half of a Yellow Warbler nest showing three layers (see Figure 4A for the separation of the layers).

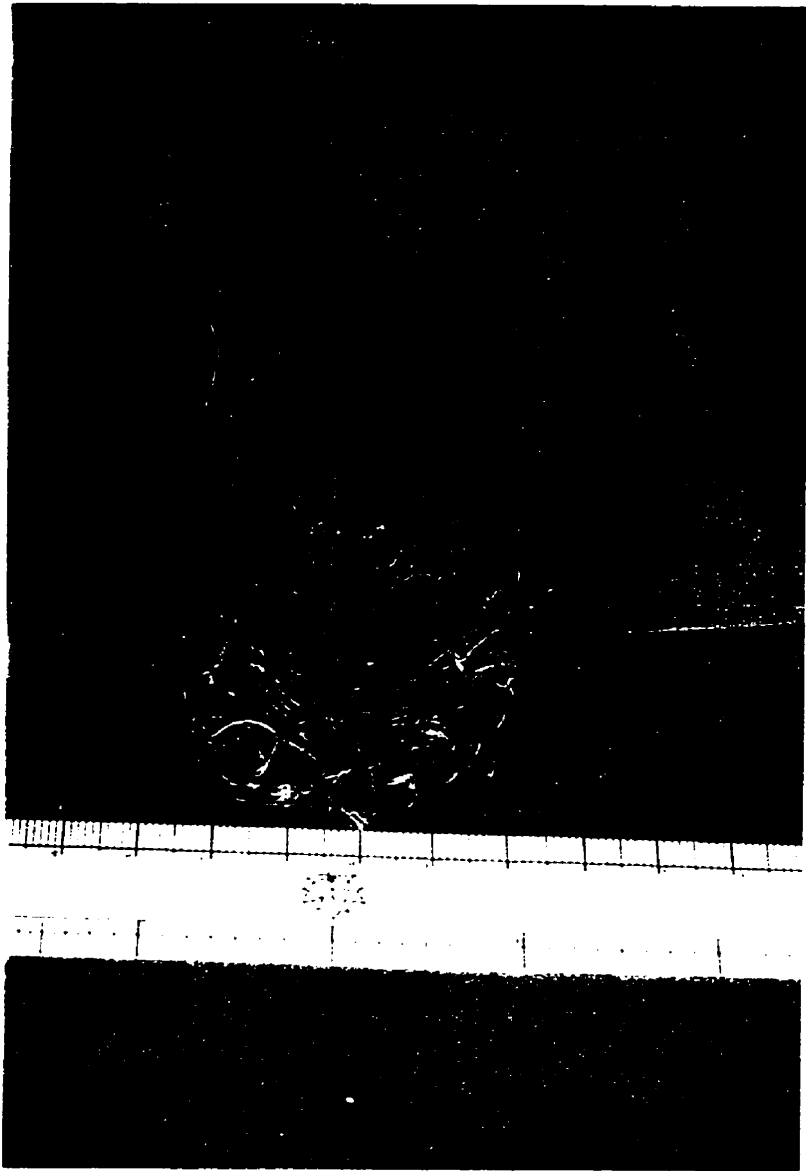


FIGURE 2. Photograph of one-half of a Yellow Warbler nest showing two layers (see Figure 4B for the separation of the layers).

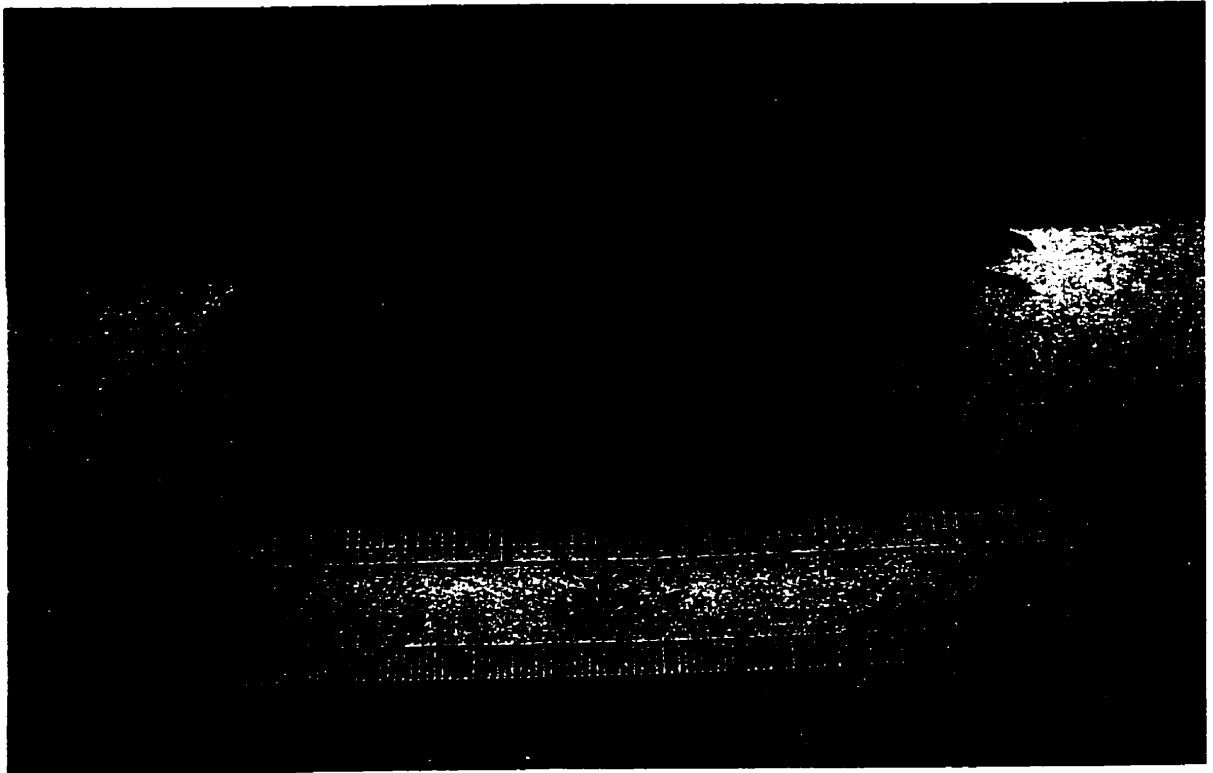


FIGURE 3. Photograph of a buried cowbird egg between the original and top nest (see Figure 5 for separation of layers).

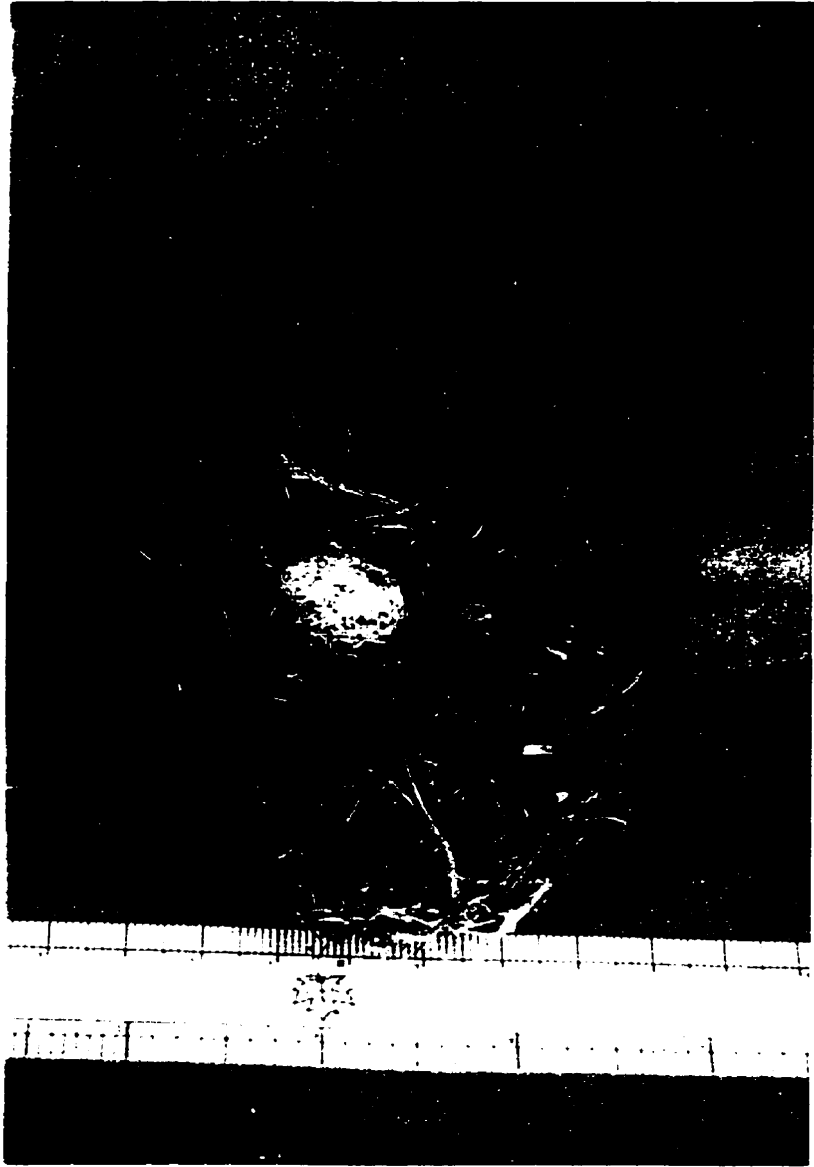
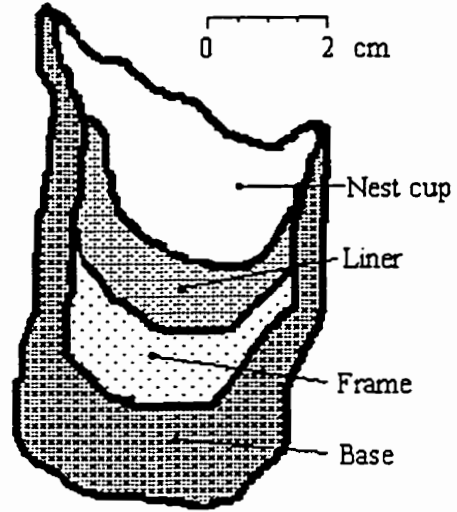


FIGURE 4. Line drawing indicating the layers of a three-layered nest from Figure 1 (A) and the two-layered nest from Figure 2 (B).

A.



B.

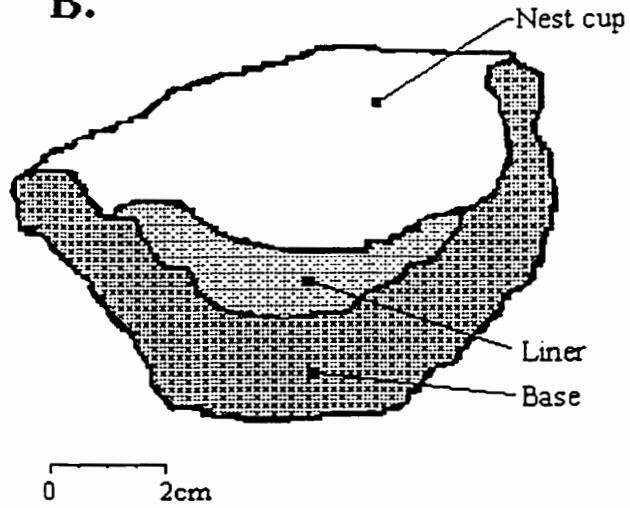
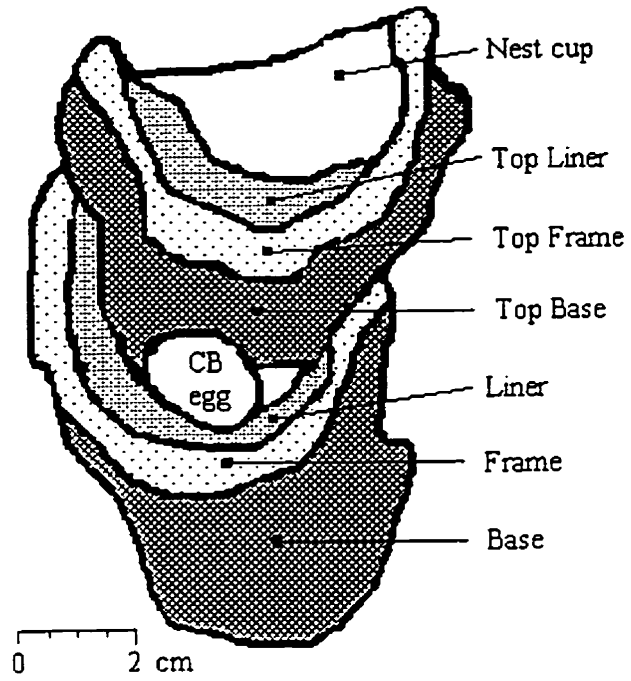


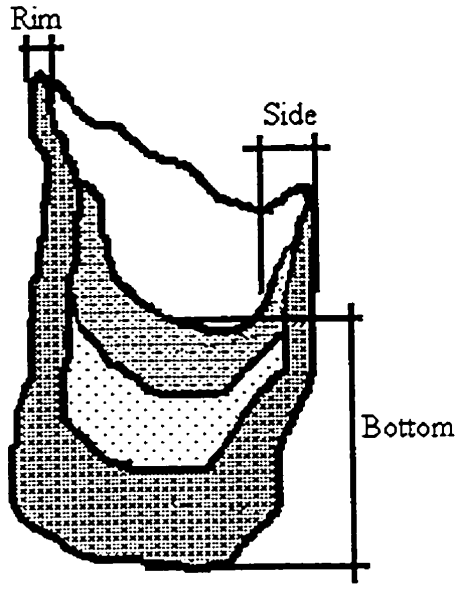
FIGURE 5. Line drawing of a Yellow Warbler burial nest showing the buried cowbird egg (CB egg) and the separation of the layers (from Figure 3).



referred to as the top (top-base, top-frame and top-liner), whereas the lower layers were referred to as the original nest (base, frame and liner) (Figures 3 and 5). One-half of the nest was used as a reference and the measurements were taken (see Figure 6 for explanation of measurements), and colour was determined for each layer (colour follows Smithe 1974). The other half was teased apart layer by layer and each piece of material within was separated and classified according to groups (see below). After separation of the whole layer, groupings for each layer were collectively weighed, to the nearest 0.05 g. Groupings that weighed less than 0.05 g were designated a set mass of 0.02 g, indicating that it was present in that layer.

All the material within the nests fell into one of six groups: nettles/hops (*Urtica dioica*, *Humulus lupulus* respectively), grass fibres (species not identified), White-tailed deer (*Odocoileus virginianus*) hair, feathers, fruits (mostly *Populus deltoides*, *Taraxacum officinale*, *Salix* spp. and *Typha* spp.) and other. Other materials included Red Fox (*Vulpes vulpes*) hair, duff (crystalline particles from feather sheaths of the young birds), invertebrates (mostly Order Diptera and occasionally chironomids and spider webs), excrement, man-made materials (fishing line, window screening, toilet paper, string, plastic), rootlets, wild cucumber (*Echinocystis lobata*) tendrils, wood/bark, red-coloured hops, moss hyphae, egg shell bits, leaves and three pieces of unknown material that were found in three nests. Red-coloured hops were separated from nettles/hops on the basis of the distinct reddish colour of the fibres (compared to a silvery-grey colour of the nettles/hops category). Invertebrates, duff and excrement were later removed from the “other” category because they were not materials that were selected by the nest builder during nest construction. The exception was spider webs within the invertebrate

FIGURE 6. Dimensions of a Yellow Warbler nest.



0 2 cm

category. Yellow Warblers collect the webs and place them on the outside of the nest and around the surrounding support branches of the nest shrub (pers. obs.).

Nevertheless, spider webs were included in the invertebrate category in which the majority of the invertebrates were of the Order Diptera. Note that most plant materials found within the nest were from the previous year. Leaves (classified under “other”), some fruits (*Populus deltoides* and *Salix* spp.) and green grass fibres (found in only 2 non-burial nests) were the only plant materials that had been produced in the present growing season.

Statistical Analysis

Nesting materials were converted to a proportion of the half nest to compensate for differences in nest mass and errors in cutting the nest in half. As the data were in proportions, they were transformed by taking the arcsine of the square-rooted proportions and expressing the data in degrees. To ensure that the data were normally distributed with equal variances, K-S Lillifores and Levene’s Test were employed, respectively (SPSS 1994).

T^2 Statistic

To analyse data that required the multi-sample comparison between two groups, a two-sample T^2 statistic (multivariate t -test) was used. It tests the null hypothesis of equivalence of two mean vectors and is performed by referring to the standard F-distribution with the appropriate degrees of freedom. This test was used to determine if there was a difference in nesting material (nettles/hops, grass, deer hair, feathers, fruits,

and other) between 1995 and 1996 nests. A two-sample T^2 statistic was then used separately on 1995 and 1996 data to determine if there was a difference in the proportion of nest materials (nettles/hops, grass, deer hair, feathers, fruits, and other) between three- and two-layered nests.

As nest size is not expressed as a proportion, it was not arcsine transformed. Instead it was found to be skewed, and hence, a log transformation ($\log+1$) was induced to make the data normally distributed with equal variances (K-S Lillifores test and Levene's Test for Equality of Variances, SPSS 1994). Then a two-sample T^2 statistic was performed on the data to determine if there was a size difference (used bottom, side and rim, see Figure 6) between two- and three-layered nests for both 1995 and 1996 nests as well as to determine if there was a size difference between nests built in 1995 and 1996.

Canonical Variates Analysis

For data that required the multi-sample comparisons with more than 2 groups, the Canonical Variates Analysis (multivariate analogue ANOVA) was used. It functions by testing the null hypothesis of the equivalence of more than two mean vectors by extracting ordination axes that serve to maximally discriminate the groups. These axes can thus be tested to determine whether the groups differ by referring to the chi-square distribution. The variables are displayed as vectors which then gives their relative importance in the discrimination space (Podani 1994). The three-layered nests of 1995 and 1996 were analyzed separately to determine whether there was a significant difference between each layer (liner, frame and base) according to the proportion of

materials found within the nest (Syntax 5.02 Scientia Publishing, Budapest). Burial nests were also analyzed using the Canonical Variate Analysis, again to determine if the six nest layers were significantly different according to the proportion of material found within each layer (Syntax 5.02 Scientia Publishing, Budapest).

Students *t*-test

Nest mass was not arcsine transformed. It was, however, found to be skewed and thus log transformed ($\log+1$) in order to make the data normally distributed with equal variances (K-S Lillifores test and Levene's Test for Equality of Variances, SPSS 1994). A students *t*-test (SPSS 1994) was performed on nest mass to determine if there was a difference in two- and three- layered nests in 1995 and 1996 nests as well as if there was a difference in mass between nests built in 1995 and 1996.

RESULTS

Of the 140 Yellow Warbler nests dissected, 113 were non-burial nests and the remaining 27 were burial nests. Seventy-seven percent of the non-burial nests consisted of three layers (Figure 1), a base, frame and liner (Figure 4A). The remaining 23% were two-layered nests, all of which appeared to be missing the frame (Figures 2 and 4B).

Yearly Differences

Significant differences in size and proportion of materials were detected between nests built in 1995 and 1996. See Appendix 5 for results and discussion of this section.

Nest Structure: Two- versus Three-layered Nests

Non-burial nests that were dissected had either two or three layers (Figures 1 and 2, respectively). There was a significant difference in the proportion of nesting materials between two- and three-layered nests in 1995 ($F = 6.197$, $p < 0.01$) but not in 1996 ($F = 1.545$, $p = 0.376$). In 1995, two-layered nests had a lower proportion of grass (main component of the frame) and a higher proportion of nettles (main component of the base) compared to the three-layered nests (Figure 7). Also, fruits were used more frequently in the two-layered nests (Figure 7). Appendix 3 and 4 lists the proportions of materials used to create Figures 7 and 8.

Two-layered nests were significantly smaller in size than three-layered nests in 1995 ($F = 6.478$, $P < 0.001$) and 1996 ($F = 3.459$, $P = 0.048$), with the base contributing to most of the difference (Figure 8). Nest mass was significantly lower in the two-layered than the three-layered nests in 1995 ($t = -2.33$, $df=63$, $P = 0.023$), but

FIGURE 7. Comparison of the proportion of nesting materials in 1995 (A) between three- ($n = 51$) and two-layered ($n = 14$) nests, and in 1996 (B) between three- ($n = 36$) and two-layered ($n = 12$) nests. Note that the left and right axis are of different scale. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*).

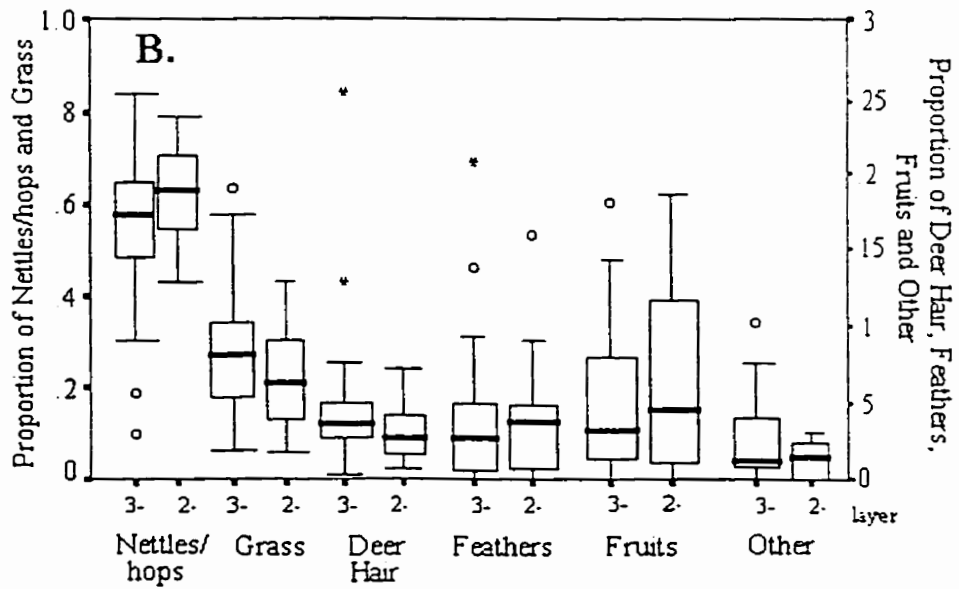
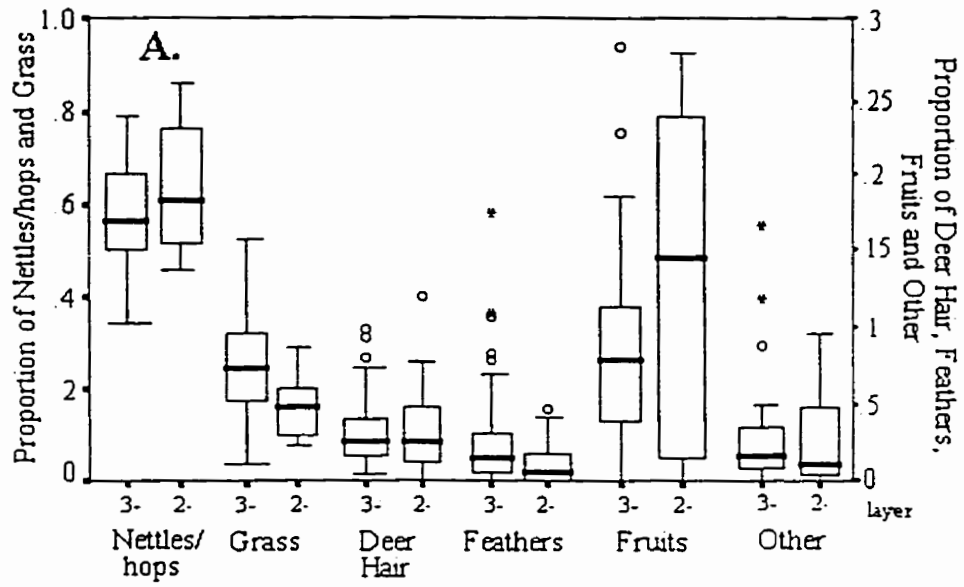
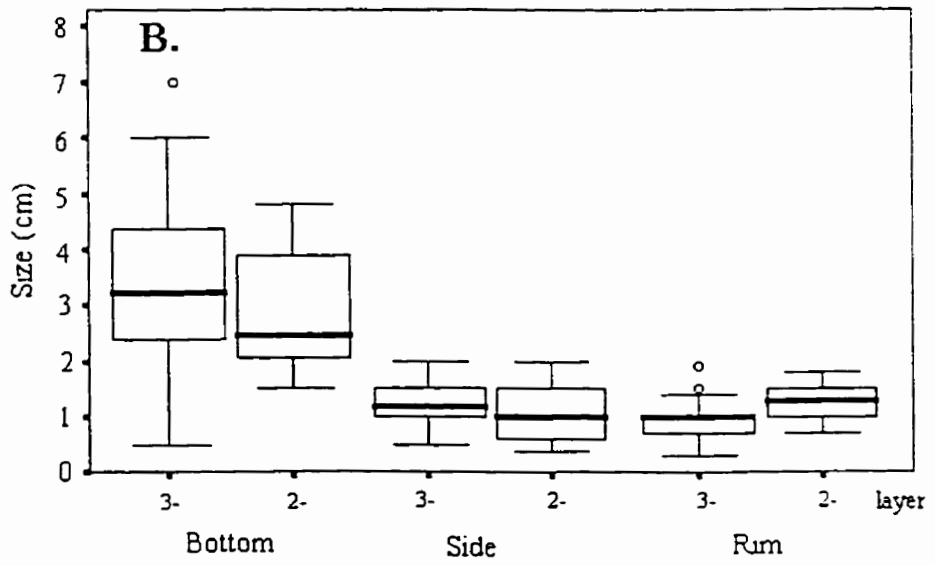
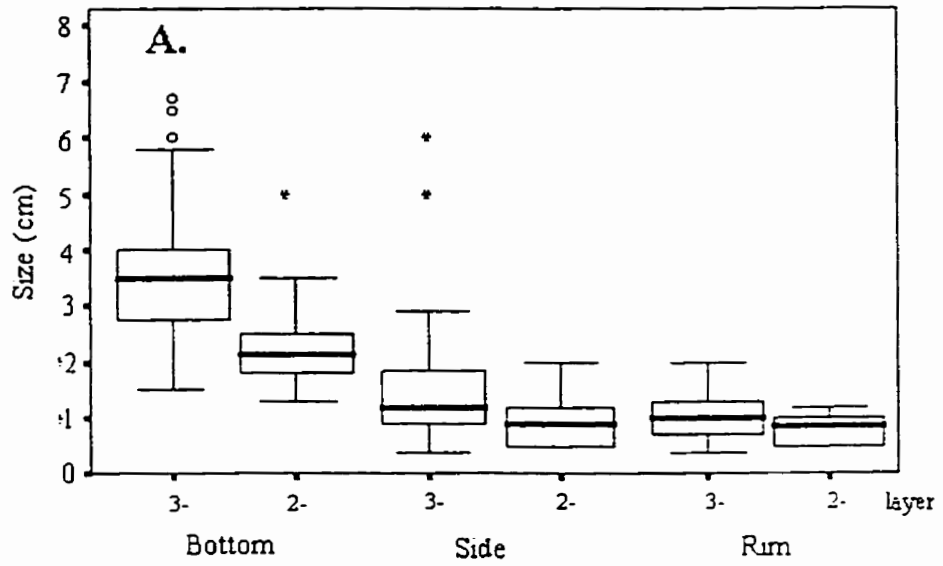


FIGURE 8. Comparison of nest size in 1995 (A) between three- (n = 51) and two-layered (n = 14) nests and in 1996 (B) between three- (n = 36) and two-layered (n = 12) nests. See Figure 7 for explanation of size. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*).



this difference was not detected in 1996 ($t = -1.01$, $df = 46$, $P > 0.05$) (Figure 9).

Three-layered Nests

Canonical Variate Analysis (Figure 10) illustrates that the relative proportion of nesting material in each layer produces distinct layers (non-overlapping 95% confidence circles around each mean). In both 1995 and 1996, the liner contains a significantly greater mass of feathers, fruits and deer hair compared to the frame and base. In 1996, there was a higher proportion of other materials in the liner, whereas in 1995, other materials contributed more to the base than the liner. The frame contained a greater mass of grass in both years, whereas the base contained mostly nettles. In 1995, however, the base also contained a greater proportion of other materials. Eighty-three percent and 92% of the variation in 1995 and 1996, respectively, can be explained by the trend observed in the first axis (i.e., relative proportion of nettles/hops; Tables 4 and 5, Figure 10).

Although materials were interwoven throughout the whole nest, the layers were easily distinguished by colour, texture and materials (Figures 1, 2 and 10). The grey colour of the base is attributable to the high proportion of nettles and hops (Figures 10 and 11). Nettles and hops had two colour values, depending on how torn the fibres were. That is, wide pieces were glaucous and finer pieces were smoke grey (Smithe 1974). The frame consisted mainly of grass and appeared more brown than the other two layers (the majority of the frames had a colour value around 30, brown; Figure 11). This is because the fibres are browner than any of the other materials found. Seed pappus and trichome colour were the most obvious parts of the fruit within the nest and

FIGURE 9. Comparison of nest mass in two- ($n = 14$) and three-layered ($n = 51$) nests built in 1995 and in two- ($n = 12$) and three-layered ($n = 36$) nests built in 1996. Note that nest mass is based on one-half nests. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*).

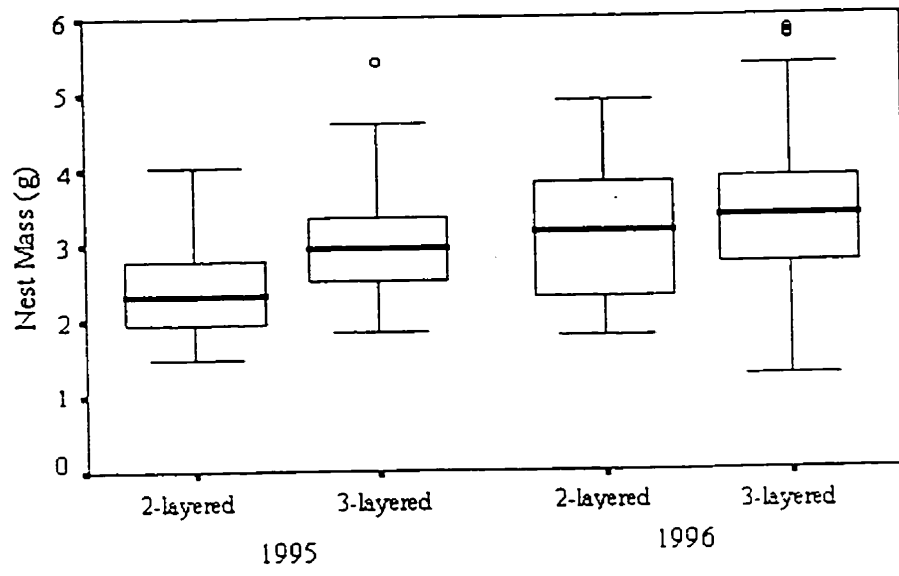


FIGURE 10. Canonical Variate Analysis of 1995 (A; n = 51) and 1996 (B; n = 36) three-layered Yellow Warbler nests displaying the separation of the nest layers (base, frame and liner) attributable to the six different nesting materials (represented by arrows). Circles represent 95% confidence intervals around the mean of each layer. Sample point symbols represent the liner (o), frame (*) and base (•).

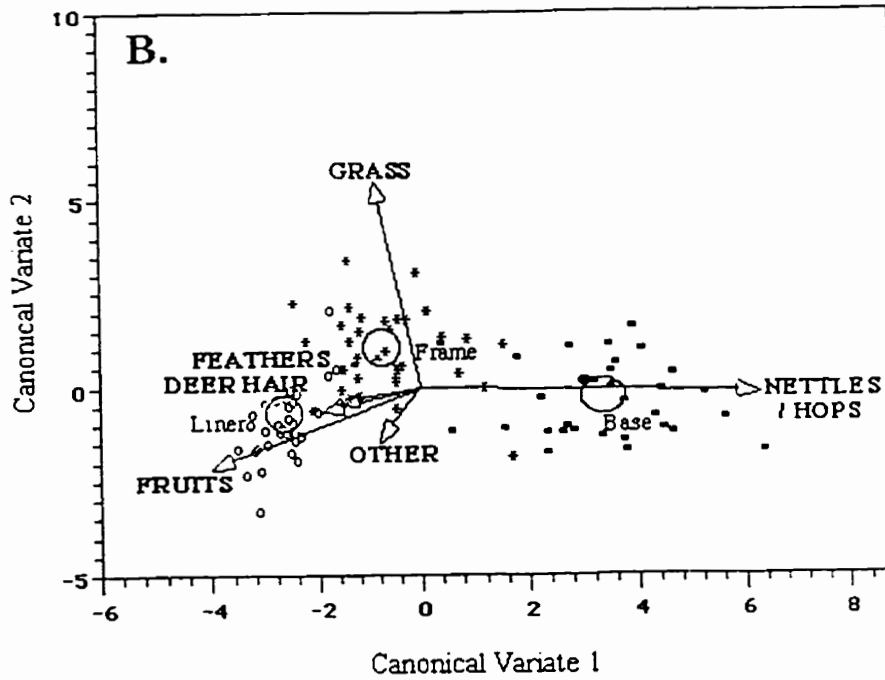
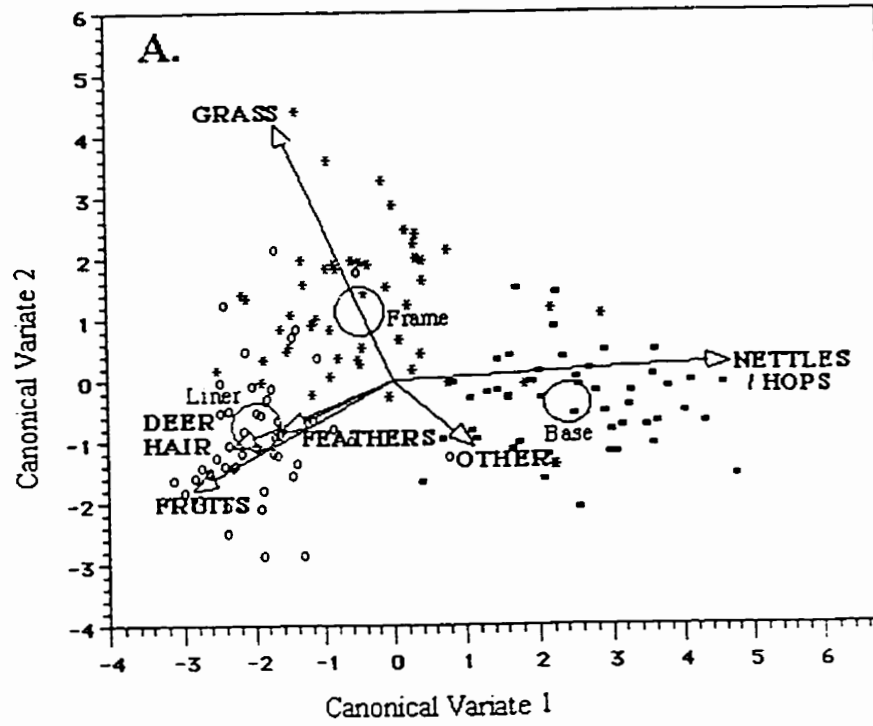


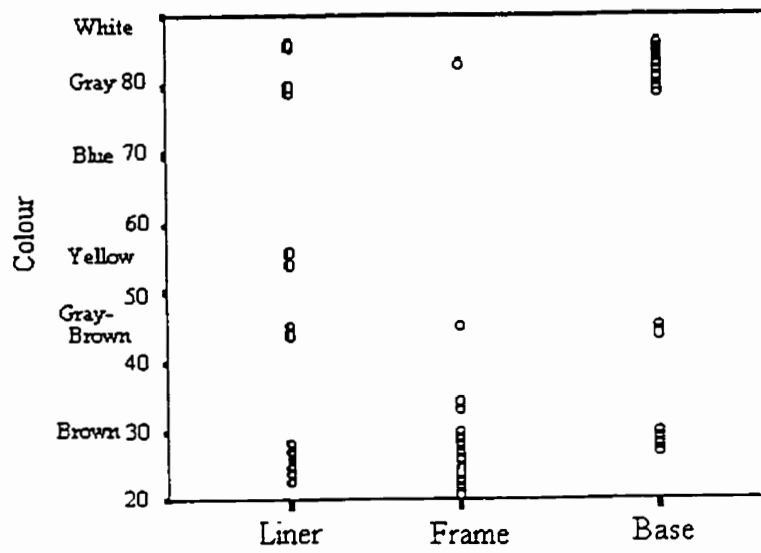
TABLE 4. Canonical Variate Analysis: eigenvalue (E.V.), canonical correlation (C.C.) and chi-square values of the first two axes for 51 three-layered Yellow Warbler nests collected in 1995 with six variables (nest groupings) and three groups (nest layers).

Axis	E.V.	E.V. as %	C.C.	Chi-square	df	P
1	3.37	82.64	0.878	296.29	12	<0.001
2	0.71	17.36	0.644	78.88	5	<0.001

TABLE 5. Canonical Variate Analysis: eigenvalue (E.V.), canonical correlation (C.C.) and chi-square values of the first two axes for 36 three-layered Yellow Warbler nests collected in 1996 with six variables (nest groupings) and three groups (nest layers).

Axis	E.V.	E.V. as %	C.C.	Chi-square	df	P
1	6.54	91.58	0.930	246.20	12	<0.001
2	0.59	8.42	0.610	46.35	5	<0.001

FIGURE 11. Colour values (Smithe 1974) for each layer of the 87 three-layered Yellow Warbler nests (1995 and 1996 data combined).



had the colour buff, cream (Smithe 1974), or white (Figure 13). Many of the nest liners appeared olive-brown due to the high proportion of cattail seeds (*Typha latifolia*). Other nest liners were whitish grey due to the high number of poplar (*Populus deltoides*) and dandelion (*Taraxacum officinale*) fruits as well as deer hair (Figure 13). Feathers were discrete (not as frequent as the other four materials and were visually different from the more weavable materials) and rarely contributed to the definition of the layers.

Mass of half-nests for 1995 and 1996 ranged from 1.86 g to 5.84 g for both years (mean \pm S.D.; 3.02 ± 0.73 and 3.50 ± 0.99 g for 1995 and 1996, respectively; Table 6). Of the total nest mass, the base had the greatest mass (1.52 ± 0.63 g, 1.95 ± 0.87 g; 1995 and 1996 respectively), followed by the frame (1995, 0.98 ± 0.56 ; 1996, 0.98 ± 0.46) and liner (0.53 ± 0.22 , 0.54 ± 0.32) (Table 6). In both 1995 and 1996, the nest bottom was the thickest portion of the nest with a mean depth of 3.59 and 3.68 cm, respectively (Table 6). The nest side and rim were a third of the size of the nest base. The nest side averaged 1.47 cm in 1995 and 1.27 cm in 1996, whereas the rim averaged 1.05 cm in 1995 and 0.90 cm in 1996 (Tables 6).

Burial Nests

As in the non-burial nests, the number of nest layers varied among the burial nests. Many (41%) of the nests had six layers, three layers below the buried egg(s) and three layers above (Figures 3 and 5, Table 7). In six-layered nests, the three layers of both the original nest and upper three layers coincided with the base, frame and liner observed in the non-burial nests. Ten burial nests consisted of five layers and usually lacked the top liner or top frame. Six nests lacked two layers, which was either the base

TABLE 6. Mean (\pm S.D.) of the mass (g) and size (cm) of three-layered 1995 (n = 51) and 1996 nests (n = 36).

Variable	Mass ^b	Size ^a		
		Bottom	Side	Rim
Whole Nest				
1995	3.02 \pm 0.73	3.59 \pm 1.23	1.47 \pm 1.02	1.05 \pm 0.41
1996	3.50 \pm 0.99	3.68 \pm 1.70	1.22 \pm 0.43	0.90 \pm 0.38
Liner				
1995	0.53 \pm 0.22	1.08 \pm 0.43	0.63 \pm 0.32	0.48 \pm 0.37
1996	0.99 \pm 0.17	2.50 \pm 0.50	1.50 \pm 0.10	2.00 \pm 0.10
Frame				
1995	0.98 \pm 0.56	0.88 \pm 0.52	0.45 \pm 0.25	0.64 \pm 0.33
1996	0.54 \pm 0.32	0.92 \pm 0.34	0.62 \pm 0.22	0.32 \pm 0.15
Base				
1995	1.52 \pm 0.63	1.73 \pm 1.08	0.61 \pm 0.62	0.67 \pm 0.35
1996	1.95 \pm 0.87	2.02 \pm 1.36	0.59 \pm 0.25	0.69 \pm 0.36

^a See Figure 6 for explanation of measurements.

^b Mass for half nest

TABLE 7. Features of the 27 burial nests. Sample sizes are in parentheses.

Nest Features	% of Nests
6 – layers	41 (11)
5 – layers	37 (10)
4 – layers	22 (6)
	Total 100 (27)
No layers missing	41 (11)
Top – liner missing	26 (7)
Top – frame missing	26 (7)
Top – base missing	15 (4)
Liner missing	0 (0)
Frame missing	15 (4)
Base missing	7 (2)
	Total 100 (27)
1 cowbird egg buried	63 (17)
2 cowbird eggs buried	4 (1)
1 to 3 Yellow Warbler eggs buried with 1 cowbird egg	32 (9 ^a)
	Total 100 (27)

^a Six nests had one, two nests had two and one nest had three Yellow Warbler eggs buried along with one cowbird egg.

or frame of either the top or bottom nest (Table 7). Despite the missing layers, the burial nests are usually almost twice the size in the bottom measurement and double the mass of non-burial nests (non-burial: Table 6; burial: Table 8).

Canonical Variate Analysis on burial nests (Figure 12) shows the material composition of each of the six layers. The liners (top and original) had similar proportion of materials (such as fruits and deer hair) as indicated by the overlapping 95% C.I. The top and original frames were similar in mass of grass (overlapping 95% C.I.). Also, both bases were composed predominantly of nettles/hops and other materials and some feathers. However, the top base had significantly more other materials and feathers, and significantly less nettles/hops than the original base (non-overlapping 95% C.I.; Figure 14). Seventy-four percent of the variation within the data (i.e., amount of fruits and amount of nettles in the layers) can be explained by the trend observed on the first canonical axis, whereas 24% can be explained by the second axis (Table 9). Thus, the first two axis were significant (Table 9) and the remaining three axis were insignificant.

Both the top and original nest were of similar colour for each layer (Figure 13) and these layers were similar in composition to the non-burial nests (Figures 11).

TABLE 8. Mean (\pm S.D.) of the mass (g) and size (cm) of 27 Yellow Warbler burial nests with six layers. Sample sizes are in parentheses.

	Mass ^b	Size ^a		
		Bottom	Side	Rim
Whole Nest (27)	4.06 \pm 1.36	4.49 \pm 2.38	not applicable	not applicable
Top Nest (27)	1.47 \pm 0.63	1.47 \pm 0.96	0.81 \pm 0.41	0.79 \pm 0.50
Top-Liner	0.7 \pm 0.05 (21)	0.76 \pm 0.28 (21)	0.47 \pm 0.26 (21)	0.30 \pm 0.23 (9)
Top-Frame	0.16 \pm 0.09 (21)	0.70 \pm 0.53 (21)	0.30 \pm 0.24 (18)	0.45 \pm 0.37 (17)
Top-Base	0.22 \pm 0.08 (23)	0.55 \pm 0.60 (17)	0.41 \pm 0.21 (18)	0.69 \pm 0.41 (17)
Bottom Nest (27)	2.58 \pm 1.12	3.02 \pm 1.85	1.24 \pm 0.47	0.78 \pm 0.47
Liner	0.10 \pm 0.06 (28)	0.75 \pm 0.48 (28)	0.50 \pm 0.27 (28)	0.36 \pm 0.17 (12)
Frame	0.20 \pm 0.10 (25)	1.36 \pm 1.51 (26)	0.46 \pm 0.26 (20)	0.45 \pm 0.29 (17)
Base	0.34 \pm 0.09 (26)	1.08 \pm 0.88 (26)	0.51 \pm 0.26 (23)	0.52 \pm 0.37 (19)

^a See Figure 6 for explanation of nest size.

^b Mass for half nest

FIGURE 12. Canonical Variate Analysis of 27 Yellow Warbler burial nests exhibiting the separation of the six nest layers attributable to the six nesting materials (represented by arrows). Circles represent 95% confidence intervals around the mean of each layer. Sample point symbols represent the liner (o), frame (*), base (^), top-liner (+), top frame (-) and top base (•).

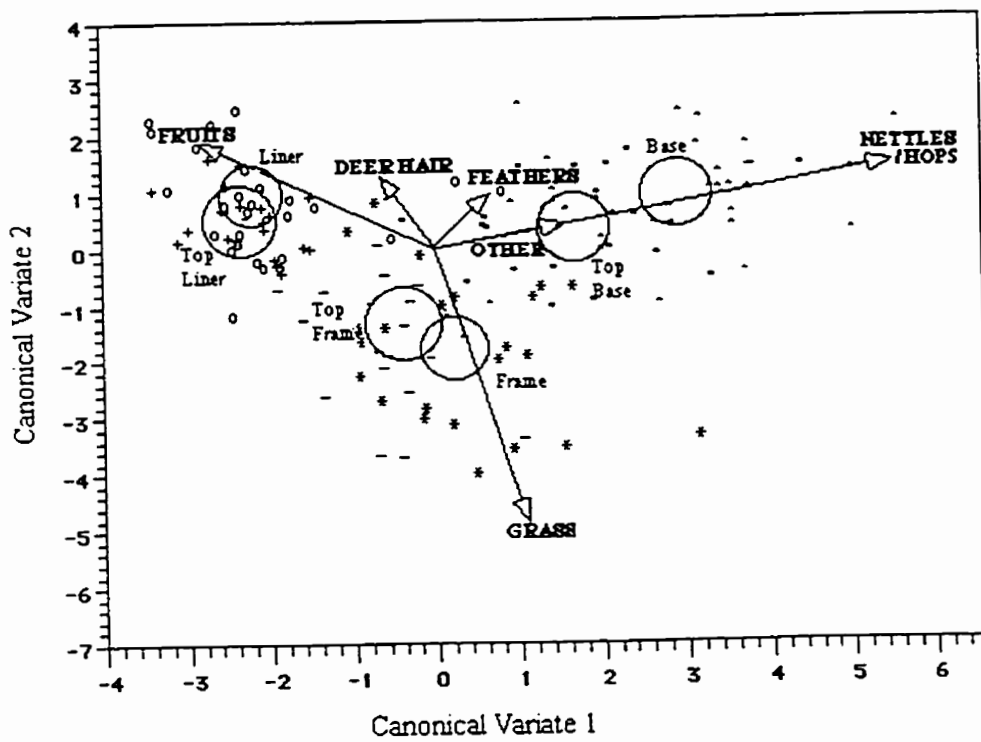
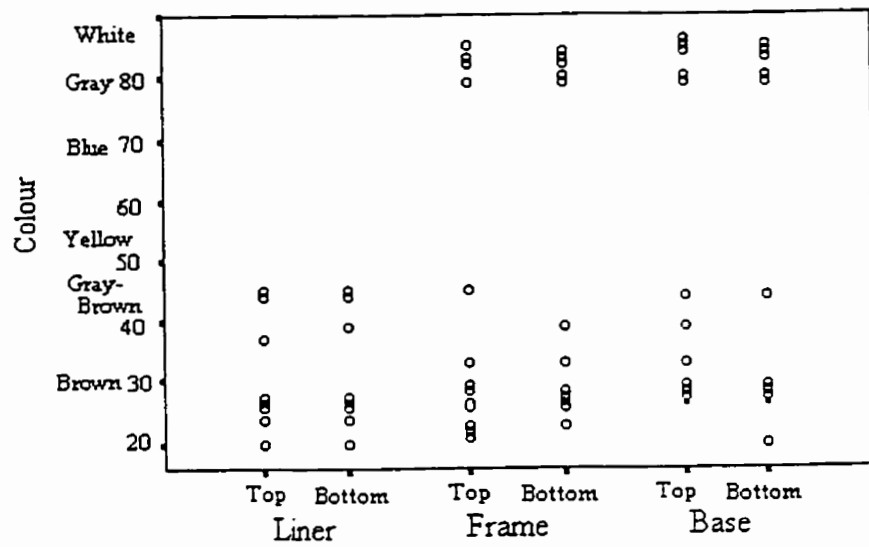


TABLE 9. Canonical Variate Analysis: eigenvalue (E.V.) , canonical correlation (C.C.) and chi-square values of the first two axes for 27 burial Yellow Warbler with six variables (nest groupings) and six groups (nest layers).

Axis	E.V.	E.V. as %	C.C.	Chi-square	df	P
1	3.87	73.52	0.892	347.15	30	<0.001
2	1.25	23.65	0.745	130.19	20	<0.001

FIGURE 13. Colour values (Smithe 1974) for the six layers of the 27 Yellow Warbler burial nests.



DISCUSSION

Nest Structure: Two- versus Three-layered Nests

Generally, Yellow Warblers at Delta Marsh built nests with three distinct layers, but 23% of the time two-layered nests were built. Three-layered nests had a distinct base, frame and liner. The liner was composed mainly of deer hair, feathers and fruits. The frame was composed mainly of grass, while the base was constructed primarily of nettles.

Materials used to build two-layered nests were similar to those used for three-layered nests. However, two-layered nests did not have a frame. Consistent with this observation, three-layered nests had a significantly higher proportion of grass than the two-layered nests. Nolan (1978) also observed the occasional absence of the middle layer in nests of the Prairie Warbler.

Three-layered nests were also larger (especially in the bottom) and heavier than two-layered nests. Observations also indicated that three-layer nests were generally more V-shaped than the two-layered nests that were relatively more U-shaped (see Figures 2 and 3). Differences in nest shape and number of layers may be a result of nest site selection. Nests in forks of willow are generally very deep and much base (nettles/hops was used, however, in 1996, deer hair was also used) is required to bring the bottom of the nest cup to an acceptable width, resulting in a V-shaped nest. Conversely, U-shaped nests are found in sites that tend to be shallower and wider, allowing a nest cup to be built with a flatter bottom. However, the increase use of grass in V-shaped nests (i.e., three-layered nest requires frame) is not clear. The Fan-shaped Warbler (*Cisticola juncidis*), fine stemmed grasses are reported to support the nest (Ueda 1984). It is has

been observed that grass provides rigidity in Yellow Warbler nests, especially in the rim. However, the need for V-shaped nests to have additional support of a frame is unclear because it presumably can rely on surrounding branches to maintain the nest shape. Nest site selection may predict the type of nest built by the Yellow Warbler and, hence, explain the dichotomy of nest shape and number of layers observed in this study.

Three-layered and Burial Nests

Rothstein (1975) hypothesized that the Yellow Warbler builds homogeneous nests with similar material used in the nest liner and frame to fool cowbirds into laying prematurely. However, nest dissections showed that although the same materials were used to build the three layers, the amounts of these materials differed significantly among layers. These differences resulted in significant visual and textural differences. Thus, the first prediction is not supported because visual homogeneity within the nest was not observed. Because cowbirds search visually for host nests (Robertson and Norman 1977), they may actually be able to use these visual and textural differences as cues to determine whether the nest is at an appropriate stage for laying (i.e., does the nest have a liner).

The second prediction of Rothstein's hypothesis states that burial is a result of premature parasitism and the female Yellow Warbler simply buries the parasitic egg in the process of nest completion. Evidence from the dissection of 27 burial nests does not support this second prediction, because a whole new nest is built, not simply the liner being extended to bury the egg(s).

Premature egg laying (i.e., as the second prediction states) may explain one of the

buried cowbird eggs observed. When this nest was dissected, it was discovered that two eggs were buried. One cowbird egg was between the original and top nest, as expected, however, another cowbird egg was suspended in the top frame indicating that the egg was laid before the second nest was finished. Although the second prediction was not supported (100% of the burial nests had a nest built upon another), premature laying may nevertheless account for a few burials observed in Yellow Warblers.

Cowbird laying observations also challenge Rothstein's hypothesis. For example, over half (59%) of the cowbird eggs are laid after clutch initiation (Sealy 1992), indicating that many cowbirds are not "tricked" into laying early. Secondly, burial often occurs when the parasitic egg is laid after clutch initiation. Sealy (1995) reported that 34% of all burials recorded occurred after the Yellow Warbler initiated her clutch. This indicates that the eggs were not laid prematurely, as nest building (as defined in Chapter 1) is terminated by the presence of the first warbler egg. Optimally, the cowbird should lay its egg on or after LD2 to decrease the risk of burial, yet lay early enough so that its eggs hatch at an appropriate time (McMaster and Sealy 1998). Rothstein (1975) did not address the timing of cowbird laying, or when Yellow Warblers bury. However, the similarity between nest liner and frame could still play a role in promoting early laying by cowbirds.

In the literature, burials have been used to describe many cases of eggs being covered over and surrounded by nesting materials resulting in the egg not being properly incubated. However, it appears that burials can be described in two ways: true burials and embedded eggs. True egg burials, as seen in most Yellow Warbler burials, involve a second nest being built over the original nest, thus covering the contents of the original

nest (i.e., host and/or parasitic eggs). This type of burial may be observed rarely in other species (see Chapter 1). Conversely, embedded eggs appear to be the result of the egg(s) being laid prematurely, and the nest builder simply finishes nest building, resulting in the eggs being partially or completely buried within the nest. Embedded cowbird eggs appear to be the main type of burial observed in other species (see Chapter 1) and as mentioned above, may be occasionally observed in Yellow Warbler nests. Finally, because the cowbird could lay prematurely at any time during nest building, embedded eggs should be found within any layer of the nest, but, most commonly within the liner with the egg being covered over with lining materials.

Based on the lack support for the predictions, the hypothesis as stated is rejected. Thus, Herrick's (1910) theory can be further examined. Unlike Rothstein's theory, in which burial occurs while the nest is being finished, Herrick states that the nest is finished and burial is a result of Yellow Warbler laying cycle being disturbed by the presence of a foreign egg.

As true burials are defined as nests built upon the original nest covering its contents, Herrick's (1910) hypothesis for explaining burial behaviour appears to have some merit. He suggested that if the breeding cycle is disturbed at the egg-laying stage, (for example, by the introduction of a cowbird egg), the warbler should desert and build another nest. The building of another nest, he claimed, would be upon the old nest because the "fear" of the disturbance is not enough to change nest sites.

Desertion originally was defined as the act of leaving the nest and nest site to build elsewhere, a behaviour observed in Yellow Warblers and other Brown-headed Cowbird acceptor species (Rothstein 1975, Clark and Robertson 1981). However, true

burials appear also to be a form of nest desertion. When parasitized, the female Yellow Warbler must first decide whether to accept or reject the nest. If rejecting the nest, then she can either build at the original site (bury the eggs) or build at a new site (traditional definition of nest desertion). Thus, true burials appear to be a form of nest desertion, not nest-site desertion.

Herrick (in Friedmann 1929) did not realize that burials involved the building of a whole new nest. Instead, he stated that the building of a new floor over the parasitic eggs should be interpreted as a new nest. Results from the present study, however, reveal that a new nest is built, not just a floor. Also, certain aspects in Herrick's hypothesis are suspect. For example, if parasitism occurs upon the completion of egg laying, according to Herrick's hypothesis, the Yellow Warbler should return to egg-laying.

Herrick (1910) also reasoned that Yellow Warblers rebuild at the same nest site because the attachment to the site is strong. Thus, the "fear" that Herrick described to cause the Yellow Warbler to desert the nest in the first place is not always strong enough to re-build at a new site. This resulted in burials. However, a strong site attachment may be better explained if there are advantages to staying at the old nest site rather than moving to a new site. The advantages of re-building at the original site versus a new site are that 1) there is no need to find new nest site, 2) it requires less time and energy to bury, and 3) the chance of being re-parasitized is reduced (see Chapter 1).

Despite these advantages, burial still may be costly because more energy apparently is required to bury than previously believed. If burials were simply additions to the liner, then its mass would be only about 0.1 g, which is the average mass of a nest

liner (Table 6 and 7). However, burials result in a whole new nest, adding approximately 1.5 g of additional material (Table 9). Although top nests are structurally similar to the bottom nests, the mass of these layers are sometimes less. Table 9 shows that the average nest base is almost double in depth compared with the top-base (0.55 vs. 1.08 cm), resulting in the top nest being generally lighter than the original nest (2.6 vs. 1.5 g, respectively). Thus the original nest seems to function as a platform, which requires relatively less material to support the new nest. With this platform, presumably less energy is required to build a true burial than to build at another site. Although using material from the old nest may considerably decrease the amount of energy required to build at a new site this option is not open to burying Yellow Warblers.

Rothstein (1975) stated that if burials are adaptive only in the context of brood parasitism, like egg ejection, it could be considered as an anti-parasitic behaviour. Depredation causes many species to desert their nests. It may be costly for a bird to re-nest in the same location after being depredated, because if the nest is highly visible to one predator, it may be to many others (Sonerud 1985), or to the same individual who already knows where the nest is. Conversely, in the context of cowbird parasitism, it is presumably of greater benefit to build a new nest at the same location (see above advantages). This indicates that building at the original nest site has no adaptive value other than in the context of brood parasitism and, according to Rothstein's (1975) criteria, it would follow that burial is an anti-parasite adaptation.

The effectiveness of burial (i.e., re-nest at the same nest site) may be related to cowbird biology. Cowbirds find and later parasitize nests at the appropriate time (Payne 1973). Female cowbirds do this by watching potential hosts from elevated perches

(Friedmann 1929, Hann 1941, Payne 1973). An enlarged hippocampus, the area of the brain responsible for location memory, allows them to remember where these nests are at a later date (Sherry *et al.* 1993). Despite these adaptations, the action of a Yellow Warbler burying does not stimulate the female cowbird to re-parasitize the nest, as reflected in the lower frequencies of parasitism at burial nests (Sealy 1995). This may be due to selection pressures against cowbirds to lay only one egg per nest site. For example, if a cowbird lays two eggs in a nest then her young would compete directly with one another resulting in lower survival rates for the young. Also, small host nests may be too crowded with more than one cowbird egg resulting in poor incubation. Finally, by spreading the eggs over many nests, the probability of all eggs being depredated decreases. At Delta Marsh, multiple parasitism in Yellow Warbler nests are uncommon (about 10%, Sealy 1995), and occur when the nest is situated between two female cowbird egg-laying ranges, resulting in one egg being laid by each female (Alderson *et al.* unpubl. data).

In Yellow Warblers, nest desertion, including both true burials and traditional nest re-location, is only observed in approximately 63% of the total nests parasitized (Sealy 1995). As true burial decreases the costs of cowbird parasitism, presumably it would be seen at a frequency closer to 100%. That burial does not occur more often indicates that nest desertion is not always the optimal solution to cowbird parasitism, even though acceptance is believed to be counter-productive (Hill and Sealy 1994). Two hypotheses attempt to explain the acceptance of cowbird parasitism, the equilibrium hypothesis (Rowher and Spaw 1988) and evolutionary lag (Rothstein 1975, 1990).

The equilibrium hypothesis proposes that accepting a parasitic egg may be the

best of a bad situation for small cowbird hosts because nest desertion is the only alternative. Rowher and Spaw (1988) assert that nest desertion carries not only the cost of re-nesting but also costs associated with delayed breeding, thus accepting parasitism may be a less costly strategy. With Yellow Warblers, the acceptance of the cowbird egg may be the best solution after LD2 and later in the season also (Clark and Robertson 1981, Sealy 1995). This could be justified with the high costs of nest desertion (including re-building) that is coupled with the decreased cost of parasitism when the nest is parasitized later in the egg-laying stage (Weatherhead 1989)

The evolutionary lag hypothesis proposes that acceptor species have not yet evolved anti-parasitic defences (Rothstein 1975, 1990). Rothstein predicts that given the strong selection pressure of cowbird parasitism, once a defence appears in a population, it would spread quickly. That Yellow Warblers reject nests with cowbird eggs at a higher rate than most acceptor species, the effectiveness of burial is indicated. However, as it does not occur at 100% of parasitized nests, other factors are clearly involved.

Overall, true burial is a unique behaviour that is only observed in Yellow Warblers. Whether it is an anti-parasitic behaviour is still debatable, but, it is interesting to note that burial is not the only interesting behaviour that Yellow Warblers display in the context of cowbird parasitism. Studies show that female Yellow Warblers do recognize female cowbirds as a unique threat by responding differently to cowbirds than to nest predators (Hobson and Sealy 1898, Gill and Sealy 1996). Female Yellow Warblers utter “seet” calls and perform nest-protection behaviour, which are only associated with the presence of a female cowbird (Hobson and Sealy 1989, Gill and Sealy 1996). Because the Yellow Warblers is the only warbler that has a distinct call and nest-

protection behaviour in response to cowbirds (Gill pers. com), this recognition may help explain why burial is unique to Yellow Warblers.

SUMMARY

The Yellow Warbler (*Dendroica petechia*) has received much attention for its habit of burying the eggs of the parasitic Brown-headed Cowbird (*Molothrus ater*). Although other species are known to bury eggs (especially cowbird eggs), the frequency has never been compiled. A review of the literature confirms that burial in other passerine species is rare and in most cases only involves the burial of cowbird egg(s). This suggests that the parasitic egg was laid prematurely in these nests and was simply buried as nest construction was completed. Few explanations have been put forth to describe the high frequency of burial observed in Yellow Warblers. The most recent was Rothstein's (1975) suggestion that burial is due to the Yellow Warbler building a nest with similar nest frame and liner so that the cowbird cannot determine when the nest is ready and parasitizes the nest prematurely. To test whether the Yellow Warbler builds a nest with similar frame and liner and to determine also whether burial involves only material of the liner, the structure of non-burial and burial nests was examined. All dissected Yellow Warblers nests had distinct layers that could be distinguished by colour and materials. Approximately three-quarters of the non-burial nests were three-layered structures (base, frame and liner), whereas the remaining nests were two-layered (base and liner). Burial nests were commonly six-layered structures, three layers below the parasitic egg and three above. The three-layers above the cowbird egg mimicked the layers below, which indicates that a complete nest was built upon the original nest. In order to bury, Yellow Warblers must first desert the contents of the original nest, not the nest site, and then build upon the original nest. Results from this study indicate that burials can be categorized into two distinct groups: true burials and embedded eggs.

True burial involves the building of a nest over the original nest and its contents (eggs) and appears to be restricted to Yellow Warblers. Conversely, embedded egg(s) seem to be the type of burial found in other species. In the majority of these cases the buried egg(s) usually only a cowbird egg, is found within the top nest layer, indicating that these egg(s) were laid prematurely.

LITERATURE CITED

- A., H.B.** 1891. Notes and queries. *Oologist* 8:15.
- Akers, L.P.** 1888. Two-storied nests of the Meadow Lark. *Oologist* 5:41.
- Allen, A.A.** 1913. An opportunity interrupted. *Bird-Lore* 15:296-300.
- American Ornithologists' Union.** 1983. Check-list of North American Birds, 6th edition. Allen Press Inc., Lawrence, Kansas. 877 pages.
- Anderson, R.T.** 1898. A discovery. *Oologist* 15:88.
- Ashworth, C.W.** 1930. California Bushtit. *Oologist* 47:43.
- Bailey, H.H.** 1925. The birds of Florida. Williams and Wilkins, Baltimore, Maryland. 146 pages.
- Bendire, C.E.** 1892. Life histories of North American birds. United States National Museum. Special Bulletin Number 1. Arno Press, New York. 518 pages.
- Bent, A.C.** 1953. Life histories of North American wood warblers, Part II. Dover Publications, Inc., New York. 734 pages.
- Bent, A.C.** 1968. Life histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies. Part Two. Dover Publications, Inc., New York. 1248 pages.
- Berger, A.J.** 1960. Some uncommon cowbird hosts. *Jack-Pine Warbler* 38:118-119.
- Bigglestone, H.C.** 1913. A study of the nesting behavior of the Yellow Warbler (*Dendroica aestiva aestiva*). *Wilson Bulletin* 25:49-67.
- Bradford, C.H.** 1928. California Bush-tit imitating the Yellow Warbler. *Oologist* 45:45-46.
- Briskie, J.V., S.G. Sealy, and K.A. Hobson.** 1990. Differential parasitism of Least Flycatchers and Yellow Warblers by the Brown-headed Cowbird. *Behavioral Ecology and Sociobiology* 27:403-410.
- Briskie, J.V., S.G. Sealy, and K.A. Hobson.** 1992. Behavioral defenses against avian brood parasitism in sympatric and allopatric host populations. *Evolution* 46:334-340.

- Brooker, M.G. and L.C. Brooker.** 1989. Cuckoo hosts in Australia. *Australian Zoological Reviews* 2:1-67.
- Brown, B.T.** 1993. Bell's Vireo (*Vireo bellii*). *In* The Birds of North America, Number 35. *Edited by* A. Poole, P. Stettenheim, and F. Gill. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.
- Brown, C.R.** 1983. Mate replacement in Purple Martins: little evidence for altruism. *Condor* 85:106-107.
- 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.
- Burtch, V.** 1898. Two-storied nest of the Phoebe. *Oologist* 15:63.
- Burtch, V.** 1910. Nesting of the Black-throated Green Warbler. *Oologist* 27:58-61.
- Chapman, F.M.** 1968. The Warblers of North America. Dover Publications, Inc., New York, NY. 307 pages.
- Charteris, G.** 1927. Rejection of Cuckoo's egg by Linnet. *British Birds* 21:180.
- Childs, J.L.** 1905. Breeding birds within the limits of the city of New York. *Warbler* 1:103-104.
- Clark, C.F.** 1988. Observations on the nesting success of Bell's Vireos in southern Arizona. *Western Birds* 19:117-120.
- Clark, K.L. and R.J. Robertson.** 1981. Cowbird parasitism and evolution of anti-parasite strategies in the Yellow Warbler. *Wilson Bulletin* 93:249-258.
- Collias, N.E. and E.C. Collias.** 1984. Nest building and bird behavior. Princeton University Press, Princeton, New Jersey. 366 pages.
- Colwell, M.A.** 1992. Wilson's Phalarope nest success is not influenced by vegetation concealment. *Condor* 94:767-772.
- Coues, E.** 1878. Field notes on birds observed in Dakota and Montana along the 49th parallel during the seasons of 1873 and 1874. *In* Bulletin of the United States Geological and Geographical Survey of the Territories. *Edited by* F.V. Hayden. Volume IV.
- Davison, J.L.** 1887. Birds laying their eggs in the nests of other birds. *Auk* 4: 263-264.

- Detroit Audubon Society.** 1953. Bird survey of the Detroit Region. 82 pages.
- Dickey, S.S.** 1941. In the mountain glades. *Oologist* 58:110-113.
- Downing, H.A. and R.L. Jeanne.** 1988. Nest construction by the paper wasp, *Polistes*: a test of sigmergy theory. *Animal Behaviour* 36:1729-1739.
- Ehrlich, W.A., E.A. Poyser, and L.E. Pratt.** 1957. Report of reconnaissance soil survey of Carberry Map sheet area. Manitoba Soil Survey, Soils Report Number 7. Winnipeg, MB. 69 pages.
- Emlen, J.T., Jr.** 1941. An experimental analysis of the breeding cycle of the Tricolored Red-wing. *Condor* 43:209-219.
- Environment Canada.** 1993. Canadian Climate Normals, 1961-1990: Volume 2, Prairie Provinces. Canadian Communications Group Publishing, Ottawa, Ontario. 266 pages.
- Friedmann, H.** 1929. The cowbirds: a study in the biology of social parasitism. C.C. Thomas, Springfield, Illinois. 421 pages.
- Friedmann, H.** 1963. Host relations of the parasitic cowbirds. *United States National Museum Bulletin* 233: 1-276.
- Friedmann, H. and L.F. Kiff.** 1985. The parasitic cowbirds and their hosts. *Proceedings of the Western Foundation of Vertebrate Zoology* 2:226-302.
- Friedmann, H., L.F. Kiff, and S.I. Rothstein.** 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. *Smithsonian Contributions to Zoology* 235:1-75.
- Gill, S.A. and S.G. Sealy.** 1996. Nest defence by Yellow Warblers: recognition of a brood parasite and an avian nest predator. *Behaviour* 133:263-282.
- Goelitz, W.A.** 1921. [Untitled]. *Oologist* 38:31.
- Goossen, J.P.** 1985. Egg-burying behaviour by a Yellow Warbler in the apparent absence of cowbird parasitism. *Blue Jay* 43:188-189.
- 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.
- Greene, I.C.** 1892. The nesting of the Blue-headed Vireo at Fitchburg, Massachusetts (*Vireo solitarius*). *Wilson Quarterly* 4:6-9.

- Griffin, W.L.** 1908. Oological freaks. *Oologist* 25:108.
- Haftorn, S.** 1978. Energetics of incubation by the Goldcrest *Regulus regulus* in relation to ambient air temperatures and the geographical distribution of the species. *Ornis Scandinavica* 9:22-30.
- Hall, J.R.** 1927. Rejection of Cuckoos' eggs by Reed Warblers. *British Birds* 21:94.
- Hanaford, A.W.** 1890. A query and answer. *Oologist* 7:16.
- Hann, H.W.** 1941. The cowbird at the nest. *Wilson Bulletin* 35:209-221.
- Harrison, H.H.** 1979. *A Field Guide to Western Birds' Nests*. Houghton Mifflin Company, Boston. 279 pages.
- Herrick, F.H.** 1910. Instinct and intelligence in birds, II. *Popular Science Monthly* 77:82-97.
- Hill D. P. and S.G. Sealy.** 1994. Desertion of nests parasitized by cowbirds: have Clay-coloured Sparrows evolved an anti-parasite defence? *Animal Behaviour* 48:1063-1070.
- Hobson, K.A. and S.G. Sealy.** 1987. Cowbird egg buried by a Northern Oriole. *Journal of Field Ornithology* 58:222-224.
- Hobson, K.A. and S. G. Sealy.** 1989. Responses of Yellow Warblers to the threat of cowbird parasitism. *Animal Behaviour* 38:510-519.
- Hohn, E.O.** 1993. Reaction of certain birds to the covering of their eggs. *Canadian Field-Naturalist* 107:224-225.
- Hopp, S.L., A. Kirby, and C.A. Boone.** 1995. White-eyed Vireo (*Vireo griseus*). In *The Birds of North America*, Number 168. Edited by A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.
- Howell, J.** 1928. Exceptional sets and nests. *Oologist* 45:138-140.
- Jacobs, J.W.** 1903. The Yellow-throated Vireo. *Wilson Bulletin* 10:17-20.
- Kedney, H.S.** 1869. The Cow Bunting. *American Naturalist* 3:550.
- Keller, V.** 1989. Egg-covering behaviour by Great Crested Grebes *Podiceps cristatus*. *Ornis Scandinavica* 20:129-131.

- Kern, M.D.** 1984. Racial differences in nests of White-crowned Sparrows. *Condor* 86:455-466.
- Kern, M.D. and A. Bushra.** 1980. Is the incubation patch required for the construction of a normal nest? *Condor* 82: 328-334.
- Kern, M.D., and C. van Riper III.** 1984. Altitudinal variations in nests of the Hawaiian Honeycreeper *Hemignathus virens virens*. *Condor* 86:443-454.
- Keyes, C.R.** 1884. Notes from central Iowa. *Ornithologist and Oologist* 9:34.
- Koehler, G.E.** 1914. A Brown Thrasher's nest. *Oologist* 31:140.
- Linsdale, J.M.** 1928. Birds of a limited area in eastern Kansas. *University of Kansas Science Bulletin* 18:517-626.
- Lippencoth, J.B.** 1903. The warblers and the vireos. *In* *Birds in their relation to man*. Edited by Weed, C.M. and N. Dearborn Publishers, Philadelphia, Pennsylvania. 380 pages.
- Loucks, W.E.** 1894. The life history and distribution of the Prothonotary Warbler in Illinois. *Bulletin of the Illinois State Laboratory of Natural History* 4:31-32.
- Lowther, P.E.** 1979. Nest selection by Brown-headed Cowbirds. *Wilson Bulletin* 91:118-122.
- Lowther, P.E.** 1983. Chickadee, thrasher, and other cowbird hosts from northwest Iowa. *Journal of Field Ornithology* 54:414-417.
- Lyon, B.E.** 1992. Egg-rejection as a defense against conspecific brood parasitism in American Coots: costs, benefits and behavioral mechanisms. Abstract from the International Conference on Behavioural Ecology, Princeton.
- MacKenzie, D.I.** 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. *Canadian Field-Naturalist* 96:61-68.
- MacKenzie, D.I., S.G. Sealy, and G.D. Sutherland.** 1982. Nest-site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. *Canadian Journal of Zoology* 60: 2212-2223.
- Maltby, F.** 1939. Twice used nests. *Oologist* 57:44-45.
- Manry, D.E.** 1992. Super dupers. *Birder's World* 6:26-32.
- Martin, H.** 1984. Zebra Finches. Grafe Unzer GmbH. Munich, Germany. 80 pages.

- Mayfield, H.F.** 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, Michigan.
- Mayfield, H.F.** 1965. The Brown-headed Cowbird, with old and new hosts. *Living Bird* 4:13-28.
- McCabe, R.A.** 1991. The little green bird ecology of the Willow Flycatcher. Rusty Rock Press, Madison, Wisconsin. 171 pages.
- McMaster, D.G. and S.G. Sealy.** 1998. Short incubation periods of Brown-headed Cowbirds: How do cowbirds hatch before Yeloo Warbler eggs? *Condor* 100:102-111.
- Mercer, W.T.** 1911. [Untitled]. *Oologist* 28:77.
- Morrison, D.F.** 1990. Multivariate statistical methods. Third Edition. McGraw-Hill, New York, NY. 495 pages.
- Morse, G.W.** 1927. Bell's Vireo. Double nest. *Oologist* 44: 23-24.
- Mumford, R.E.** 1952. Bell's Vireo in Indiana. *Wilson Bulletin* 64:224-233.
- Nice, M.M.** 1929. The fortunes of a pair of Bell Vireos. *Condor* 31:13-18.
- Nice, M.M.** 1937. Studies in the life history of the Song Sparrow, 1. *Trans. Linnaean Society of New York* 6: 1-328.
- Nicholson, W.H.** 1927. Twice used nests. *Oologist* 34:134.
- Nickell, W.P.** 1958. Brown-headed Cowbird fledged in nest of Catbird. *Wilson Bulletin* 70:286-287.
- Nickell, W.P.** 1965. Some natural and artificial materials used in the nests of common birds in Michigan. *Jack-Pine Warbler* 43:70-78.
- Nolan, V., Jr.** 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithological Monographs* 26: 1-595.
- Norman, R.F. and R.J. Robertson.** 1975. Nest-searching behavior in the Brown-headed Cowbird. *Auk* 92:610-611.
- Norris, R.T.** 1947. The Cowbirds of Preston Frith. *Wilson Bulletin* 59:83-103.
- Nyc, F.F.** 1940. Texas notes. *Oologist* 57:113-115.

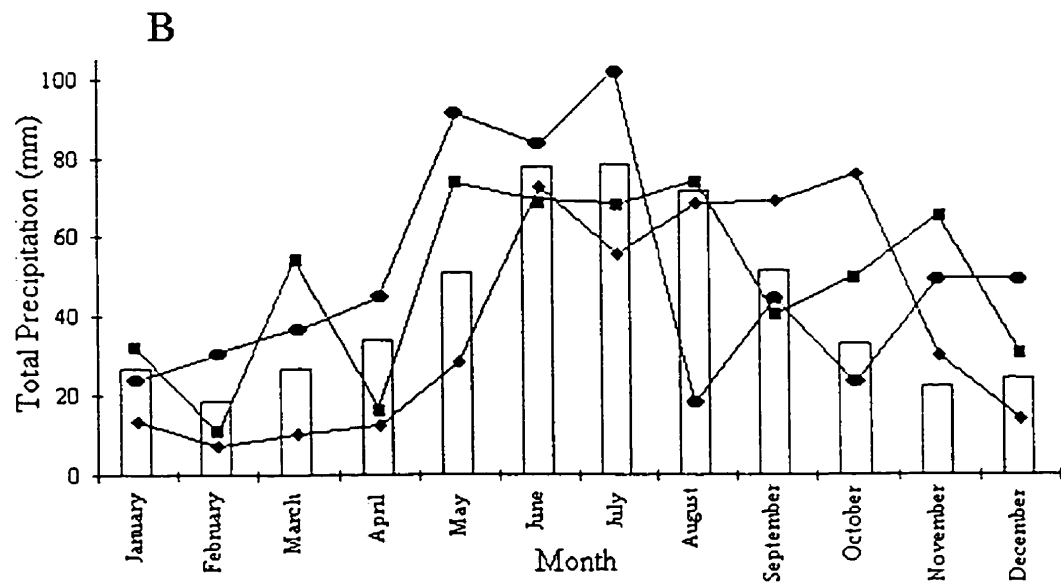
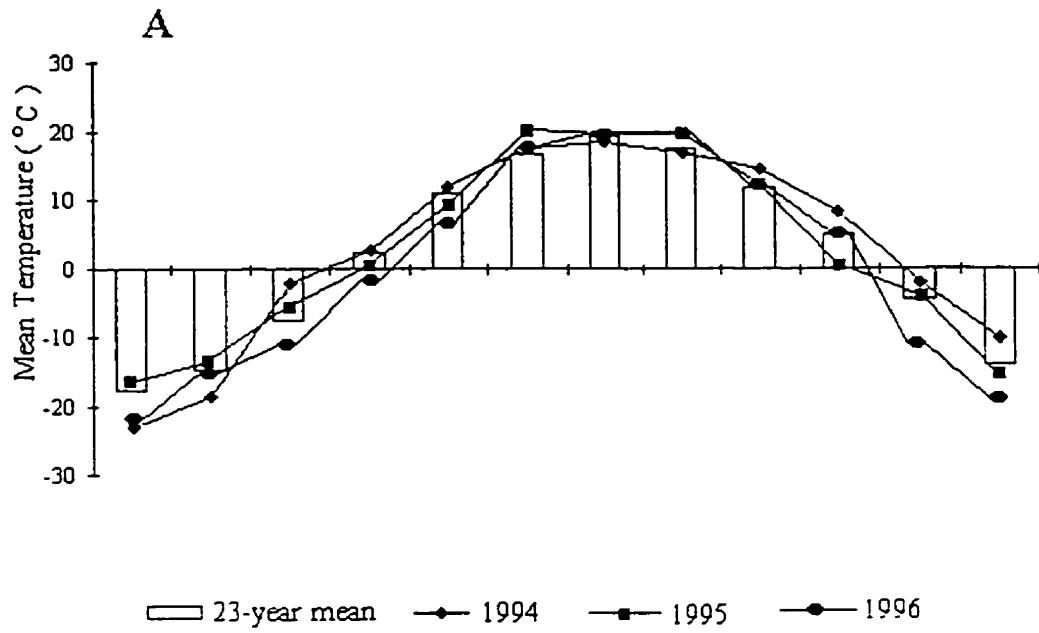
- Parshall, S.E.** 1884. The cowbird nuisance. *Ornithologist and Oologist* 9:138.
- Paton, H.** 1968. Bird notes from Oxbow. *Blue Jay* 26:61.
- Payne, R.B.** 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird, in central California. *Condor* 75:80-99.
- Payne, R.B.** 1977. The ecology of brood parasitism in birds. *Annual Review of Ecology and Systematics* 8:1-28.
- Peabody, P.B.** 1926. Nest-parasitism, with the Mourning Dove. *Oologist* 43:115-116.
- Pelton, C.W.** 1912. Bobolink nest. *Oologist* 29:211-212.
- Perry, T.D.** 1884. Painted Bunting or Nonpariel. *Oologist* 1:21.
- Pettingill, O.S, Jr.** 1985. *Ornithology in laboratory and field*, 5th Edition. Academic Press, Inc., New York. 403 pages.
- Pitelka, F.A. and E.J. Koestner.** 1942. Breeding behavior of Bell's Vireo in Illinois. *Wilson Bulletin* 54:97-106.
- Ramsay, A.O.** 1987. Thermal adaptations of the Carolina Wren. *North American Bird Bander* 12: 64.
- Reed, W.** 1926. Woodchuck. *Oologist* 43:140.
- Richter, C.H.** 1926. More two in one. *Oologist* 43:45-46.
- Robertson, R.J. and R.F. Norman.** 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. *Condor* 78:166-173.
- Robertson, R.J. and R.F. Norman.** 1977. The function and evolution of aggressive host behavior towards the Brown-headed Cowbird (*Molothrus ater*). *Canadian Journal of Zoology* 55:508-518.
- Rohwer, S. and C.D. Spaw.** 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evolutionary Ecology* 2:27-36.
- Robinson, W.D.** 1995. Louisiana Waterthrush (*Seiurus motacilla*). In *The Birds of North America*, Number 151. Edited by A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington D.C.

- Rothstein, S.I.** 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250-271.
- Rothstein, S.I.** 1986. A test of optimality: egg recognition in the Eastern Phoebe. *Animal Behaviour* 34:1109-1119.
- Rothstein, S.I.** 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics* 21:481-508.
- Rowe, J.S.** 1972. Forest regions of Canada. Canadian Forestry Service Publication Number 1300. Department of the Environment, Ottawa, Ontario.
- S., J.R.** 1884. Jottings. *Oologist* 1:24.
- Sage, J.H. and L.B. Bishop.** 1913. The Birds of Connecticut. Connecticut State Geological and Natural History Survey Bulletin 20: 1-370.
- Samuals, E.A.** 1867. Ornithology and Oology of New England.
- Savage D.L.** 1894. Cowbird. *Iowa Ornithologist* 1:29-44.
- Schlegel, M.** 1916. Ingenious disposal of cowbirds' eggs. *Country Life in America* X: 74-76.
- Schrantz, F.H.** 1943. Nest life of the Eastern Yellow Warbler. *Auk* 60: 367-387.
- Schwilling, M.D.** 1951. Parula Warbler nesting in Kansas. *Condor* 53:100-101.
- 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., K.A. Hobson, and J.V. Briskie.** 1989. Responses of Yellow Warblers to experimental intraspecific brood parasitism. *Journal of Field Ornithology* 60:224-229.
- Sherry, D.F., M.R.L. Forbes, M. Khurgel, and G.O. Ivy.** 1993. Females have a larger hippocampus than males in the brood-parasitic Brown-headed Cowbird. *Proceedings of the National Academy of Science, USA.* 90:7839-7843.

- Smithe, F.B.** 1974. *Naturalist's Color Guide*. American Museum of Natural History, New York.
- Sonerud, G.A.** 1985. Nest hole shift in Tengmalm's Owl *Aegolius funereus* as a defence against nest predation involving long-term memory in the predator. *Journal of Animal Ecology* 54:179-192.
- Southern, W.E.** 1958. Nesting of the Red-eyed Vireo in the Douglas Lake Region, Michigan. *Jack-Pine Warbler* 36:105-130 and 185-207.
- Spicker, S.** 1887. Nesting under difficulties. *Ornithologist and Oologist* 12:38.
- Stoner, E.A.** 1938. A Black Phoebe's nest with eggs of three species. *Condor* 40:42.
- Strauss, A.E.** 1993. Some observations of nesting Yellow Warblers. *Bird Observer* 21:211-212.
- Tate, J., Jr.** 1970. Nesting and development of the Chestnut-sided Warbler. *Jack-Pine Warbler* 48:57-65.
- Terrill, L. M.** 1961. Cowbird hosts in southern Quebec. *Canadian Field-Naturalist* 75:2-11.
- Thompson, E.E.** 1891. *The birds of Manitoba*. Government Print Office, Washington, D.C. 643 pages.
- Ticehurst, N.F.** 1927. Rejection of Cuckoo's egg by Tree-Pipit. *British Birds* 21:94-95.
- Ueda, K.** 1984. Successive nest building and polygyny of Fan-tailed Warblers *Cisticola juncidis*. *Ibis* 126:221-229
- Valera, F., H. Hoi, and B. Schleicher.** 1997. Egg burial in Penduline Tits, *Remiz pendulinus*: its role in mate desertion and female polyandry. *Behavioral Ecology* 8:20-27.
- W., C.B.** 1884. Oological items. *Oologist* 1:35.
- Weatherhead, P.J.** 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. *Auk* 106:358-366.
- Walkinshaw, L.H.** 1961. The effects of parasitism by the Brown-headed Cowbird on *Empidonax* flycatchers in Michigan. *Auk* 78:266-268.

- Walkinshaw, L.H.** 1983. Kirtland's Warbler: the natural history of an endangered species. Cranbrook Institute of Science, Bloomfield Hills, Michigan. 207 pages.
- Weaver, F.G.** 1949. Wood Thrush. Pages 101-123. *In* Life histories of North American thrushes, kinglets, and their allies. *Edited by* A.C. Bent. United States National Museum Bulletin Number 196.
- Weeks, L.T.** 1922. A deceived Yellow Warbler. *Auk* 39:266.
- Weeks, H.P., Jr.** 1994. Eastern Phoebe (*Sayornis phoebe*). *In* The Birds of North America, Number 95. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, D.C.
- Wiens, J.A.** 1971. "Egg-dumping" by the Grasshopper Sparrow in a Savannah Sparrow nest. *Auk* 88:185-186.
- Welty, J.C.** 1975. The life of birds. W.B. Saunders Co., Philadelphia, PA. 623 pages.
- Wharram, S.V.** 1926. Christmas birds. *Oologist* 43:9-10.

APPENDIX 1. Daily mean temperatures and total precipitation for the 23-year mean (1967-1990), 1994, 1995 and 1996 (from Environment Canada). Weather data from 1994 were included because the majority of the plant materials used to build 1995 nests grew in 1994.



APPENDIX 2. Proportion (\pm S.D.) of nesting materials found in the 1995 ($n = 51$) and 1996 ($n = 36$) three-layered Yellow Warbler nests.

	Nesting Materials ^a					
	Nettles / Hops	Grass	Deer hair	Feathers	Fruits	Other
Whole Nest						
1995	0.58 \pm 0.11	0.25 \pm 0.11	0.03 \pm 0.02	0.03 \pm 0.03	0.08 \pm 0.06	0.03 \pm 0.03
1996	0.56 \pm 0.15	0.28 \pm 0.13	0.05 \pm 0.04	0.04 \pm 0.04	0.05 \pm 0.05	0.02 \pm 0.03
Liner						
1995	0.02 \pm 0.02	0.06 \pm 0.05	0.02 \pm 0.01	0.02 \pm 0.03	0.06 \pm 0.05	0.01 \pm 0.02
1996	0.56 \pm 0.15	0.28 \pm 0.13	0.05 \pm 0.04	0.04 \pm 0.04	0.05 \pm 0.05	0.02 \pm 0.03
Frame						
1995	0.13 \pm 0.13	0.15 \pm 0.09	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.02	0.01 \pm 0.01
1996	0.09 \pm 0.06	0.16 \pm 0.09	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01
Base						
1995	0.43 \pm 0.16	0.04 \pm 0.03	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.02
1996	0.45 \pm 0.16	0.06 \pm 0.05	0.01 \pm 0.03	0.01 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01

^a Proportion for half nest.

APPENDIX 3. Proportion (\pm S.D.) of nesting materials found in the 1995 (n = 14) and 1996 (n = 12) two-layered Yellow Warbler nests.

		Nesting Materials ^a					
		Nettles / Hops	Grass	Deer hair	Feathers	Fruits	Other
Whole Nest							
1995		0.64 \pm 0.14	0.16 \pm 0.06	0.04 \pm 0.03	0.01 \pm 0.02	0.13 \pm 0.11	0.02 \pm 0.03
1996		0.62 \pm 0.11	0.22 \pm 0.11	0.03 \pm 0.02	0.04 \pm 0.05	0.07 \pm 0.06	0.01 \pm 0.01
Liner							
1995		0.05 \pm 0.05	0.09 \pm 0.04	0.03 \pm 0.03	0.01 \pm 0.01	0.10 \pm 0.09	0.01 \pm 0.01
1996		0.04 \pm 0.04	0.09 \pm 0.06	0.02 \pm 0.01	0.03 \pm 0.04	0.05 \pm 0.05	0.01 \pm 0.01
Base							
1995		0.59 \pm 0.11	0.06 \pm 0.04	0.01 \pm 0.01	0.01 \pm 0.01	0.03 \pm 0.04	0.02 \pm 0.03
1996		0.58 \pm 0.11	0.13 \pm 0.11	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.02	0.01 \pm 0.01

^a Proportion for half nest.

APPENDIX 4. Proportion (\pm SD) of nesting materials found in the 27 Yellow Warbler burial nests.

	Nesting Materials ^a					
	Nettles / Hops	Grass	Deer Hair	Feathers	Fruits	Other
Whole Nest	0.46 \pm 0.18	0.32 \pm 0.15	0.02 \pm 0.01	0.03 \pm 0.04	0.12 \pm 0.08	0.04 \pm 0.06
Top Nest	0.16 \pm 0.10	0.13 \pm 0.08	0.01 \pm 0.01	0.01 \pm 0.02	0.04 \pm 0.03	0.02 \pm 0.03
Top - Liner	0.01 \pm 0.01	0.02 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.03	0.01 \pm 0.01
Top - Frame	0.03 \pm 0.07	0.07 \pm 0.07	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01
Top - Base	0.12 \pm 0.09	0.04 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.02
Bottom Nest	0.30 \pm 0.13	0.19 \pm 0.09	0.01 \pm 0.01	0.02 \pm 0.02	0.04 \pm 0.03	0.02 \pm 0.03
Liner	0.01 \pm 0.02	0.03 \pm 0.02	0.01 \pm 0.01	0.01 \pm 0.01	0.05 \pm 0.05	0.01 \pm 0.02
Frame	0.04 \pm 0.04	0.12 \pm 0.08	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.01 \pm 0.01
Base	0.24 \pm 0.12	0.04 \pm 0.03	0.01 \pm 0.01	0.01 \pm 0.02	0.01 \pm 0.02	0.01 \pm 0.01

^a Proportion for half nest.

APPENDIX 5. Results and Discussion of yearly differences between nests built in 1995 and 1996.

RESULTS

There was a significant difference in the total proportion of materials used to construct nests between 1995 and 1996 ($F = 3.853$, $P = 0.003$). This difference was primarily due to the higher proportion of fruits in the nesting materials in 1995 compared to 1996 (Figure 14). Also, the proportion of feathers, deer hair, grass and nettles was higher in 1995 compared to 1996 (Figure 14).

Nest dimensions were not significantly different between years ($F = 0.872$, $P = 0.964$ Figure 15A). However, 1995 nests were significantly lighter than 1996 nests ($t = -2.84$, $df = 111$, $P = 0.0005$; Figure 15B).

DISCUSSION

Nests built in 1995 and 1996 differed significantly in their mass and proportion of materials. This difference may have been due to the weather and/or the availability of certain nesting materials between the two years.

When seeking for nesting materials, birds are believed to be opportunistic, however, they prefer certain materials when available (such as wool and animal hair; Kern and van Riper 1984, Pettingill 1985). At Delta Marsh, animal hair appears to be a preferred material, especially when readily available. In the winter and spring of 1996, lower than average temperatures and higher than average precipitation (snow) (see Appendix 1), may have resulted in high deer mortality. In the study area

FIGURE 14. Comparison of the proportion of materials in nests built in 1995 ($n = 65$) and 1996 ($n = 48$). Note that the left and right axes are of different scale. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*).

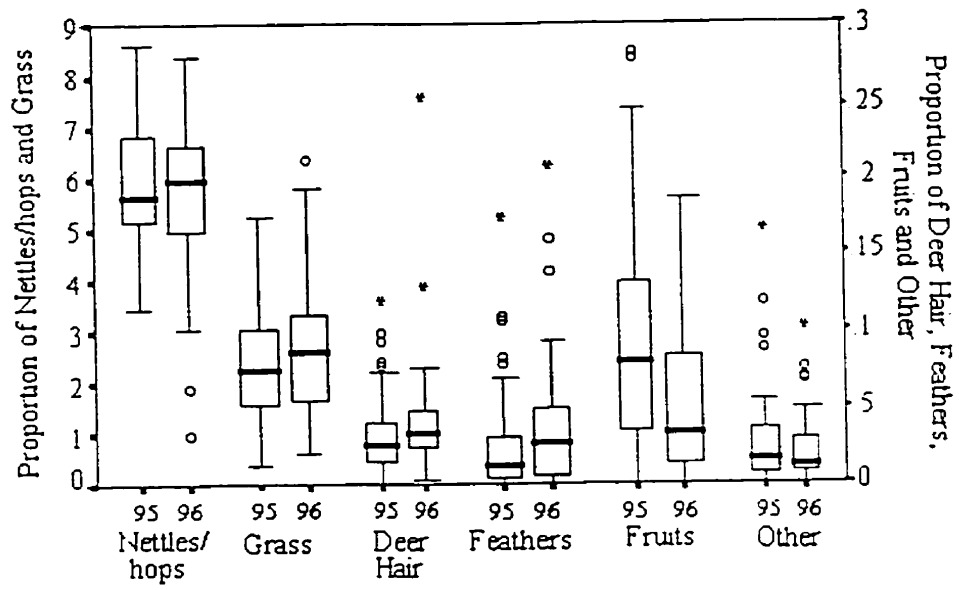
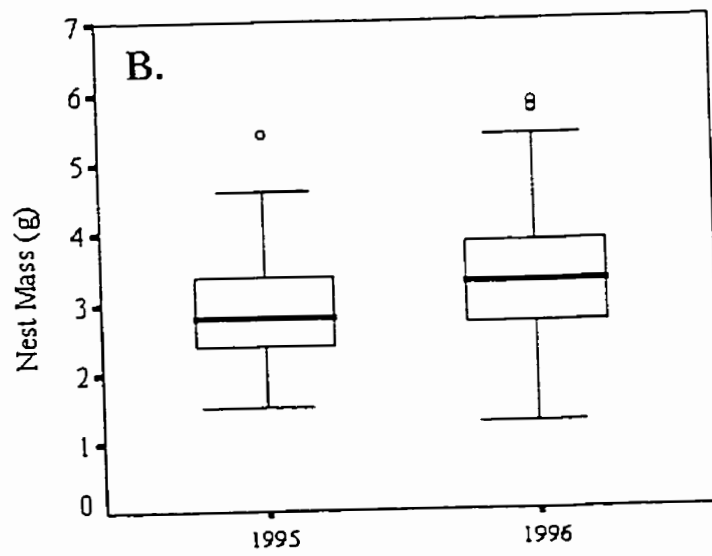
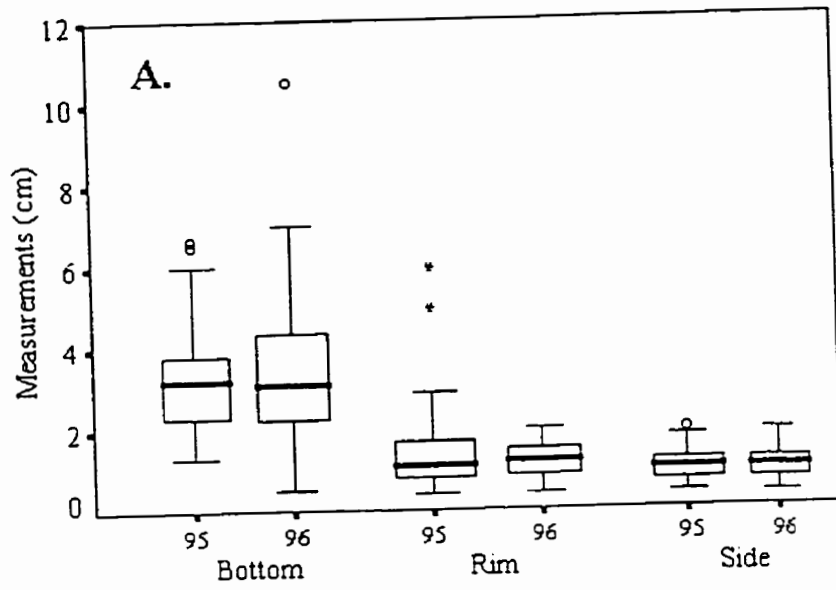


FIGURE 15. Comparison of nest size (A) and mass (B) of nests collected in 1995 (n = 65) and 1996 (n = 48). Note that nest mass is based on one-half nest. See Figure 6 for explanation of size. Boxplot represents median, 25th and 75th percentiles, whiskers extend to the highest and lowest values, excluding outliers (o) and extreme values (*).



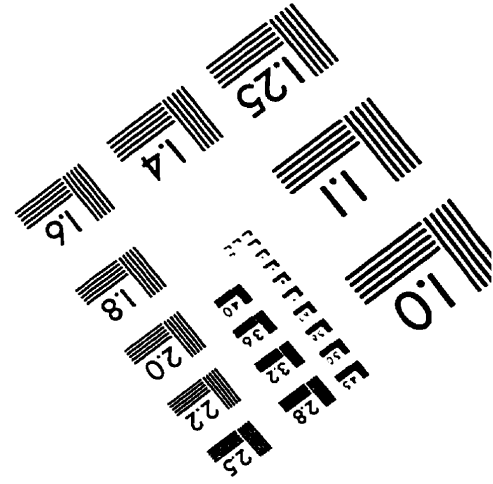
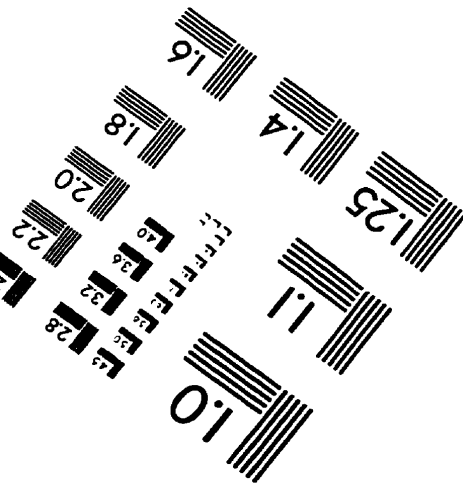
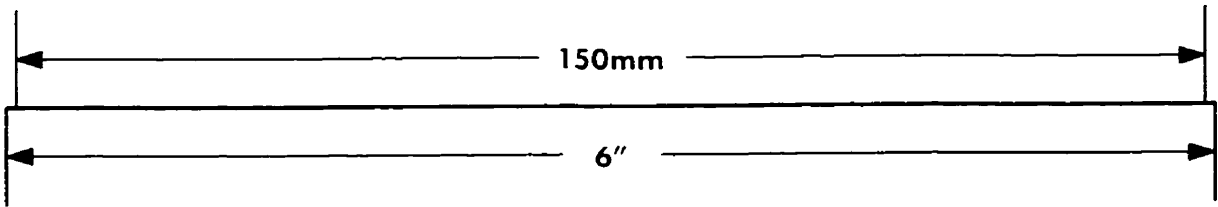
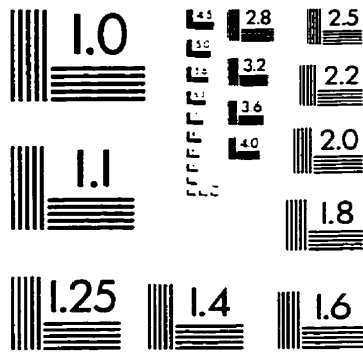
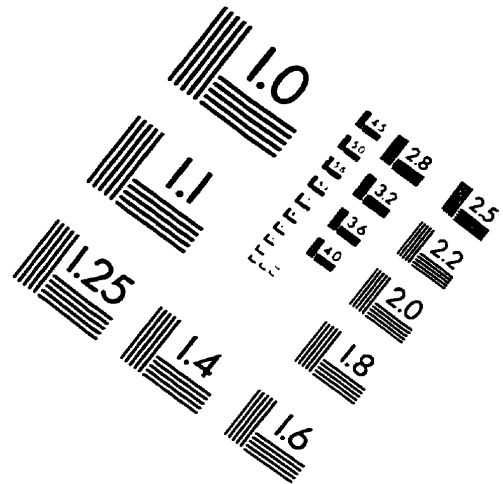
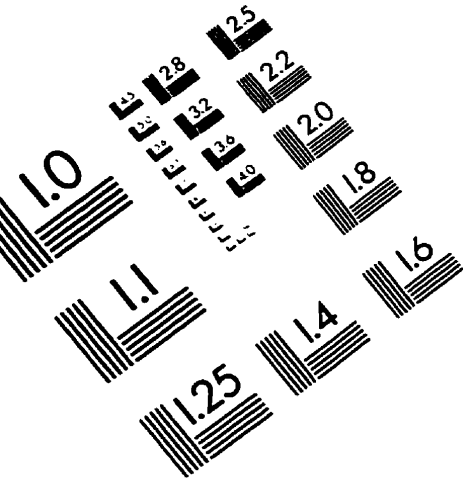
(approximately 5-km strip), three deer carcasses were found. This created an abundance of deer hair that was not seen in 1995, and was readily utilized by nesting Yellow Warblers.

Animal hair is also preferentially used by in other species. Welty (1975) noted that at the turn of the century, the Chipping Sparrow (*Spizella passerina*) was known as the Hairbird because it used generous amounts of horse hair in constructing its nest. However, with the gradual disappearance of the horse from rural areas, the Chipping Sparrow has substituted fine grasses for the nest lining. Reed (1926) also noted an extreme example of preferential use of animal hair. He observed a Tufted Titmouse (*Parus bicolor*) plucking hair from the back of a live groundhog while the bird's mate sat close by with a bill already full of hair.

Differences in temperature have also been reported to alter the use of certain materials and change the shape and size of nests. Among three races of White-crowned Sparrow (*Zonotrichia leucophrys*), nest size increased, external appearance changed and more insulative materials were used as climatic conditions became cooler (Kern 1984). Carolina Wrens (*Thryothorus ludovicianus*) also use lighter and smaller nesting materials as the breeding season becomes warmer (Ramsay 1994). The Prairie Warbler has been reported to adapt its nest size according to seasonal temperature changes (Nolan 1978). In this study, a yearly difference in nest size was not observed, however, the proportion of materials and hence mass did differ significantly between years. Of the entire nest, proportionally more fruits were used in 1995 than 1996 (0.08 and 0.05, respectively), while more deer hair was used more in 1996 than 1995 (0.05 and 0.03, respectively). The mass difference between these two materials (deer hair heavier and the wind borne

fruits of cattails and willow lighter) could have accounted for the significant difference between years. In conjunction with readily available deer hair, spring temperatures in 1996 were cooler than average (Appendix 1). This may have induced the Yellow Warblers to seek and utilize a higher proportion of warmer nesting materials. In warmer spring and summers (such as in 1995, Appendix 1), along with the unavailability of animal hair, lighter materials such as fruits, appear to be readily substituted.

IMAGE EVALUATION TEST TARGET (QA-3)



APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved