PATTERNS OF HOST NEST USE BY BROWN-HEADED COWBIRDS PARASITIZING SONG SPARROWS AND YELLOW WARBLERS

BY

CELIA M. M^{c}LAREN

A thesis presented to the University of Manitoba in fulfillment of the thesis requirements for the degree of Master of Science in the Department of Zoology

Winnipeg, Manitoba
© August 2000

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.

0-612-53191-0

Canada

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION PAGE

Patterns of Host Nest use by Brown-Headed Cowbirds Parasitizing Song Sparrows and Yellow Warblers

BY

Celia M. M^{c}Laren

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

CELIA M. MCLAREN © 2000

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/practicum 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.

Celia M. McLaren

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

Celia M. McLaren

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

ABSTRACT

I investigated patterns of host nest use by Brown-headed Cowbirds (*Molothrus ater*) parasitizing two common hosts, the Song Sparrow (*Melospiza melodia*) and the Yellow Warbler (*Dendroica petechia*), at Delta Marsh, Manitoba. I examined two non-exclusive aspects of host nest use: susceptibility of nests to discovery by nest-searching cowbirds and factors influencing host nest selection. Patterns of parasitism and multiple parasitism on Song Sparrows were determined by following the nesting attempts of this host during two breeding seasons and using molecular genetic techniques to quantify the number of female cowbirds laying eggs in parasitized nests. Host selectivity was indicated by non-random distributions of parasitisms among nests both temporally and spatially, although the frequency of cowbird eggs laid at inappropriate stages was high and cowbirds did not avoid parasitizing already-parasitized nests. Multiple parasitism was the result of a single female re-parasitizing a nest almost as often as it was the result of multiple females parasitizing the same nest. I report three major findings concerning inappropriately laid eggs in multiply parasitized nests: 1) inappropriately-timed cowbird eggs were laid later in the season than appropriately-timed eggs, 2) inappropriately-timed eggs tended to be those laid in nests parasitized by more than one female, and 3) fewer nests were available when eggs were laid in nests multiply parasitized by the same female, which were initiated earlier than nests parasitized by multiple females. These results suggest that the two types of multiple parasitism on Song Sparrow nests may be the result of different factors: nests multiply parasitized by one female are the result of a female facing low nest availability, whereas nests parasitized by more than one female are frequently the result of females laying indiscriminately.

I assessed the importance of both nest habitat and microhabitat as well as host activity in influencing the likelihood of parasitism of Song Sparrow and Yellow Warbler nests by measuring several vegetation and behavioural characteristics of nests that were unparasitized, parasitized once, and parasitized more than once by the same female and by more than one female (i.e. multiple parasitism). None of the individual variables measured was significantly related to parasitism, but non-significant trends consistent across years and between species suggest that concealment and host conspicuousness may be important, but that quantifying them is difficult and complex. A significant relationship between nest mass and parasitism probability in Song Sparrows further supports this suggestion, in that nest mass should represent the intensity of nest-building activity as a whole.

ACKNOWLEDGMENTS

The greatest expression of gratitude for the production of this thesis I wish to extend my supervisor, Dr. Spencer Sealy. Your unreserved welcome brought me here, your supreme patience and dedication carried me through everything, your unlimited knowledge and wisdom raised me to far greater understanding of birds and biology than I arrived with and your kind encouragement and support as a mentor have made the whole experience enjoyable.

I also gratefully acknowledge the other members of my committee, Dr. Norm Kenkel, Dr. Scott Forbes and Dr. Richard Baydack for their advice and support during the production of my thesis. Dr. Kenkel's enthusiastic expertise in multivariate statistics and open office door gave me the confidence to produce sensible results from an enormous data set.

In addition, I am indebted to Dr. H. Lisle Gibbs for his contributions that in large part helped to produce this thesis. Your encouragement and faith in me and your expertise and insight in the lab and in discussions have been indispensable and appreciated.

I thank the Staff of the University of Manitoba Field Station (Delta Marsh), especially manager Russ Mead, for providing wonderful working and living comfort during all the times I spent there. In particular, I appreciate Doreen Greening and Shirley Dinwoodie for being the next best thing to mothers and always showing an interest. I thank the officers of the Portage Country Club, the Delta Waterfowl and Wetlands Research Station, and the Bell Estate for allowing field work to be conducted on their property.

Fieldwork is never an easy task, and searching for Song Sparrow nests can be dreary, frustrating and unrewarding, so I am grateful for the assistance of Cara Gillard, Dean Jeske, Sara Lelièvre, Janice Lorenzana, Kevin Shonk, Robyn Underwood, Todd Underwood, and Bonnie Woolfenden. Special commendations to Cara, Sara, Jan, and Robyn for bearing the curtain in the woods, and to Robyn for staying awake in the blinds. Thanks to Lilie DeSousa for all her help when the molecular world seemed to fall apart.

My labmates also deserve a section of acknowledgments unto themselves and to each I extend the warmest of thanks. Janice Lorenzana has been the most understanding, thoughtful and supportive friend I never knew existed until I met her. Cori Schuster provided inspiration and understanding along the way. Kevin Ellison has contributed through his unending interest and his cowbird discussions. Foremost of all, Todd Underwood has been unquestionably giving, encouraging, and helpful and his friendship has been one of the best parts of being a Sealyite.

Last, but certainly foremost in my heart, I wish to thank my parents, Brian and Veronika McLaren, whose love, patience, support, and encouragement to be successful in the endeavours I chose and who are unquestionably the foundation of who I am and what brought me where I am.

Funding for this project was provided by NSERC research grants to S.G. Sealy and H.L. Gibbs and by a Society of Canadian Ornithologists Taverner Award.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

GENERAL INTRODUCTION

The parasitic Brown-headed Cowbird (*Molothrus ater*, hereafter cowbird) is a host generalist that has been reported to parasitize more than 220 species across its range, and at least 140 of these host species are known or suspected to have raised cowbirds at least to fledging (Friedmann and Kiff 1985). Cowbirds use different hosts across geographic regions and in different habitats (Lowther 1993). Frequency and intensity of parasitism also varies greatly within a host species (e.g. Wiens 1963, Southern and Southern 1980, Fleischer 1986, Smith and Myers-Smith 1998).

Much research has focussed on the effect of cowbird parasitism on the success of the host species (see Lorenzana and Sealy 1999 for review), but there are few data on the cowbird's reproductive success in the nests of different hosts. Quality of a potential host species depends on whether hosts accept or reject cowbirds eggs (Rothstein 1975), their mode of feeding offspring (e.g. Eastzer et al. 1980), the type of food their young are fed (e.g. Middleton 1977, Kozlovic et al. 1996) and/or their size (e.g. Weatherhead 1989). Although cowbirds apparently avoid unsuitable hosts (e.g. Friedmann 1963; Rothstein 1975, 1976; Sealy and Bazin 1995), the basis by which they recognize suitable hosts is unknown. More importantly, the extent to which cowbirds select the most appropriate nests within a host community remains unclear (but see Grant 1998). Natural selection should favour cowbirds that distribute their eggs to maximize their reproductive success (Rothstein 1976, Payne 1977b).

To reproduce, a host generalist such as the cowbird must locate and select nests belonging to appropriate host parents from a pool of potential host species nesting at a particular site (Briskie et al. 1990). Some descriptions exist of how cowbirds locate nests (e.g. Nice 1937, Norman and Robertson 1975, Wiley and Wiley 1980), but this literature is largely anecdotal. In addition, there is almost no information on how laying females select nests from among those available. Whether this selection is random continues to be debated. Many studies have reported a preferential use of one or more host species by cowbirds, but few have attempted to explain observed patterns (e.g. Briskie et al. 1990, Hahn and Hatfield 2000). Within a host species, highly variable parasitism frequencies are also common, but these variations lack adequate explanations (Smith and Myers-Smith 1998).

Multiple parasitism occurs when more than one cowbird egg is laid in the same host nest, either by the same female laying more than one egg in a nest or by more than one female laying in the same nest. Frequencies of multiple parasitism within a host community or on a particular host species may also be an index of host preference or, alternatively, an indication of a shortage of suitable alternative host nests. Because multiple parasitism reduces cowbird success (Rothstein and Robinson 1998, Trine 2000), cowbirds should avoid laying in already-parasitized nests. Nonetheless, most studies of the distribution of cowbird eggs within a host community have shown a random distribution, where multiple parasitism occurs as frequently as expected by chance (Ortega et al. 1994 and references therein).

Some studies have reported no preference for particular hosts among host species that vary in quality and others document host use patterns that are driven primarily by density of the parasite (McGeen 1972, Fretwell 1977, Fleischer 1985, Hoover and Brittingham 1993). However, results of most studies agree that relative host abundance alone does not explain frequency of parasitism (e.g. Elliott 1978, Fleischer 1986, Briskie et al. 1990, Alderson et al. 1999a). Variable levels of parasitism and multiple parasitism both within host communities and across populations of individual host species indicate cowbirds may adaptively select particular hosts from among those available (Robinson et al. 1995, Smith and Myers-Smith 1998, Trine 2000). Use of unsuitable hosts may be a best-of-a-bad-lot strategy that occurs as a consequence of the low cost of egg production in cowbirds (Ankney and Scott 1980) and/or the result of parasitism by young females (Rothstein 1976). Alternatively, the observed patterns might be the result of other factors related to cowbird search strategies, such as nest microhabitat features, host defenses, or nest type. In any event, host selection is in contrast to the "shotgun" strategy that suggests brood parasites lay their eggs in any nest they happen upon (e.g. Friedmann 1929, 1963, Rothstein 1976, Carter 1986, Kattan 1997).

The goal of this study was to examine patterns of host nest use by cowbirds. Use of a host nest (i.e. parasitism) probably involves two processes: the location of nests and the selection from those of the nest in which to lay an egg (Thompson and Gottfried 1981). In Chapter 1, I addressed the issue of host selection by examining the proximate causes and patterns of parasitism and multiple parasitism on the Song Sparrow (*Melospiza melodia*). At Delta Marsh, the Song Sparrow is an abundant, frequently parasitized cowbird host (S. Sealy unpubl. data). I focussed on this host because it is commonly and consistently multiply parasitized (Alderson et al. 1999a, Woolfenden 2000) and appears to be a preferred host (Woolfenden 2000), whereas other common hosts are either rarely or inconsistently multiply parasitized. My specific objectives were to determine the frequency of occurrence of multiple parasitism by one female versus several females, and to compare host and parasite breeding phenologies, timing and synchronization of parasitism events and the relationship between both types of multiple parasitism and temporal patterns of nest availability. In Chapter 2, I evaluated potential cues used by cowbirds to locate and parasitize host nests. I assessed the importance of nest habitat and host behaviour in explaining patterns of parasitism on two host species with different nest types, but which breed in the same habitat, the Song Sparrow and the Yellow Warbler (*Dendroica petechia*). Cowbird nest-searching tactics may differ when searching for nests of different hosts. Thus, the Yellow Warbler was included to compare whether patterns of parasitism on Song Sparrows that were characterized in Chapter 1 and which could be explained by either habitat or host behaviour were upheld in a second common host. I attempted to address the different processes of location versus parasitism by separating nests into three categories: unparasitized, singly parasitized, and multiply parasitized and also by identifying multiply parasitized nests as those parasitized more than once by the same female and those parasitized by more than one female. Nests parasitized by multiple females necessarily have been located by multiple females.

STUDY SITE AND SPECIES

The study site consisted of the marshland and woodland habitat at the University of Manitoba Field Station (Delta Marsh) (50° 11' N, 98° 19'W) and portions of the adjacent properties of the Portage Country Club, Delta Waterfowl and Wetlands Research Station, Bell Estate, and the village of Delta. Field work was conducted from May to July in 1998 and 1999. I searched for nests of Song Sparrows and Yellow Warblers primarily within the dune-ridge forest and adjacent marsh edge along the southern shore of Lake Manitoba, from Cram Creek east through the village of Delta to the Delta

Waterfowl and Wetlands Research Station (see map in Sealy 1980; see MacKenzie 1982 and MacKenzie et al. 1982 for description of the study site). Song Sparrows nest on or close to the ground within nettles (*Urtica dioica*), burdock (*Arctium* spp.), Virginia creeper (*Parthenocissus inseria*), and grasses in the ridge and within willows (*Salix* spp.), reeds (*Phragmites australis*) and cattails (*Typha* spp.) of the marsh and marsh-ridge interface, as well as along roadsides and lawns. Yellow Warblers nest within the small trees and shrubs of the ridge (e.g. willows, elderberries (*Sambucus* spp.), snowberry (*Symphoricarpos albus*), roses (*Rosa* spp.)) as well as within the willows and phragmites of the marsh (see Goossen and Sealy 1982, MacKenzie et al. 1982).

CHAPTER 1: TEMPORAL PATTERNS OF HOST AVAILABILITY AND MULTIPLE PARASITISM IN BROWN-HEADED COWBIRDS

INTRODUCTION

Brown-headed Cowbirds (*Molothrus ater*, hereafter cowbirds) rely on individuals of other species to raise their offspring. Brood parasitism requires cowbirds to locate nests and select one daily in which to lay an egg from among the pool of nests they have found (Thompson and Gottfried 1981). Little is known about how a laying female cowbird selects nests from among those available and how availability of host nests influences patterns of laying.

Until recently, cowbirds have been described as laying indiscriminately among host nests (e.g. Friedmann 1929, Rothstein 1976, 1990). Alternatively, non-random laying may occur if cowbirds select hosts likely to fledge their offspring. Although several potential hosts may nest in a given area, not all will be suitable choices, because of diet or behavioural incompatibilities (e.g. Middleton 1977, Eastzer et al. 1980, Kozlovic et al. 1996). Hosts also vary in their tolerance of parasitism and the frequency of rejection or desertion by the host may influence cowbird choice (e.g. Young 1963, Rothstein 1975, Briskie et al. 1990, Sealy and Bazin 1995, Grant 1998). Unequal ease in locating nests by cowbirds may mean some hosts are not used because of high nest-searching costs, regardless of their relative abundance (e.g. Briskie et al. 1990, Smith and Myers-Smith 1998). Finally, cowbirds may avoid laying eggs in previously parasitized nests (Ortega et al. 1994). Nests parasitized previously should be avoided if cowbirds are selective, because even in host species that successfully raise more than one cowbird, each additional cowbird egg in a nest may reduce cowbird hatching and fledging success (Rothstein and Robinson 1998, Trine 2000).

Indications of host preference suggest that cowbirds may adaptively select host nests from among those available (e.g. Briskie et al. 1990, Smith and Myers-Smith 1998, Alderson et al. 1999a, Hahn and Hatfield 2000). Unsuitable hosts may be used when suitable nests are not available, as a consequence of the low cost of egg production in cowbirds (Ankney and Scott 1980, Kattan 1997) and/or as a result of parasitism by young females (Rothstein 1976, Hahn et al. 1999). Unsuitable nest choice also includes eggs wasted when they are laid in nests at inappropriate stages for parasitism (Kattan 1997, Strausberger 1998, Mermoz and Reboreda 1999). The occurrence of inappropriately timed eggs has generally been considered as a rare event that results as a "a last resort in an emergency" (Friedmann 1929:186-187). In contrast, the Shiny Cowbird (*M. bonariensis*) appears to exhibit host preference (e.g. Mason 1986, Mermoz and Reboreda 1999), but in general this parasite follows a "shotgun" strategy in which females neither select high-quality hosts nor synchronize their laying with them (Post and Wiley 1977, Kattan 1997).

Multiple parasitism occurs when more than one cowbird egg is laid in the same host nest, either by the same female laying more than one egg in a nest or by more than one female laying in the same nest. The frequency of multiple parasitism may reflect host preference or, alternatively, indicate a shortage of suitable host nests (Smith and Myers-Smith 1998). Because multiple parasitism usually reduces cowbird productivity, (Rothstein and Robinson 1998, Trine 2000), a cowbird female should not reparasitize a nest or, if she can recognize a parasitized nest, avoid laying in one parasitized by another female (Ortega et al. 1994, Hahn et al. 1999). In either case, the distribution of cowbird eggs among nests should differ from random. Nonetheless, most studies in different communities revealed a random distribution of cowbird eggs that conforms to a Poisson distribution (reviewed in Ortega et al. 1994). Multiple parasitism that results when more than one female cowbird lays in the same nest (hereafter multiple female nests) may occur in areas of high cowbird density if suitable nests are in short supply (Smith and Myers-Smith 1998) or if female cowbirds cannot recognize an already-parasitized nest (Ortega et al. 1994, Hahn et al. 1999). In contrast, multiple parasitism involving the same female parasitizing a nest more than once (hereafter single female nests) should occur only when the number of suitable nests is limited (Martinez et al. 1998, Alderson et al. 1999a). In either scenario, the degree to which females maintain exclusive laying areas should influence frequencies of multiple parasitism (Martinez et al. 1998a, Soler et al. 1998, Alderson et al. 1999a, Hahn et al. 1999). Few estimates exist of the frequency at which either type of multiple parasitism occurs. Published estimates are based on studies that assume individual female cowbirds lay eggs that are morphologically distinct (e.g. McGeen and McGeen 1968, Elliott 1977) or on genetic studies in which sample sizes were small (Alderson et al. 1999a, Hahn et al. 1999, Woolfenden 2000).

To view patterns of parasite laying as strategies, it must be assumed that female cowbirds distinguish among hosts and assess the suitability of hosts (Briskie et al. 1990). On a crude scale, cowbirds clearly exhibit some choice of hosts because parasitism of unsuitable hosts is rare (Friedmann and Kiff 1985). Many researchers believe that some wastage of eggs or improper nest choice is an unavoidable cost of the generalist laying strategy (Rothstein 1976, Carter 1986, Weatherhead 1989). Understanding causes of multiple parasitism and the use of unsuitable hosts requires information on laying strategies of individual female cowbirds (e.g. Alderson et al. 1999a). Until highly variable genetic markers such as DNA microsatellite loci became available, this information was largely observational and anecdotal. Recently, use of these techniques to describe the laying patterns of individual female parasites has begun to provide answers about the spatial and temporal distribution of eggs in host nests (e.g Martinez et al. 1998a, Alderson et al. 1999a, Hahn et al. 1999, Woolfenden 2000). These studies suggest that the realized fecundity of cowbirds may be lower than previously thought, and as a result, selection for adaptive laying strategies by individual females should be high.

In this chapter, I investigated patterns of parasitism by Brown-headed Cowbirds on Song Sparrows (*Melospiza melodia*) at Delta Marsh. As a primary objective, I determined the frequency of occurrence of multiple parasitism by a single female versus several females. In addition, I compared host and parasite breeding phenologies, timing and synchronization of parasitisms, and the relationship between both types of multiple parasitism and temporal patterns of nest availability.

METHODS

Host nest monitoring

Details of the study site and species are given in the general introduction and reproductive parameters of Song Sparrows in each year are in Appendix 1. In 1998, Song Sparrow nests were searched for opportunistically throughout the site, with no effort made to find all nests. In 1999, Song Sparrow nests fell into one of two groups: those found within a "core area", 1000 m X 400 m, where I attempted to find all active Song Sparrow nests, and nests found "outside the core area", where they were sought opportunistically. I intensively searched for nests in the core area daily, and as a result I was aware of the location of all singing males and, hence, potential nests. In addition, conducting point counts and mapping territories of Song Sparrows in a previous year yielded an estimate of approximately 35 Song Sparrow nests in the core area (Woolfenden 2000), and I found 37. Considering nesting attempts after failure, I believe I found most nests initiated during the cowbird laying season within the core area.

Nests were numbered and marked 1-2 m away with flagging tape and checked daily to detect cowbird parasitism and to record the date of clutch completion, depredation, abandonment or fledging. Nests were not checked during rain, wind > 30 km/hour, or when it was < 10°C. Nests were not visited until after 0730, after Song Sparrows had laid (D.G. McMaster et al. unpubl. data). Depredated, abandoned, and fledged nests were checked every few days for up to a week until 2-3 days post-completion or failure to detect parasitisms.

Breeding phenologies

Nest stage was determined by recording host laying events or by backdating from hatch at nests found during incubation. Nests found with complete clutches that failed before hatch were assumed to have been found on the first day of incubation. This method provided the most conservative estimate for calculations of nest availability (see below) that are based on the length of time a nest was active. Likewise, nests depredated or abandoned between visits more than one day apart were assumed to have been depredated/abandoned on the day following the last day the nest was known to be active.

Laying date and timing of laying of eggs relative to those of the host were known for 22 of 65 (34%) cowbird eggs in 1998 and 64 of 101 (63%) eggs in 1999. The remainder were estimated as follows. If the nest was found with a complete host clutch and initiation date was known by backdating from hatch, I assumed any cowbird egg(s) in the nest was laid on the date corresponding to the midpoint of the host laying cycle (i.e. day 3 for a five-egg clutch, day 2 for a four-egg clutch) or, if two eggs laid by the same cowbird female were present, I assumed they were laid on host laying days 2 and 3. If cowbird egg(s) appeared in a nest with a complete clutch between nest checks separated by more than one day, I assumed the egg was laid on the midpoint of the range (if on two possible days, I assumed the earlier date). If stage of host nest was also unknown, date of cowbird laying was estimated by assuming additionally that the day the nest was found was the first day of incubation (see above). The latter estimate involved fewer than five cowbird eggs each year and these dates were not included in the determination of the number of cowbird eggs laid at inappropriate stages. Also, only nests with known initiation dates were used in the comparison of nest initiation date among unparasitized, singly parasitized, and multiply parasitized nests.

Cowbird egg sampling

Upon discovery, all cowbird eggs were removed from nests and replaced with plaster-of-Paris or wooden models painted to resemble cowbird eggs, to maintain clutch volume, prevent abandonment, and maintain the status of parasitism of the nest.

All cowbird eggs were labeled, candled with a flashlight to assess development (Lokemoen and Koford 1996) and incubated at 37.5°C for up to 10 days to ensure adequate tissue development (McMaster and Sealy 1998). Sufficiently-developed eggs were removed from the incubator, sealed in plastic bags, and stored at -20°C. In 1998, newly hatched cowbird chicks were used in another study and, hence, not all eggs incubated were available for genetic sampling. In both years, priority for genetic analyses was given to eggs from multiply parasitized nests and only these eggs were used in the analyses of timing and synchronization of parasitism.

DNA Extraction, PCR Amplification and Genotyping

Of the 65 eggs collected in 1998, 20 from multiply parasitized nests were available for genetic analyses, and 12 yielded sufficient DNA. In 1999, of the 101 eggs collected, 88 were from multiply parasitized nests. Of these, 86 were available for genetic analyses, and 76 yielded sufficient DNA. Eggs that did not yield DNA were either infertile or did not develop. DNA was isolated from tissue samples removed from the collected eggs by organic solvent purification (Sambrook et al. 1989). Allelic variability and genotypes were assessed using nine microsatellite loci, including five cowbird-specific loci, two isolated from Yellow Warblers (*Dendroica petechia*), and two isolated from Swainson's Thrush (*Catharus ustulatus*). I used polymorphic loci from these additional species to improve resolution and the power to determine kinship probabilities. Procedures for genotyping are described in detail in Alderson et al. (1999b). Briefly, I used ^{33}P end-labelled primers to amplify loci from DNA using polymerase chain reaction (PCR). PCR products were resolved by electrophoresis on 6% denaturing polyacrylamide gels at 70W for approximately 2 hours. I then dried gels and exposed them to x-ray film overnight. I determined product sizes by comparing them to a clone of known size or an individual of known genotype run on the same gel.

Sibling kinship assessment

I examined sibling relationships among groups of eggs found in the same host nest using kinship analyses based on estimates of pairwise relatedness (*r*, see Queller and Goodnight 1989) using the program KINSHIP 1.1.2 (Goodnight et al. 1997). Results of the genotyping yielded 31 nests containing more than one cowbird egg with sufficient genotypic information to resolve sibling relationships (all from 1999). I used population allele frequencies for the five cowbird and two Yellow Warbler loci from the adult cowbird population sampled at Delta Marsh since 1994 (Woolfenden unpubl. data). Allele frequencies for the two thrush loci were assessed from a sample of 20 randomly selected adult cowbirds (10 males, 10 females) captured and bled in 1998 and 1999. The program KINSHIP used these allele frequencies to generate null distributions and expected 95% confidence intervals for full-sibling, half-sibling, and unrelated pairwise relationships using 5000 randomizations. I compared the observed *r*-values for pairs of eggs with the range of expected *r*-values for each type of kin group to infer genealogical relationships. *R*-values falling within overlap regions for different kin groups were dealt with as follows. I classified as full-siblings only those pairs of individuals with *r*-values above the upper 95% confidence interval for half-siblings. I also used KINSHIP significance testing for null distributions of various kinship levels. I used a significance level of $\alpha = 0.05$, with a Bonferroni correction for 53 multiple comparisons (i.e. 0.05/53). I classified as unrelated all pairs that fell within the overlap between unrelated and half-siblings that failed to reject the null hypothesis in a likelihood test of half-sibling versus unrelated ($p>0.05$). In all cases, 95 % confidence testing based on *r*-values and likelihood tests produced matching results. These criteria were used to minimize the occurrence of Type I errors (i.e. misclassifying unrelated or half-siblings as full-siblings, or unrelated as half-siblings). These methods should conservatively identify definitive full-siblings or unrelated pairs of individuals.

Synchrony of cowbird laying

The first day of host laying (LD 1) is the day the first host egg was laid. The first day of incubation (ID 1) in host nests was the day following clutch completion (i.e. the day by which the total number of eggs in the nest had been present for two consecutive days). I considered any cowbird eggs that appeared in active nests before LD 1 up to and including ID 2 as appropriately laid. I chose these criteria because Song Sparrow and cowbird incubation periods are approximately 12 days (calculated from the laying of the last egg in sparrows, Nice 1937) and, hence, cowbird eggs laid after ID 2 will not hatch (Nice 1937, G. McMaster pers. comm). Inactive nests include abandoned nests (either unattended nests that never received a host egg or contained eggs cold to the touch for at least two consecutive days), depredated nests, and nests that had fledged young.

I compared appropriateness of cowbird laying in each category of multiply parasitized nest using two-sided Fisher's exact tests. I combined nests found in the core area and outside the core area to increase sample sizes, and because there is no reason to expect differences in cowbird synchrony between areas. I performed two analyses: 1) by nest, where each nest was scored as all eggs laid appropriately or one or more laid inappropriately, and 2) by egg, where each egg was scored as appropriately or inappropriately laid. In the latter case, only eggs subsequent to the first egg in the nest were considered, unless both eggs appeared the same day, in which case neither was included. Two or more eggs laid by the same female in a single nest were scored as "single female eggs" (see below) even if they were laid along with one or more eggs by a different female.

Nest availability

I considered any Song Sparrow nest containing real or model eggs a nest available for parasitism. The number of nests that contained neither real nor artificial cowbird eggs was the number of unparasitized nests available. Nest availability within three-day intervals was the maximum number of nests available on any of the three days in the interval. The number of nests initiated in each three-day interval was the sum of the number of nests initiated on each of the three days in the interval. For multiple regressions (see below), I performed separate analyses for each year on all nests, within and outside the core area. Although this measure of availability does not reflect actual numbers of nests available when not all nests were found, I assumed that across three-day intervals, the number of nests available is an accurate index of the real number available. This index should suffice to detect seasonal patterns of parasitism that may be related to availability. For logistic regression analyses (see below), I used only a subset of the nests found in 1999, for the following reasons. In 1999, nest monitoring was more frequent and, hence, laying dates of cowbird eggs were known more precisely. The subset of nests considered is those found within the core area where I located most active Song Sparrow nests in that area. Hence, the number of other nests active on any given day of a nest's cycle is an appropriate estimate of Song Sparrow nest availability. This estimate was used to determine how availability influences the occurrence of either type of multiple parasitism.

Statistical analyses

Differences between nest initiation dates were compared using one-way ANOVA among parasitism categories (unparasitized, singly parasitized, and multiply parasitized) and *post hoc* LSD tests among pairs. Difference in laying date of cowbird eggs that involved either type of multiple parasitism (egg laid in a nest by the same female or egg laid by a different female) was tested using the Mann-Whitney U-test. A parasitism event, defined as the laying of a cowbird egg into a host nest, is a multiple parasitism only if a cowbird egg is already present in the nest. Hence, I considered all cowbird eggs subsequent to the first laid in a nest and included only those for which laying date was known precisely. I determined whether the number of nests initiated, the total number of nests available or the number of unparasitized nests available best predicts the number of parasitism events occurring in three-day intervals throughout the season using step-wise multiple regression with parasitism events as the dependent variable. I used a probability of $p \leq 0.05$ to enter a variable in the model and $p \geq 0.1$ to remove a variable. Associations among the variables were measured using Spearman rank correlations.

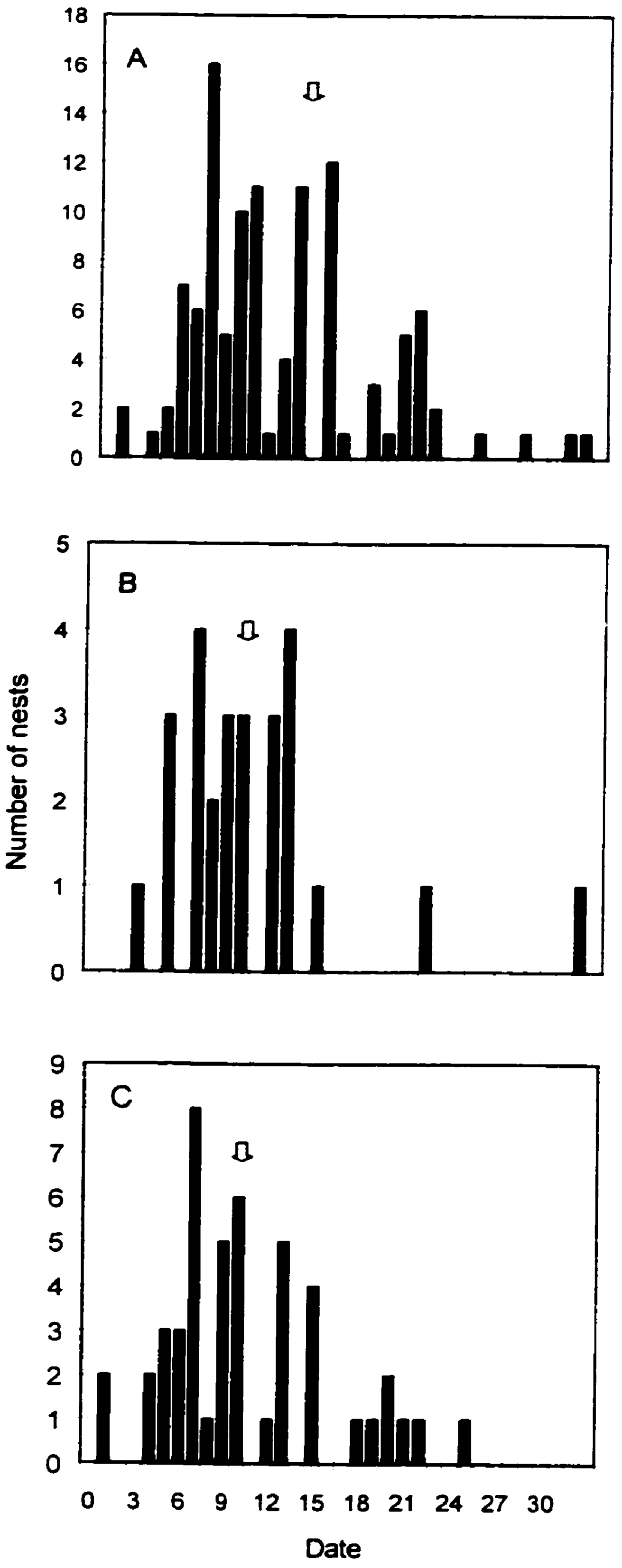
I tested the effect of nest availability on the probability that an egg was laid in a nest along with an egg(s) from another female or a subsequent time by the same female by performing logistic regressions, modified from the method described in Martinez et al. (1998a). For nests parasitized more than once by the same female or by multiple females on different days, only the second and subsequent eggs were considered. For nests parasitized more than once on the same day, all eggs were considered. The dependent variable was coded as 0 for eggs laid in nests along with an egg by the same female and 1 for eggs laid in nests along with an egg by another female. A logistic model was fitted using the maximum likelihood method (Sokal and Rohlf 1995). I used total number of Song Sparrow nests available and number of unparasitized Song Sparrow nests available the day the egg was laid as independent variables.

RESULTS

Timing and distribution of cowbird eggs

The earliest Song Sparrow nests initiated were 13 May 1998 and 18 May 1999. Mean initiation date for 1998 and 1999 were 19 May and 26 May, respectively. This 5-7 day delay in nest initiations between years was mirrored in parasitisms, because the first cowbird egg laid was correspondingly later (17 May 1998 versus 24 May 1999). I combined years by standardizing dates within years, where date of the first Song Sparrow egg = day 1. The mean initiation date significantly differed among parasitism categories ($F = 4.47$, $df = 2,107$, $P = 0.01$), where mean initiation date of unparasitized nests was significantly later than mean initiation date of either singly or multiply parasitized nests (Figure 1).

Figure 1. The frequency distributions of clutch initiation dates for A) unparasitized, B) singly parasitized, and C) multiply parasitized Song Sparrow nests. Years were combined standardizing dates between years, where date of the first Song Sparrow egg = day 1 (day 1 = 13 May in 1998, 18 May in 1999). Arrows indicate mean date in each category.

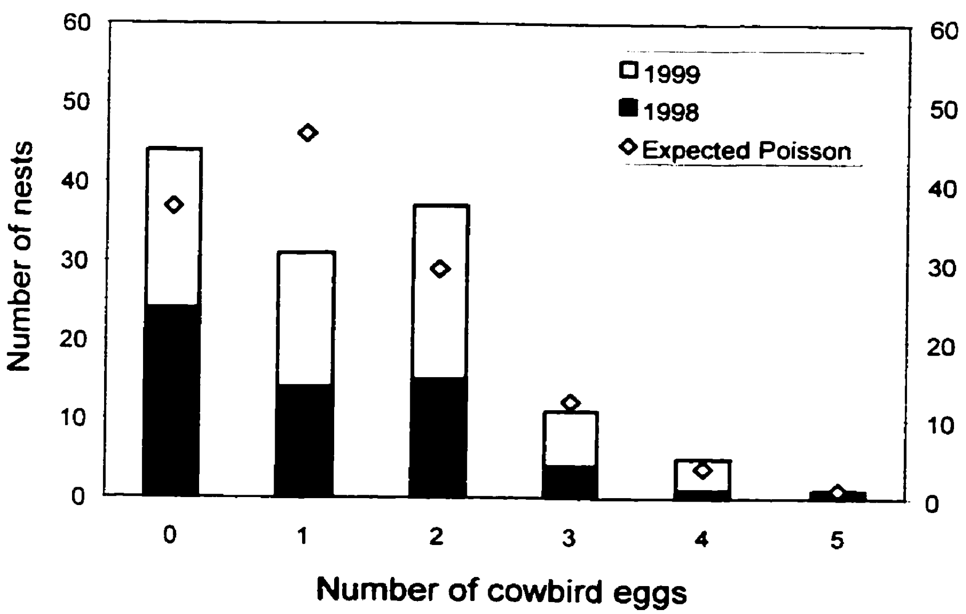

A
B
C
Number of nests
Date
0
2
4
6
8
10
12
14
16
18
0
1
2
3
4
5
0
1
2
3
4
5
6
7
8
9
0
3
6
9
12
15
18
21
24
27
30

The distribution of cowbird eggs among Song Sparrow nests showed no detectable difference between years (Kolmogorov-Smirnov test, P = 0.89; Figure 2), so I combined them. The combined distribution differed significantly from a random Poisson series ($\chi^2 = 9.0$, df = 3, $p < 0.01$; Figure 2). Fewer nests contained one egg and more nests contained two eggs than expected by chance, suggesting that the second cowbird egg in a nest is often placed non-randomly. Applying Mayfield's (1965) correction for the underestimate of the number of nests with one egg that may result if these nests are abandoned does not affect the results. Lowther (1984) described a different correction to the null distribution for the number of nests containing no cowbird eggs, based on the distinction between those that remained undiscovered by cowbirds and those that cowbirds found but did not lay in. Applying this correction requires an estimation from the data of the mean number of cowbird eggs per nest discovered by cowbirds. In the current data set, estimates of this parameter are highly variable and, hence, application of this correction is not appropriate.

Kinships

The relatedness distributions for unrelated individuals, half-siblings, and full siblings (Figure 3) and their associated 95% confidence intervals (Table 1) overlap extensively. Hence, I considered full-siblings only those pairs of individuals where a KINSHIP test of full-siblings versus half-siblings/unrelated was yielded $p<0.00094$ ($p<0.0001$ with a Bonferroni correction for 53 comparisons), or when the null hypothesis was not rejected but the pair had an *r*-value greater than the upper 95% confidence limit

Figure 2. The distribution of Brown-headed Cowbird eggs in Song Sparrow nests in 1998 and 1999 and the expected random Poisson distribution (based on both years combined).



60
50
40
30
20
10
0
Number of nests
□ 1999
■ 1998
◇ Expected Poisson
0
1
2
3
4
5
Number of cowbird eggs

Figure 3. Probability distributions for relatedness values between simulated pairs of individuals (*r*; Queller and Goodnight 1989) that are specified as unrelated, half-siblings or full-siblings, drawn from a set of alleles at nine loci. Allele frequencies are based on a sample of unrelated adult cowbirds captured at Delta Marsh since 1994.

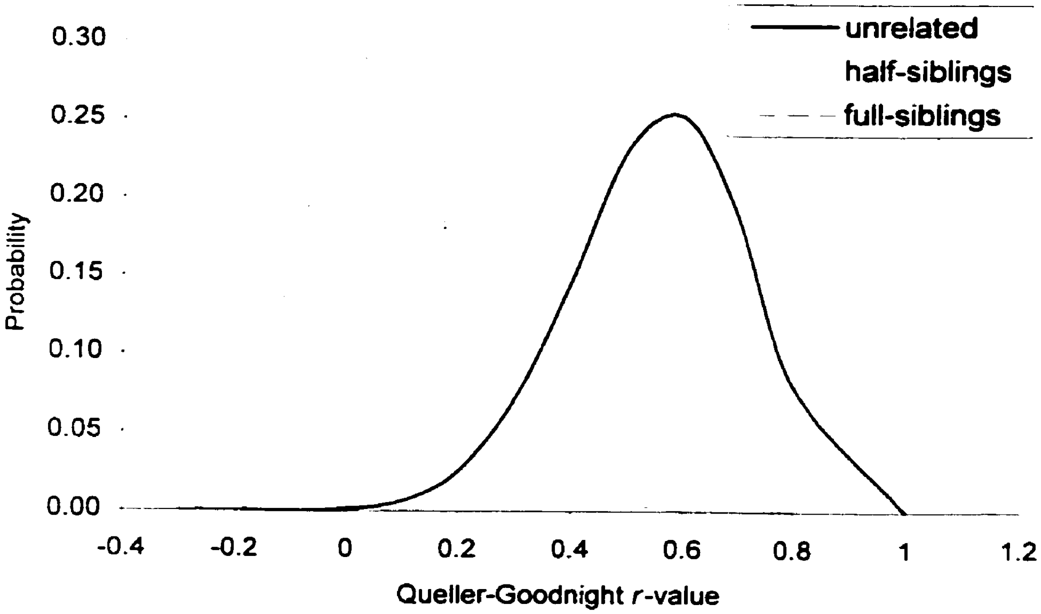

unrelated
half-siblings
full-siblings
Probability
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
1.2
Queller-Goodnight *r*-value

Table 1. Lower and upper 95% confidence limits for relatedness values for different kinship levels. The probability that two individuals share an allele by descent from their mother or father are indicated by r_m and r_p, respectively. The other possibility for half-siblings is equivalent to the one indicated.

			95% confidence limits	
Relationship	r_m	r_p	lower	upper
Full-siblings	0.5	0.5	0.2384	0.7528
Half-siblings	0.5	0.0	0.0015	0.4967
Unrelated	0.0	0.0	-0.2005	0.2612

for half-siblings (0.4967). Power of these tests for the uncorrected p-value was 0.807; i.e. less than 20% of pairs were classified as unrelated when in fact they were full-siblings. Unrelated pairs of individuals are those rejected (p>0.01) by the KINSHIP test for half-siblings versus unrelated or with an *r*-value less than 0.0015. Relatedness values for pairs of individuals from multiply parasitized nests are listed in Appendix 2. In one case, two eggs in one nest were designated full-siblings on the basis of a high *r*-value, although KINSHIP significance was only p<0.01. This classification was verified by additional information from exclusion analysis on potential maternal genotypes from the adult cowbird population (K. Shonk et al. unpubl. data).

Using these guidelines, I classified 31 multiply parasitized Song Sparrow nests, 15 within the core area and 16 outside the core area (Table 2). Of all nests, 10 (32%) contained cowbird eggs that were full-siblings (i.e. eggs were laid by one female) and 21 (68%) contained two or more eggs that were laid by more than one female. Of the latter group, five nests contained more than two cowbird eggs, of which two were laid by the same female (= "single female eggs"; see methods and below) and the remainder by a different female. Also, in five nests containing more than two cowbird eggs, the third (and fourth) egg(s) yielded no DNA. However, in only one of these cases were the eggs that yielded DNA laid by the same female and, hence, the missing information could result in a change of category for this case only.

Synchrony of cowbird laying and multiple parasitism

Many cowbird eggs in both years were not synchronized with the Song Sparrow nest cycle or were laid in inactive nests. In 1998, of 39 eggs for which the laying stage

Table 2. Number of multiply parasitized Song Sparrow nests within and outside the core area that contained cowbird eggs all laid by the same female, laid by more than one female or a combination[a].

Type of multiple parasitism	Within core	Outside Core	Total[b]
All eggs from one female	4	6	10
All eggs from different females	9	7	16
2+ eggs from one female, 1+ eggs from at least one other female	2	3	5

[a] All SFNs contained two (genotyped) cowbird eggs; for numbers of MFNs of each type containing 2, 3 or 4 cowbird eggs, see Appendix 2.

[b] Two additional multiply parasitized nests of other species were analyzed, but are not shown: one Orchard Oriole (*Icterus spurius*) nest on the core area contained two cowbird eggs from different females and one Red-winged Blackbird (*Agelaius phoeniceus*) nest outside the core area contained two cowbird eggs from the same female.

was known, 14 (36%) were inappropriately laid and in 1999, 28 of 101 eggs (28%) were inappropriately laid. These estimates are conservative, because nests were considered abandoned only if unattended with cold eggs for at least two consecutive days. Thus, for example, in two nests likely abandoned before they received any host eggs, only the second and third cowbird eggs in the nest were inappropriately laid, and two other nests found with two cold cowbird eggs were not considered in the sample.

Multiply parasitized nests that received inappropriately laid cowbird eggs were more likely the result of multiple females (multiple female nests) rather than the same female parasitizing a nest again (single female nests) (Fisher's exact test, $P = 0.02$). This result is supported by looking at subsequent-to-first eggs laid in these multiply parasitized nests. In this analysis, eggs laid by a female in a nest already containing a cowbird egg laid by another female tended to be more likely inappropriately laid than the second egg laid in a nest by the same female, although the difference is not significant (Fisher's exact test $P = 0.08$).

Mean Julian initiation date of nests that received one or more inappropriately laid cowbird egg (148.5 ± 1.9, $n = 16$) was not significantly different than mean initiation date of nests that received only appropriately laid cowbird egg(s) (148.0 ± 1.5, $n = 24$) (Mann-Whitney U-test, $U = 175.5$, $P = 0.6$). However, the laying date of inappropriately laid eggs (157.9 ± 2.0, $n = 25$) was significantly later than the laying date of appropriate eggs (153.3 ± 1.5, $n = 35$) (Mann-Whitney U-test, $U = 286$, $P = 0.03$).

Timing of cowbird laying and multiple parasitism

Although inappropriately timed eggs were both more likely laid in multiple female nests and laid later, cowbird eggs appearing in multiple female nests were not laid significantly later in the season (mean Julian date = 157.4 ● 2.8, n = 15) than eggs laid in single female nests (mean Julian date = 154.7 ± 3.0, n = 10), when data from outside and within the core area are combined (Mann-Whitney U-test, U = 62.5, P = 0.5). However, combining areas masks a real trend, because the trend in each area is in the opposite direction. Methodologically, there may be justification not to combine areas: nests within the core area were found later into the breeding season, whereas nest searching outside the core area was discontinued earlier. A comparison of initiation dates of nests found in each area confirmed a difference, although it is not statistically significant (mean Julian date; core area: 153.6 ± 3.7, n = 7, outside core area: 147.9 ± 2.0, n = 16; U = 28.5, P = 0.06). Nonetheless, examining the trends in each area separately removes this potential bias. Outside the core area, eggs appearing in multiple female nests were laid significantly later (160.1 ± 4.1, n = 9) than eggs laid in single female nests (149.0 ● 1.4, n = 6) (U = 9, P = 0.03). In contrast, within the core area, eggs appearing in multiple female nests were generally laid earlier (153.3 ± 3.1, n = 6) than eggs in single female nests (163.3 ± 4.8, n = 4), but not always and, hence, the trend is not significant (U = 4.5, P = 0.11). These results suggest that multiple female nests occur throughout the season, some earlier ones with appropriately timed eggs and some later ones with inappropriately timed eggs.

Nest availability

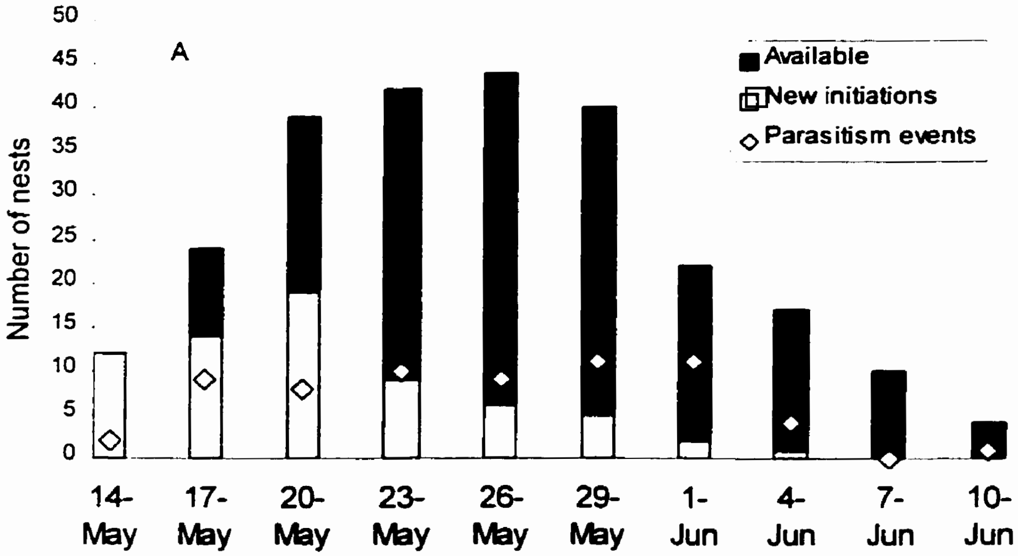
Seasonal variation in the number of parasitism events is best explained by the number of unparasitized nests in 1998 (regression $R^2 = 0.71$, model $F = 19.6$, $df = 1,8$, $P = 0.002$) and by the total nests available in 1999 (regression $R^2 = 0.74$, model $F = 37.7$, $df = 1,13$, $p < 0.001$). However, significant correlations among the independent variables result from interdependence among the variables entered into the regression models (Table 3). In both years, the number of parasitism events is correlated with both total number of nests available and the number parasitized, which, in turn, are significantly correlated with each other (Table 3, Figure 4). Hence, it is impossible to infer mechanistically whether cowbirds respond to total available nests or specifically to the unparasitized portion. Nonetheless, the number of parasitism events is not correlated in either year with the number of nests initiated (Table 3, Figure 4).

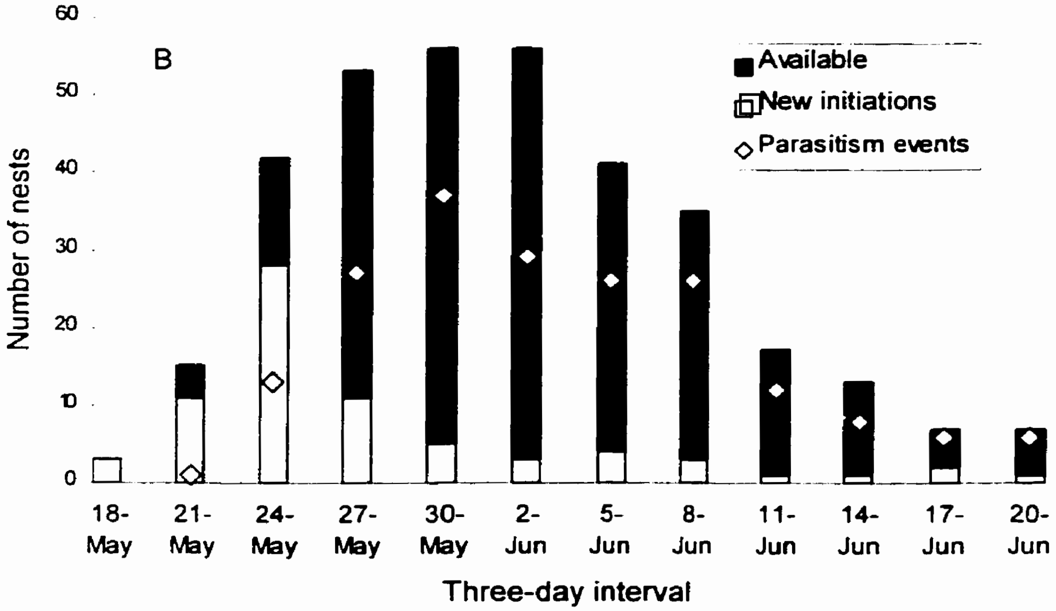
Together, the total number of Song Sparrow nests available and the number of unparasitized nests available had a significant positive effect on the probability that a cowbird egg was laid in a nest along with an egg by a different female (final model $\chi^2 = 6.87$, $df = 2$, $P = 0.03$), although neither variable alone had a significant effect (maximum likelihood estimates of the slope parameters, nests available: $B = -0.21$, $P = 0.12$, unparasitized nest available: $B = 0.53$, $P = 0.09$). However, when fewer unparasitized nests were available, subsequent eggs were more likely laid in a nest by the same female than by another female (mean number of unparasitized nests available 7.4 ± 3.8 versus 13.5 ± 2.4).

Table 3. Spearman rank correlation coefficients among four variables describing Song Sparrow and cowbird breeding phenologies in 1998 (upper value) and 1999 (lower value). An asterisk indicates significance of $p < 0.01$ (0.05 with Bonferroni correction).

	Nests available	Nests parasitized	Nests initiated
Nests available	-		
Nests parasitized	0.891*	-	
	0.891*		
Nests parasitized	0.547	0.255	-
	0.734*	0.442	
Nests parasitized	0.744*	0.768*	0.330
	0.842*	0.856*	0.569

Figure 4. Total number of Song Sparrow nests available, the proportion of those nests that are new initiations and the total number of parasitism events occurring within three-day intervals over the season in A) 1998 and B) 1999. Spearman rank correlations between these variables are listed in Table 3.


A
Number of nests
0
5
10
15
20
25
30
35
40
45
50
■ Available
◫ New initiations
◇ Parasitism events
14-May
17-May
20-May
23-May
26-May
29-May
1-Jun
4-Jun
7-Jun
10-Jun


B
Number of nests
0
10
20
30
40
50
60
■ Available
◫ New initiations
◇ Parasitism events
18-May
21-May
24-May
27-May
30-May
2-Jun
5-Jun
8-Jun
11-Jun
14-Jun
17-Jun
20-Jun
Three-day interval

DISCUSSION

Timing and distribution of cowbird eggs

Parasitized nests were not evenly distributed across the season (Figure 1). Earlier nests were parasitized more frequently than later nests, and nests that received more than one cowbird egg were initiated earlier than nests that received one cowbird egg. Wolf (1987) found a similar trend in Dark-eyed Juncos (*Junco hymenalis*). In contrast, multiple parasitism was more frequent late in the host season in Song Sparrows on Mandarte Island (Smith and Arcese 1994), and was correlated with a decline of available nests. These authors tested this relationship by comparing the number of available nests in weeks with only single and with multiple parasitism. A similar test at Delta is not possible, because of the difference in the density of cowbirds parasitizing the population, such that both types of parasitism occur to some extent in all intervals throughout the season. However, multiple parasitism earlier in the season at Delta Marsh may be related to changes in nest availability because the departure from random laying of eggs in nests indicates many more nests with two cowbird eggs than expected. Nests that escaped parasitism may have remained undiscovered because later nests are more difficult for cowbirds to locate when cover is thicker (see Chapter 2).

Parasitism and nest availability

The positive correlation between nest availability and the number of parasitism events suggests that cowbirds at Delta Marsh respond to the breeding cycle of Song Sparrows. Song Sparrows are likely the most important host at Delta Marsh, in terms of the total number of cowbird eggs that are laid in their nests (Alderson et al. 1999a, Woolfenden 2000), although several other suitable host species breed at higher densities (Sealy unpubl. data). Song Sparrows apparently are preferred hosts, because they are the only host parasitized more frequently and intensively than expected based on availability alone (Alderson et al. 1999a). In a year-by-year analysis of parasitism on three major hosts in this avian community, this preference was documented in each year only for Song Sparrows and not for Red-winged Blackbirds (*Agelaius phoeniceus*) or Yellow Warblers (Woolfenden 2000). My analysis additionally indicates that cowbirds respond to Song Sparrow nest availability within a season, and adds credence to these studies at Delta Marsh that suggest a preference for parasitism on Song Sparrows.

Other studies of cowbird parasitism similarly have pointed to preference for a particular host within an avian community. Mermoz and Reboreda (1999) showed that Shiny Cowbirds responded to the availability of nests of the Brown-and-Yellow Marshbird (*Pseudoleistes virescens*) because the incidence of parasitism was correlated with the number of host nests in the laying stage. Similarly, Clotfelter and Yasukawa (1999a,b) found parasitism frequency on Red-winged Blackbirds was correlated with the number of nests each year. However, neither of these studies definitively documented a preference for a particular host species over other potential hosts, because other hosts bred on the study areas, but patterns of parasitism on them were not examined. Although these studies documented a response by cowbirds to the host studied, demonstration of host preference requires evidence of use beyond that predicted by nest availability. Indeed, Wiens (1963) found no apparent relationship between cowbird laying and availability of nests of eight host species. The results of these studies that indicate either positive or no relationship between parasitism and host nest availability are not in contrast to studies that have found a negative relationship between host densities and parasitism levels (e.g. Fretwell 1977, Clark and Robertson 1979, Zimmerman 1983, Freeman et al. 1990). In these studies, the measure of cowbird breeding activity was parasitism frequency, whereas the positive relationships documented by Mermoz and Reboreda (1999), Clotfelter and Yasukawa (1999a,b), and the present study use parasitism events as a measure of cowbird response. Mermoz and Reboreda (1999) noted that the increased response they documented could have arisen as a result of more female cowbirds involved in the parasitic events or each female laying more eggs. In either case, an increase in cowbird laying activity could be masked by a disproportionate increase in host nest density, producing a negative correlation when parasitism frequency is the variable measured. At Delta Marsh, the resident female cowbird population is fairly stable once breeding is initiated (Woolfenden 2000). However, because apparently not all female cowbirds breed, it is unclear which alternative better explains the positive relationship between parasitism and nest availablity. Moreover, although Song Sparrows appear to be the preferred host at Delta Marsh (Alderson et al. 1999a, Woolfenden 2000) and cowbirds respond to the availability of their nests, the availability of nests of other host species likely influences parasitism patterns. Cowbirds may respond to particularly conspicuous species within a host community (Barber and Martin 1997) and use these as indicators of host densities. At Delta Marsh, Woolfenden (2000) found that total host abundance (Song Sparrows, Red-winged Blackbirds, and Yellow Warblers) was positively correlated with frequency of parasitism on Yellow Warblers, and suggested cowbirds responded to abundance of Red-winged Blackbirds. Tracking within-year nest availability of all potential hosts in the avian community is necessary to clearly identify how cowbirds respond to host nest availabilty.

Although availability of all active Song Sparrow nests and availability of unparasitized nests were both significantly correlated with parasitism events (Table 3), the results indicate total nest availability adequately predicts parasitism events. Correlation coefficients between parasitism events and both availability variables were approximately the same, but there was also a significant correlation between the total number of nests available and the proportion of those nests that were parasitized. This result is not surprising because as the total number of nests increased early in the season, the cumulative number of parasitism events increased as well and, hence, the proportion of nests parasitized also must have increased. Furthermore, cowbirds did not avoid laying in already-parasitized nests. The distribution of cowbird eggs per nest differed from a random Poisson, and there were more multiply parasitized nests than expected by chance, in contrast to the number predicted if females avoid already-parasitized nests. In addition, multiple parasitism occurred even when there were unparasitized nests available. In contrast, Smith and Arcese (1994) reported lower than expected frequency of multiple parasitism on Song Sparrows, but their insular host population was visited by at most three female cowbirds per year. One possible explanation for the discrepancy between these results is that an individual female may not re-parasitize a nest when alternative nests are available (see Smith and Arcese 1994), but that female cowbirds may not be able to recognize a nest parasitized by another cowbird.

Characteristics of multiple parasitism

Timing and synchronization

The frequency of unsynchronized parasitisms (30% of all cowbird eggs laid in Song Sparrow nests, both years combined) is one of the highest documented for any host species. In most records, frequencies of inappropriate laying involve less than 10% of all cowbird eggs laid (Berger 1951, Mayfield 1960, Strausberger 1998). Frequencies between 10-20% have also been reported (Klaas 1975, Nolan 1978, Wolf 1987, Sealy 1992). In only four studies were frequencies comparable to the present study (Davis 1994, 23% in eight grassland hosts, Scott and Lemon 1996, 24% in Song Sparrows, Weatherhead 1989, 28% and Freeman et al. 1990, 22% in Red-winged Blackbirds). Freeman et al. (1990) observed that nests in marshes surrounded by more trees had fewer cowbird eggs laid inappropriately and concluded that cowbirds perching near the marsh gain information on when to parasitize nests. I recorded no cowbirds laying during the host nestling stage, although such cases have been documented in several species (e.g. Leopold 1924, Berger 1951, Mumford 1959, Furrer in Friedmann et al. 1977, Davis 1994, Sealy 1995).

The number of nests initiated was not significantly related to the number of parasitism events in either year, but the number of nests available was significantly correlated with parasitism events. My definition of an available nest included all nests containing eggs, not only those in the laying stage. These results suggest that cowbirds do not preferentially parasitize nests during host laying, either because they are unable to assess stage or because they are forced to lay at other stages because of a lack of other known nests. Weatherhead (1989) similarly suggested evolutionary lag as an explanation for the lack of refinement in timing of parasitism on Red-winged Blackbirds, suggesting that selection for the ability to ascertain stage of the host nest has been slow. In another cowbird species, poor synchronization resulting in "shotgun" parasitism by Shiny Cowbirds may be the result of the difficulty cowbirds have in gaining access to cavity or domed nests (Kattan 1997, Mermoz and Reboreda 1999). The two examples of poor synchronization in Red-winged Blackbirds may be similarly explained, if group defense by colonially nesting blackbirds prevents cowbirds from monitoring nests (Robertson and Norman 1977, Folkers and Lowther 1985). This explanation, however, does not likely explain the result in Song Sparrows and other grassland ground-nesting hosts. Perhaps cowbirds are less likely to monitor ground-nests because of the search costs associated with relocating these nests to determine contents or because of the inability to observe host behaviour at them from a distant perch.

If nests are both less available and more difficult to locate later in the season, one might expect more inappropriately laid eggs later in the season (Friedmann 1929, Hoy and Ottow 1964). This prediction was supported when examining the laying dates of individual eggs, but not in the analysis of initiation dates of nests classified as either all eggs appropriately timed or some eggs inappropriately timed. The latter test eliminated bias that is inherent in the contrast, because inappropriately laid eggs include those laid later in the host nest cycle and, hence, also later in the season. This test may still be somewhat biased, however, because eggs for which laying dates were not known precisely were not included. These eggs tended to be laid earlier in the host cycle (i.e. they were in nests found after clutch completion, but before hatch) and, hence, appropriate and therefore also laid earlier in the season. In any event, lower availability of nests later in the season does not seem to explain the inappropriate layings.

This is the first study to examine the frequency at which cowbird eggs are inappropriately laid and what factors may influence this behaviour (see Strausberger 1998). I report three major findings concerning inappropriately laid eggs in multiply parasitized nests: 1) inappropriately-timed cowbird eggs were laid later in the season than appropriately-timed eggs, 2) inappropriately-timed eggs tended to be those laid in nests parasitized by more than one female, and 3) fewer nests were available when eggs were laid in nests multiply parasitized by the same female, which were initiated earlier than nests parasitized by multiple females. Thus, if few nests are available early in the season an individual female cowbird may re-parasitize a nest. Later in the season, when nests may be more difficult for cowbirds to locate (see Chapter 2), some females may also return to re-parasitize a nest. In contrast, particularly later in the season, some females indiscriminately lay in inappropriate nests, including already-parasitized nests. I could not test whether nest availability was related to inappropriate laying, because both kinds of parasitism occur on most days throughout the season. Also, I could not identify whether the non-selective females were the same females that laid synchronized eggs earlier or involved other non-selective females.

Timing and availability

The finding that fewer nests were available when eggs were laid in parasitized nests by the same female than when eggs were laid in a nest parasitized by a different female is in contrast to Martinez et al.'s (1998a) findings. These authors found that frequency of parasitism and multiple parasitism in general are influenced by nest availability, because synchronous host breeding reduces the probability each nest is parasitized (Martinez et al. 1996). However, they found that nests re-parasitized by the same female Great Spotted Cuckoo (*Clamator glandarius*) tended to occur independently of Black-billed Magpie (*Pica pica*) nest availability. They suggested these nests are re-used because they are preferred in some way, perhaps related to host quality (Soler et al. 1995). Even so, in a previous year at the same site, Martinez et al. (1998b) suggested that availability may instead influence host choice: multiply parasitized nests were mostly "shared" nests containing eggs laid by different females, and temporal patterns of egg laying suggest cuckoos parasitize Carrion Crows (*Corvus corone*) when Magpie nests are not available. Similarly, Strausberger (1998) suggested multiple parasitism may point to host preference. My results suggest that the two types of multiple parasitism are the result of different factors: nests are parasitized more than once by the same female when few new nests are available, whereas nests parasitized by more than one female frequently involve females laying indiscriminately. A female may multiply parasitize a nest because it is preferred over another nest of a lower-quality host species. This assumes that a female remembers the nests she has parasitized. Although there is indirect evidence based on relative hippocampus size that female cowbirds have the capacity to remember nest locations (Sherry et al. 1993), there is little evidence to validate the assumption directly.

Although estimates of potential cowbird fecundity abound, estimates of realized fecundity are few. Recent genetic studies have indicated that the realized fecundity of cowbirds may be much lower than potential fecundity estimates suggested (Alderson et al. 1999b, Hahn et al. 1999, Woolfenden 2000). Rothstein (1976) originally proposed that cowbirds are physiologically constrained to produce a series of eggs even on days when nests were not available. Later, Ankney and Scott (1980) suggested that cowbirds produce an egg only when a nest is available. Other studies are similarly contradictory. Oviducal analyses have led to the suggestion that atresia may occur if no nests are available (Payne 1965, 1998; Scott and Ankney 1983). However, studying cowbirds in captivity, Holford and Roby (1993) found egg production was uncorrelated with nest availability. Hahn et al. (1999) proposed that a female may eat her egg if no nest is available, but there is no evidence that this occurs. If cowbirds are forced to produce eggs even when no suitable nest is available, Strausberger (1998) suggested that they may "make the best of a bad situation" and reparasitize an already-parasitized nest. However, his data did not support this hypothesis, nor did he find evidence that cowbirds laid at inappropriate times. Hahn et al. (1999:216) speculated that multiple parasitism resulted from "opportunistic laying by a yearling female cowbird". They cited Darley's (1983) observation that younger females usually do not hold a home range and suggested these females parasitize any conspicuous nest, irrespective of parasitism status or stage. While multiple parasitism may be a consequence of a non-territorial system or a system involving some non-territorial individuals (Martinez et al. 1998a, Alderson et al. 1999a), there is no information on the ages of the females involved. Yearling female cowbirds arrive at breeding sites later (Darley 1983, Woolfenden 2000) and delay breeding (Fleischer et al. 1987). It is possible, therefore, that later-laid and inappropriately timed cowbird eggs at Delta Marsh are laid by younger females. In any event, the possibility that there are two types of cowbird females, selective egg-layers and indiscriminate egg-layers, must be considered when cowbird fecundity is discussed. Reports of average fecundity based on all females in the population may be misleading if researchers are able to collect more eggs from females that lay many well-timed eggs than from females that lay many ill-timed eggs.

Describing the laying behaviour of individual female cowbirds as optimal strategies in a game theory sense requires an understanding of several different aspects of single and multiple parasitism (Payne 1977a): the criteria used by cowbirds to rank the quality of host nests, differences among individual females in nest-searching experience, differences in the ability to maintain territories, and the contributions of different females to multiply parasitized nests. I have provided data to clarify the last point. More information on the first three will help contribute to a general understanding of selection pressures acting on reproductive behaviour of cowbirds.

CHAPTER 2: SUSCEPTIBILITY OF HOST NESTS TO BROOD PARASITISM: HOW DO COWBIRDS LOCATE NESTS?

INTRODUCTION

The host generalist strategy of Brown-headed Cowbirds (*Molothrus ater*; hereafter cowbirds) allows for considerable variation in individual reproductive success that can be manifested through host choice and successful synchronization with host laying. As a consequence, cowbirds should maximize their laying options by continually searching for new opportunities for parasitism. Observations and experiments on how cowbirds locate nests are few and the relative importance of various observed nest-searching strategies remains unclear. Three methods that cowbirds use to locate nests have been described: 1) observation of hosts building their nests is widely considered the most important (e.g. Friedmann 1929, Nice 1937, Hann 1941, Berger 1951, Southern 1958, Payne 1973, Norman and Robertson 1975, Thompson and Gottfried 1981), but 2) female cowbirds may actively search for nests by walking silently about the habitat where nests are likely to be found (Norman and Robertson 1975, Gates and Gysel 1978, Wiley and Wiley 1980), and 3) female cowbirds may flutter about the vegetation to flush host females from their nests (Norman and Robertson 1975, Wiley and Wiley 1980). These methods suggest that the type and amount of vegetative cover of the habitat, especially around nests, influences parasitism risk.

The scale of vegetative cover that most influences risk of discovery depends on how cowbirds search for nests. If cowbirds only actively search for nests, the sight of a nest is critical, and cover immediately around the nest should be related to parasitism risk. In contrast, if cowbirds passively observe hosts, the sight of nest building activities of the hosts is important and the risk of parasitism would be affected only if vegetative cover concealed host activities. Here, cover throughout the nesting territory may be important (Larison et al. 1998, Uyehara and Whitfield 2000). However, habitat type may override the importance of concealment at either scale, if cowbird abundance or habitat preference varies by habitat type (Burhans 1997, Spautz 1999).

Most studies that have examined the habitat features at the nest have concluded that concealment alone is not a good predictor of the likelihood of parasitism (e.g. Anderson and Storer 1976, Gochfeld 1979, Buech 1982, Clotfelter 1998, but see DellaSala 1985, Burhans 1997, Larison et al. 1998). Some structural features of the territory may increase parasitism probability if observations of host activity are important and if these features improve the ability of cowbirds to observe hosts (e.g. Anderson and Storer 1976, Gochfeld 1979, Brittingham and Temple 1996, Romig and Crawford 1995, Larison et al. 1998, but see Freeman et al. 1990). Despite a growing number of studies addressing these issues, the proximate cues that cowbirds use to locate nests still are not known.

Independent of habitat features, secretive host behaviour around the nest may be a beneficial antiparasite strategy if cowbirds cue into this behaviour to locate nests (Ricklefs 1969, Uyehara and Narins 1995). The nesting cue hypothesis (Robertson and Norman 1977, Gill et al. 1997) predicts that host defensiveness toward cowbirds near a nest increases the likelihood of discovery. Specifically, the nesting cue hypothesis requires that hosts respond to cowbirds at some distance from their nests and that the aggressive behaviours intensify as the nest is approached (Neudorf and Sealy 1992).

More generally, any activities associated with the nest may provide cues for cowbirds (Banks 1997). This activity may include trips to and from the nest by the hosts (Hann 1941, Gochfeld 1979, Banks 1997) or vocalizations near it (Uyehara and Narins 1995, Banks 1997, Clotfelter 1998). Studies using artificial nests without direct or indirect evidence of host activity have not elicited parasitism (e.g. Laskey 1950, Thompson and Gottfried 1976, 1981, Grieef 1995). Similarly, studies indirectly testing the importance of host activity using artificial nests with eggs added daily and/or taxidermic models of hosts with or without song also have rarely elicited parasitism (e.g. Lowther 1979, Wiley 1988, Yahner and DeLong 1992, Grieef 1995).

In this chapter, I examine the importance of habitat concealment of the nest and host activity in influencing the likelihood of parasitism on two host species with different nest types, but which breed in the same habitat. The Song Sparrow (*Melospiza melodia*) and the Yellow Warbler (*Dendroica petechia*) are two of the most frequently parasitized host species at Delta Marsh (S. Sealy unpubl. data). I hypothesized that concealment of host nests affects vulnerability to parasitism in two ways: concealment of the nest proper may reduce the risk of discovery if cowbirds actively search for nests or concealment within the greater nest area may conceal activity of hosts if cowbirds locate nests by passively observing host activity. Because the Song Sparrow nests in both the treeless marsh and forested dune ridge, I tested the influence of habitat type on the relationship between parasitism and concealment. In addition, I examined the characteristics of nests susceptible to parasitism using contrasts beyond the simple comparison of unparasitized versus parasitized nests used in most previous studies. The relationship between concealment and susceptibility may be complex, because discovery of a nest by cowbirds may not always be interpreted by the number of cowbird eggs in the nest. Hence, I compared concealment of Song Sparrow nests that were unparasitized, parasitized once, and parasitized more than once by the same female and by more than one female (i.e. multiple parasitism).

My goals were 1) to identify a measure of nest concealment that accurately represents the view of a nest-searching cowbird by (a) measuring vegetation during the time a nest is susceptible to parasitism and (b) characterizing several measures of concealment in the microhabitat of the nest and within the broader nest habitat, 2) to assess whether surreptitious behaviour of hosts reduces susceptibility to parasitism and what aspects of behaviour might provide cues to nest-searching cowbirds, and 3) to examine the relationship between habitat and behaviour in determining susceptibility of nests to parasitism.

METHODS

Vegetation Sampling

Vegetation characteristics at Song Sparrow and Yellow Warbler nests were measured from May to July, 1998 and 1999. I measured vegetation as soon as possible after a nest was discovered, but not before host clutches were complete. This protocol permitted an accurate assessment of concealment at the stage cowbirds are likely to locate and parasitize most nests (see Burhans and Thompson 1998). All nests included in the sample were exposed to parasitism for at least the laying stage, when most cowbird eggs are laid (see Chapter 1, see also Sealy 1995, Woolfenden unpubl. data), so parasitism intensity (i.e. the number of cowbird eggs laid in the nest) could be accurately assigned. In 1999, I measured vegetation as soon as possible after the termination of a nesting attempt, not while nests were active as in 1998, to further reduce the risk of abandonment associated with extended visits while measuring vegetation. Preliminary analysis of 1998 data indicated that most vegetation variables did not change significantly over intervals of a week or less, and the difference in date waiting for nest termination was rarely longer than 7-8 days. All measurements were taken between 1300 and 2100 hours, Central Standard Time.

Song Sparrow

I followed James and Shugart's (1970) methodology, but modifications noted below are based on Burhans (1997), Burhans and Thompson (1998), and Larison et al. (1998). Consistent with all of these studies, I established a 0.04-ha circular plot (radius = 11.3 m) centred on the nest. I paced approximately 11 m from the nest in each of the cardinal directions and marked the endpoints. I measured the following variables (Table 4): (1) lateral vegetation density, at two scales (Larison et al. 1998): (a) in the nest microhabitat ("at 5 m"). Positioned approximately 5 m from the nest, I photographed a 0.5-m x 2-m cloth held 1 m in front of the nest, in each of the four cardinal directions. The cloth had a grid of 50 10-cm x 10-cm squares in each of the bottom half (<1 m above ground) and top half (1-2 m above ground). The proportion of squares 50% or more obscured by vegetation in each half was an estimate of vegetation cover < 1 m (bottom) and 1 m-2 m (top). For each height category, I considered the mean, minimum, and maximum of the four values from each cardinal direction as variables. I included minima and maxima, because using only a mean value may obscure extremes that occur in any

Table 4. Summary of vegetation variables measured at Song Sparrow (SOSP) and Yellow Warbler (YWAR) nests at Delta Marsh, 1998-1999.

Vegetation variable	1998	1999
Density 0-1 m (at 5 m) [a]	SOSP & YWAR	SOSP
Minimum density 0-1 m (at 5 m)	SOSP & YWAR	SOSP
Maximum density 0-1 m (at 5 m)	SOSP & YWAR	SOSP
Density 1-2 m (at 5 m)	SOSP & YWAR	SOSP
Minimum density 1-2 m (at 5 m)	SOSP & YWAR	not measured
Maximum density 1-2 m (at 5 m)	SOSP & YWAR	SOSP
Density 0-1 m (at 11 m)	SOSP & YWAR	not measured
Minimum density 0-1 m (at 11 m)	SOSP & YWAR	not measured
Maximum density 0-1 m (at 11 m)	SOSP & YWAR	not measured
Density 1-2 m (at 11 m)	SOSP & YWAR	not measured
Minimum density 1-2 m (at 11 m)	SOSP & YWAR	not measured
Maximum density 1-2 m (at 11 m)	SOSP & YWAR	not measured
Mean percent ground cover around nest[b]	SOSP	SOSP
Minimum ground cover around nest	SOSP	SOSP
Maximum ground cover around nest	SOSP	SOSP
Percent ground cover over nest	SOSP	SOSP
Total number of stems	SOSP	not measured
Distance to nearest perch (m)	SOSP & YWAR	not measured

one or more direction, whereas to a nest-searching cowbird, any exposed view of the nest (e.g. no cover on one side of a nest) may increase its detectability (Burhans and Thompson 1998); (b) in the nest habitat ("at 11 m"). Likewise, I photographed the cloth held 5 m in front of the nest in each cardinal direction, from 11 m. As above, for each height category, I used the mean, minimum, and maximum of the four values from each cardinal direction as variables. 2) Percent ground cover. I peered through an ocular tube with a 10-cell grid drawn on the eyepiece, held at approximately 1 m above ground, to measure percent ground cover. I sampled directly over the nest and at 5 m from the nest in each of the four cardinal directions and approximately 7 m in each of four intermediate directions. These points are defined by the midpoints and corners, respectively, of a square centred on the nest, and represent an unbiased sample of cover throughout the 0.04-ha plot. I counted the proportion of cells 50% or more obscured by vegetation as an estimate of ground cover. I included all standing and fallen, live or dead vegetation, but not fallen trees or large branches. Ground cover over the nest and the mean, minimum, and maximum of the eight measurements around the nest were used as variables. 3) Total number of stems in the plot. I recorded the number of living and dead trees in each of three size categories (0-5, 5-10 and >10 cm dbh) within the 0.04-ha plot. 4) Distance to nearest perch. I recorded the distance to the nearest suitable cowbird scanning perch. A scanning perch was any shrub, tree or human-made structure standing >1 m above the surrounding vegetation (Romig and Crawford 1995). Levels of parasitism may increase with proximity of perches from which cowbirds can observe host activity (Burhans 1997).

I used *post hoc* examination of the photographs to assign nests to the marsh, ridge or interface. I included interface as a third habitat type, because assignment of nests in this area of overlap to either marsh or ridge was questionable. The open, treeless marsh is bordered by encroaching willows (*Salix* spp.), which also invade the forested ridge. Considering nests in this area separately allowed me to highlight differences between marsh and ridge nests in either parasitism or concealment. I also justified the separation of nests into different habitat types because parasitism frequencies and patterns tended to differ in each habitat. Parasitism frequency was highest in the marsh and lowest in the ridge in both years, although the differences were not statistically significant (proportion of nests parasitized, years combined: marsh 75% (27/36), interface 65% (30/46), ridge 54% (15/28); $\chi^2 = 0.38$, df = 2, $P > 0.05$). In contrast, multiple parasitism was more common in the ridge in 1998 and less common in the ridge in 1999, although these differences also were not significant (proportion of parasitized nests receiving more than one cowbird egg: 1998, marsh 70% (12/17), interface 78% (11/14), ridge 57% (4/7); 1999, marsh 60% (6/10), interface 56% (9/16), ridge 88% (7/8); $\chi^2 = 0.60$, df = 4, $P > 0.05$). However, there was a significant difference in the type of multiple parasitism (i.e. all cowbird eggs laid by one female (hereafter single female nests) or eggs laid by more than one female (hereafter multiple female nests, see chapter 1) in marsh versus interface (calculated in 1999 only, number of SFNs out of total multiply parasitized nests: 1 of 11 single female nests in marsh versus 6 of 13 single female nests in interface, Fisher Exact Test, $P = 0.05$; there were too few multiply parasitized nests of known type in the ridge to compare).

I assigned nests to each habitat type according to the following criteria. Marsh nests were in habitat characterized predominantly by cattails (*Typha* spp.) or phragmites (*Phragmites australis*), and had no trees within approximately 20 m. Nests in the interface were in habitat with either cattails/phragmites cover or grasses (predominately *Scolochloa festucacaea*) and nettles (*Urtica dioica*) or a combination, were within approximately 11 m of at least one woody-stemmed tree of diameter no greater than approximately 10 cm, and had trees of larger diameter within at least 20 m. Ridge nests were characterized by grass, nettle or burdock (*Arctium* spp.) cover, and the presence of trees of at least 10 cm in diameter within approximately 11 m.

For several reasons, I did not combine data from each year for any of the vegetation analyses. First, nesting phenology differed between years (see Chapter 1) and a subjective assessment of vegetation indicated years were not comparable: in 1999, a mild, sunny April was followed by a cool, wet May, and Song Sparrows delayed nest initiations, but vegetation had already begun to grow. A comparison of four variables measured in both years indicated significant differences between years (Table 5) and, hence, data were not pooled.

I used the results collected in 1998 to determine which variables were most important in describing vegetative concealment of nests as they relate to parasitism probability. In 1999, I reduced the number of variables I measured to increase the power of the tests (see Table 4). I considered vegetation density only in the microhabitat (at 5 m) and used the mean and maximum in the top half (1-2 m) and the mean, minimum, and maximum in the bottom (< 1 m) half as variables. I also included ground cover over the nest and the mean, minimum, and maximum of eight measurements of ground cover around the nest, as above.

Yellow Warbler

I measured vegetation at Yellow Warbler nests from May to July, 1998, following the same procedures as above. I included the mean, minimum, and maximum vegetation density < 1 m and 1-2 m in both the nest microhabitat and in the nest habitat as variables. I also included total number of stems and nearest perch distance.

Table 5. Comparison between years of four vegetation variables measured at Song Sparrow nests.

Vegetation variable	Means ± SE (n)		*t*	df	p
	1998	1999			
Density 0-1 m (at 5 m)	56.70 ± 1.92 (57)	69.94 ± 2.07 (63)	5.11	118	<0.0001
Density 1-2 m (at 5 m)	15.31 ± 2.03 (57)	9.78 ± 1.75 (63)	3.42	118	0.0009
Mean percent ground cover around nest	55.00 ± 3.00 (55)	75.36 ± 2.58 (63)	0.89	113	0.38
Percent ground cover over nest	78.70 ± 3.72 (52)	76.82 ± 2.94 (63)	5.60	116	<0.0001

Data analysis

I used the arcsine square root transformation for all percentage variables. Other variables were judged to be normally distributed using graphical procedures. I tested for seasonal changes in each vegetation variable using regression analyses with Julian date of the measurements as the independent variable. Because some variables significantly positively increased over time, I used the standardized residuals from the regression of all variables in comparing among parasitism categories. I performed one-way ANOVA to test for univariate differences among group means (groups: unparasitized = U, singly parasitized = S, and multiply parasitized = M) and *post hoc* LSD tests between pairs if there were significant differences. I used the software SYNTAX, program ORDIN, to test for multivariate patterns in parasitism probability. I performed principal components analysis (PCA) on vegetation variables. In 1998, I performed the multivariate analyses on a subset of nine of the vegetation variables for Song Sparrow nests (the nine variables also measured in 1999) and a subset of five variables for Yellow Warbler nests (I eliminated minima and maxima, because the univariate p-values for these variables were high and they were autocorrelated with their associated means). In 1999, I included all nine variables measured at Song Sparrow nests and performed separate multivariate analyses for nests in marsh, ridge, and interface. A separate multivariate analysis was performed on multiply parasitized Song Sparrow nests that could be identified as either single female nests or multiple female nests (see Chapter 1), to compare concealment at nests multiply parasitized by a single female with nests parasitized by multiple females.

All statistical tests were two-tailed. Differences among group means were judged significant using Bonferroni corrections for multiple comparisons and *post hoc* comparisons between pairs were judged significant at $\alpha = 0.05$. Means ● SE are reported for summary statistics.

Host activity

Behaviour

I observed host behaviour around the nest during the nest-building stage, otherwise as soon as possible after nest discovery. If cowbirds lay most of their eggs during the host's laying period, discovery of nests must occur during either the nest-building or egg-laying stages and, hence, if cowbirds use host behaviour to locate nests, activity during these stages should be important (Banks 1997). Most Song Sparrow nests were observed during the laying stage, whereas all Yellow Warbler nests were observed during building. Observation bouts were one hour between 0600 and 1200 hours, Central Standard Time. On arrival at a nest, I set up and immediately entered a blind, but waited 10 minutes before beginning the observation bout. I recorded the following behaviours (after Banks 1997): the number of trips to the nest site per unit time by either sex (Song Sparrows are monomorphic, but male and female Yellow Warblers are distinguishable), the duration of nest visits in seconds, the direction of flights (one of eight possible cardinal directions) to and from the nest, and the location and distance of all perches within the 0.04-ha plot centred on the nest used en route, whether I could see the female carrying nest material, the number of male song repetitions given within the 0.04-ha plot, and whether the female chipped or uttered nest departure calls.

Nest mass

To test whether nest-building behaviour in general provides cues for nest-searching cowbirds, I used nest mass as a correlate for building behaviour (Uyehara 1996). This approach assumes that hosts vary in the length of time spent building nests and that a constant amount of material is brought to the nest on each trip. Heavier nests then indicate more trips to the nest or a longer duration of nest-building activity. In 1999, I collected Song Sparrow nests after the termination of nesting attempts. I attempted to pick up all nest material and material woven into the nest, but attached to the substrate was severed at the nest surface. I removed extraneous material (e.g. eggshell fragments, leaves blown in) and bagged the nests for storage. I oven-dried all nests in paper bags at approximately 80°C, until the mass did not change for two consecutive measurements 24 hours apart and recorded mass to the nearest 0.1 g.

Data analyses

I used Mann-Whitney U-tests to test for univariate differences between group means (groups: unparasitized = U, parasitized = P) for all behaviour variables, except presence/absence of female vocalizations and seen/not seen carrying material, which I tested using Fisher's exact test. I used the software SYNTAX, program ORDIN, to test for multivariate patterns in parasitism probability. I used principal components analysis (PCA) to test for multivariate patterns explaining parasitism.

If materials used to construct nests differed among habitat types and these materials differed in mass, then relationships between parasitism and nest mass might be obscured by differences across habitat types. Hence, I performed one-way ANOVA to test for differences in nest mass among habitat types (ridge, marsh, and interface) and among parasitism groups (unparasitized = U, singly parasitized = SP, parasitized multiply by one female (single female nests) = SFN, and multiply parasitized by more than one female (multiple female nests) = MFN) and *post hoc* LSD tests when significant to determine which groups differed.

All statistical tests were two-tailed. Differences among group means were judged significant using Bonferroni corrections for multiple comparisons and *post hoc* comparisons between groups were judged significant at $\alpha = 0.05$. Means ± SE are reported for summary statistics.

RESULTS

Vegetation sampling

Song Sparrow

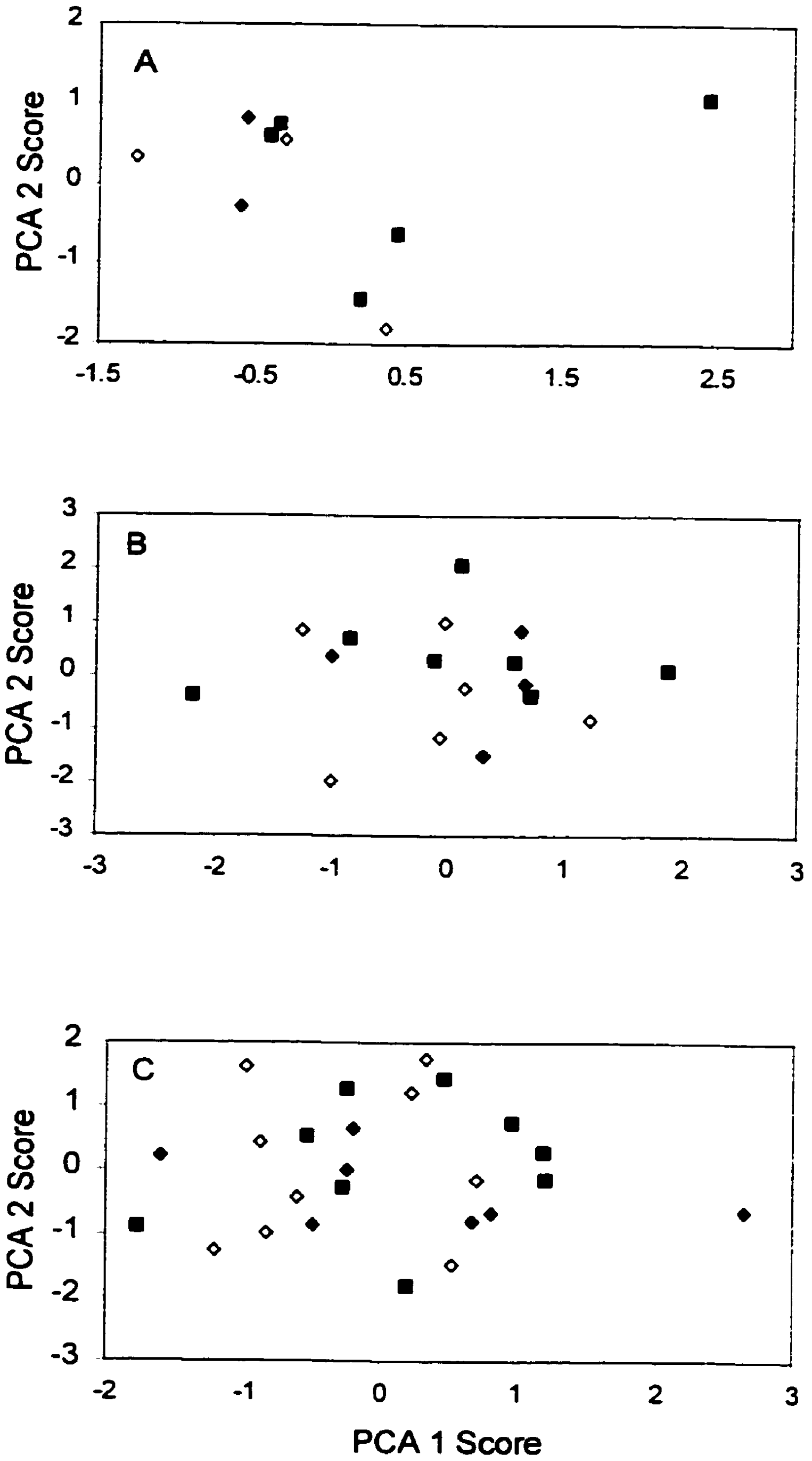
Unparasitized, singly parasitized, and multiply parasitized Song Sparrow nests did not differ significantly in any of the 18 habitat and microhabitat vegetation variables measured in 1998 (Table 6). The difference among groups for minimum percent ground cover around the nest approached significance ($F = 3.20$, $df = 2, 52$, $P = 0.049$), but using the Bonferroni correction, the means were not statistically different. The non-significant trend was paralleled in mean percent ground cover: multiply parasitized nests tended to have a greater ground cover than either parasitized or unparasitized nests. Multivariate analyses of nine variables revealed no particular trends that explained parasitism (Figure 5).

Table 6. Comparisons among means for 18 habitat and microhabitat vegetation measurements at unparasitized, singly parasitized, and multiply parasitized Song Sparrow nests in 1998.

Vegetation variable	Means ± SE			*F*	p
	Unparasitized	Singly parasitized	Multiply parasitized		
Distance to nearest perch (m)	1.89 ± 0.32	1.77 ± 0.38	1.98 ± 0.46	0.05	0.95
Density 0-1 m (at 5 m)	54.12 ± 2.80[a]	52.78 ± 4.81[c]	61.54 ± 2.89	2.10	0.13
Minimum density 0-1 m (at 5 m)	34.18 ± 3.87[a]	28.83 ± 5.62[c]	42.27 ± 3.90	1.52	0.23
Maximum density 0-1 m (at 5 m)	76.36 ± 3.97[a]	69.83 ± 5.84[c]	80.99 ± 3.55	1.46	0.24
Density 1-2 m (at 5 m)	14.59 ± 2.59[a]	15.08 ± 1.40[c]	16.18 ± 3.23	0.23	0.79
Minimum density 1-2 m (at 5 m)	0.18 ± 0.18[a]	0.00 ± 0.00[c]	0.55 ± 0.33	0.99	0.38
Maximum density 1-2 m (at 5 m)	44.36 ± 6.79[a]	33.00 ± 11.52[c]	37.36 ± 6.98	0.54	0.58
Density 0-1 m (at 11 m)	63.95 ± 3.36	64.74 ± 5.38	67.94 ± 3.05	0.50	0.61
Minimum density 0-1 m (at 11 m)	45.81 ± 4.12	36.91 ± 7.97	40.36 ± 5.41	0.25	0.78
Maximum density 0-1 m (at 11 m)	88.29 ± 2.95	79.45 ± 7.32	90.18 ± 2.55	0.38	0.69
Density 1-2 m (at 11 m)	25.52 ± 4.37	28.41 ± 7.57	28.70 ± 3.98	0.20	0.82
Minimum density 1-2 m (at 11 m)	2.38 ± 1.58	3.27 ± 3.08	1.36 ± 0.52	0.10	0.91
Maximum density 1-2 m (at 11 m)	56.95 ± 8.05	53.82 ± 13.03	66.45 ± 6.88	0.35	0.71
Mean percent ground cover around nest	50.45 ± 5.20	51.70 ± 4.69	61.82 ± 4.71	1.56	0.22
Minimum ground cover around nest	13.33 ± 5.27	5.45 ± 3.90	24.09 ± 5.72	3.20	0.049
Maximum ground cover around nest	92.86 ± 3.10	94.45 ± 2.82	90.45 ± 3.57	0.51	0.60
Percent ground cover over nest	85.24 ± 5.15[b]	83.00 ± 7.00[d]	70.00 ± 6.62[b]	1.70	0.19
Total number of stems	24.45 ± 7.31	15.55 ± 4.41	27.86 ± 7.37	0.56	0.57

[a] n = 23, [b] n = 21, [c] n = 12, [d] n = 10

Figure 5. Relationship of vegetation characteristics at Song Sparrow nests in three habitat types in 1998 in two dimensions, based on a multivariate analysis of nine vegetation variables using Principal Components Analysis. See Table 4 for list of variables included in the analysis and see methods for categorization of habitat types: A) marsh, B) ridge, and C) interface. Open diamonds = unparasitized, closed diamonds = singly parasitized, and closed squares = multiply parasitized.


A
B
C
PCA 2 Score
PCA 1 Score
2
1
0
-1
-2
-1.5
-0.5
0.5
1.5
2.5
3
-3
-2
-1
0
1
2
3

Similarly, unparasitized, singly parasitized, and multiply parasitized Song Sparrow nests did not differ significantly in any of the nine habitat and microhabitat vegetation variables in 1999 (Table 7). Multivariate analyses of the nine variables revealed no particular trends that explained parasitism, neither among unparasitized, singly parasitized, and multiply parasitized nests in any of the three habitat types (Figure 6) nor between nests multiply parasitized by the same female and nests parasitized by more than one female, in all three habitat types combined (Figure 7).

Yellow Warbler

Unparasitized, singly parasitized, and multiply parasitized Yellow Warbler nests did not differ significantly in any of 13 habitat and microhabitat vegetation variables (Table 8). Vegetation density 1-2 m above ground in the nest habitat (at 11 m) tended to be greater at multiply parasitized nests than at either unparasitized or singly parasitized nests, but singly parasitized nests tended to be the least concealed. Multivariate analysis of five variables revealed no trends (Figure 8).

Host activity

Behaviour

I watched 23 Song Sparrow nests: 2 in the building stage, 12 during laying, and 9 during early incubation. Activity of the hosts at these nests was limited and difficult to detect. For example, at several nests, I did not observe any nest visits during the watch and when one did occur during a watch, individuals often walked for several metres through the vegetation to reach nests, so I was unable to record accurately the direction or time of arrival at the nest. As a result, I obtained data for only three activity variables:

Table 7. Comparisons among means for 9 vegetation measurements at unparasitized, singly parasitized, and multiply parasitized Song Sparrow nests in 1999.

Vegetation variable	Means ± SE			*F*	p
	Unparasitized (n = 15)	Singly parasitized (n = 18)	Multiply parasitized (n = 30)		
Density 0-1m (at 5m)	66.87 ± 4.78	73.08 ± 3.74	69.60 ± 2.89	0.60	0.55
Minimum density 0-1m (at 5m)	43.87 ± 7.68	52.11 ± 4.70	50.60 ± 4.09	0.65	0.53
Maximum density 0-1m (at 5m)	84.80 ± 4.63	88.22 ± 3.68	83.80 ± 2.81	0.52	0.59
Density 1-2m (at 5m)	13.57 ± 3.66	11.58 ± 5.49	6.80 ± 1.59	1.35	0.27
Maximum density 1-2m (at 5m)	30.27 ± 7.56	25.11 ± 8.38	20.80 ± 4.98	0.34	0.71
Mean percent ground cover around nest	72.83 ± 5.05	72.83 ± 5.05	72.83 ± 5.05	1.55	0.22
Minimum ground cover around nest	38.67 ± 8.27	33.89 ± 6.96	50.33 ± 5.56	2.19	0.12
Maximum ground cover around nest	96.67 ± 2.11	95.00 ± 2.94	98.33 ± 0.84	0.67	0.51
Percent ground cover over nest	82.67 ± 4.83	67.78 ± 6.34	79.33 ± 4.07	2.00	0.14

Figure 6. Relationship of vegetation characteristics at Song Sparrow nests in three habitat types in 1999 in two dimensions, based on a multivariate analysis of nine vegetation variables using Principal Components Analysis. See Table 4 for list of variables included in the analysis and see methods for categorization of habitat types: A) marsh, B) ridge, and C) interface. Open diamonds = unparasitized, closed diamonds = singly parasitized, and closed squares = multiply parasitized.

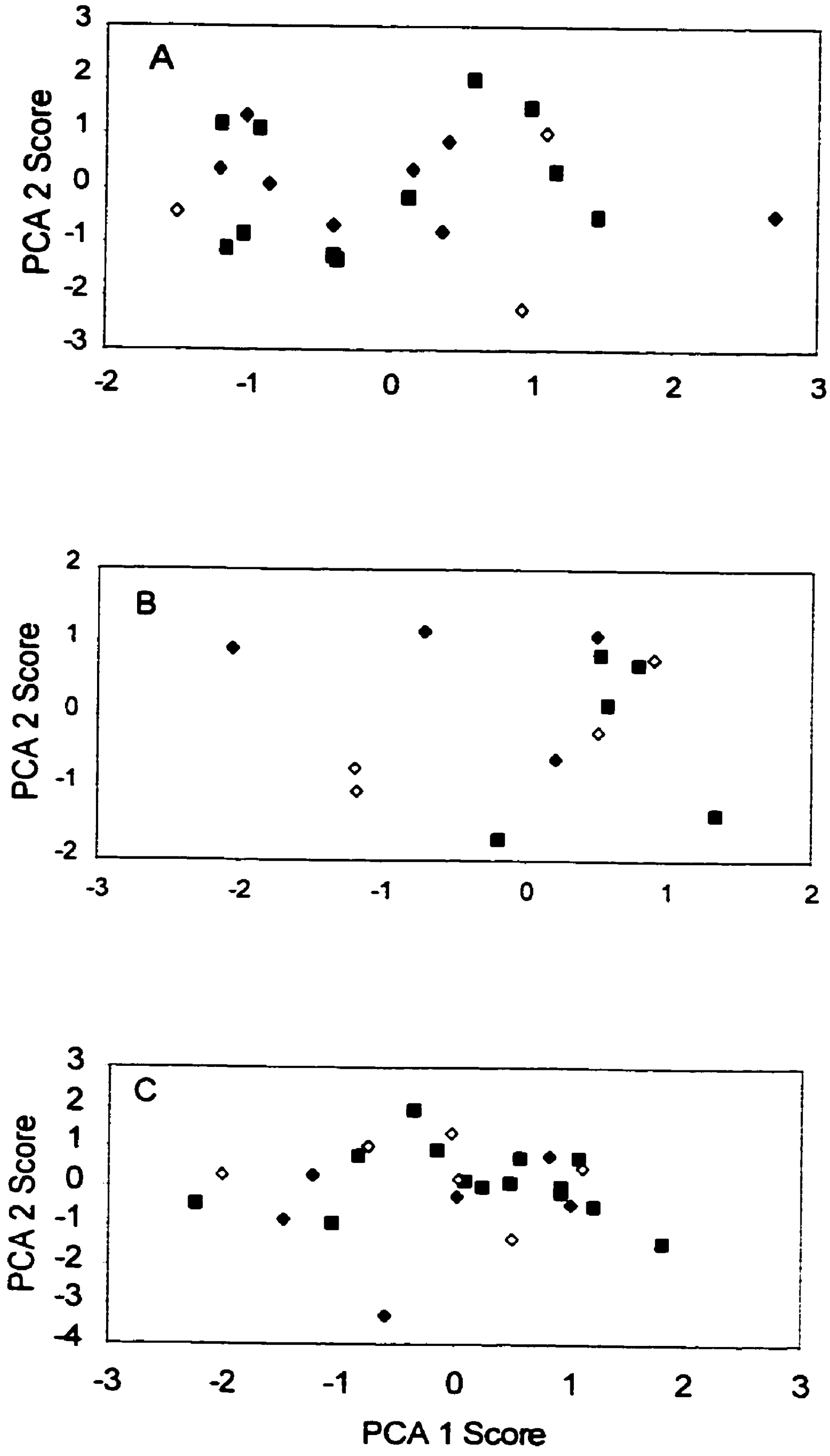

A
PCA 2 Score
3
2
1
0
-1
-2
-3
-2
-1
0
1
2
3
B
PCA 2 Score
2
1
0
-1
-2
-3
-2
-1
0
1
2
C
PCA 2 Score
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
PCA 1 Score

Figure 7. Relationship of vegetation characteristics at 26 multiply parasitized Song Sparrow nests in two dimensions, based on a multivariate analysis of 9 vegetation variables using Principal Components Analysis. Open squares = nests parasitized by more than one female, closed diamonds = nests multiply parasitized by one female.

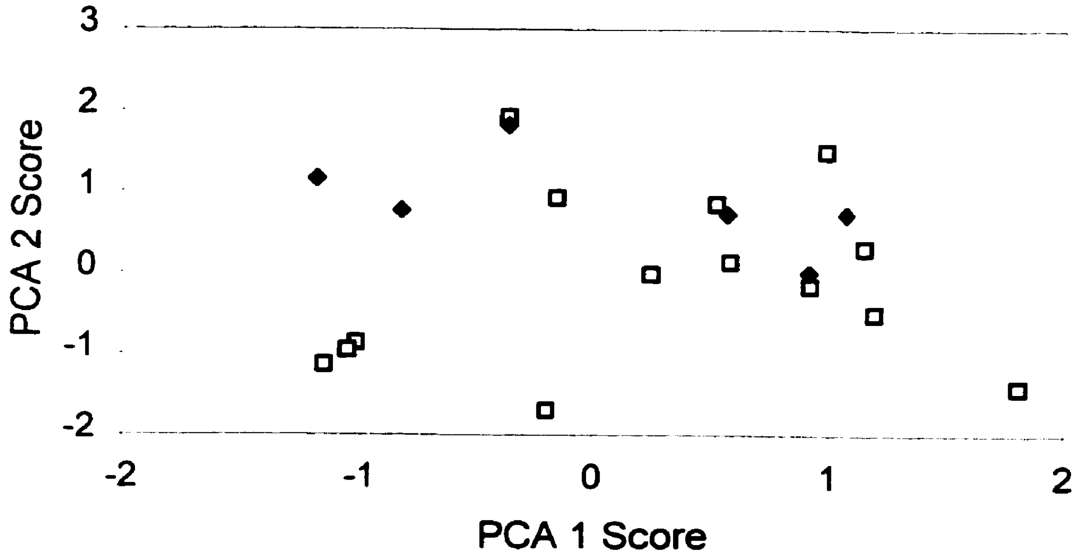
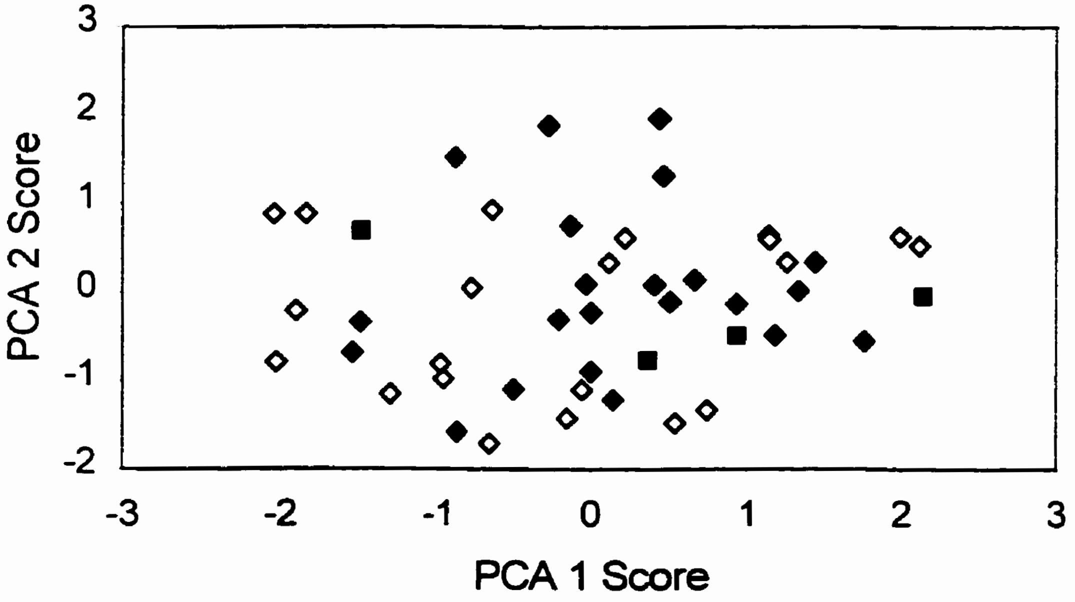

3
2
1
0
-1
-2
PCA 2 Score
-2
-1
0
1
2
PCA 1 Score

Table 8. Comparisons among means for 13 habitat and microhabitat vegetation measurements at unparasitized, singly parasitized, and multiply parasitized Yellow Warbler nests in 1998.

	Mean ± SE				
Vegetation variable	Unparasitized (n = 23)	Singly parasitized (n = 22)	Multiply parasitized (n = 4)	*F*	p
Distance to nearest perch (m)	0.57 ± 0.14	0.80 ± 0.25	0.38 ± 0.12	0.60	0.55
Density 0-1m (at 5 m)	87.11 ± 1.91	86.09 ± 2.93	85.63 ± 6.00	0.07	0.93
Minimum density 0-1m (at 5 m)	63.74 ± 6.18	70.00 ± 5.73	69.50 ± 10.94	0.46	0.64
Maximum density 0-1m (at 5 m)	98.70 ± 0.73	98.36 ± 0.63	96.00 ± 2.16	1.90	0.16
Density 1-2m (at 5 m)	48.39 ± 4.45	45.07 ± 4.52	37.88 ± 8.39	0.51	0.60
Minimum density 1-2m (at 5 m)	11.57 ± 4.94	12.18 ± 3.88	14.50 ± 8.14	0.14	0.86
Maximum density 1-2m (at 5 m)	82.87 ± 3.51	80.09 ± 4.97	66.50 ± 4.99	1.35	0.27
Density 0-1m (at 11 m)	84.35 ± 2.56	83.50 ± 3.12[a]	94.38 ± 3.88	1.84	0.17
Minimum density 0-1m (at 11 m)	58.61 ± 7.20	62.10 ± 6.45[a]	87.50 ± 6.13	1.57	0.22
Maximum density 0-1m (at 11 m)	99.13 ± 0.48	97.52 ± 1.18[a]	100.00 ± 0.00	1.07	0.35
Density 1-2m (at 11 m)	50.74 ± 4.07	40.07 ± 4.98[a]	64.25 ± 8.09	3.01	0.059
Minimum density 1-2m (at 11 m)	13.04 ± 4.25	7.05 ± 2.29[a]	29.50 ± 16.48	1.64	0.20
Maximum density 1-2m (at 11 m)	88.70 ± 3.98	74.48 ± 7.24[a]	97.50 ± 2.50	2.37	0.10

[a] n = 21

Figure 8. Relationship of vegetation characteristics at 47 Yellow Warbler nests in 1998 in two dimensions, based on a multivariate analysis of 9 vegetation variables using Principal Components Analysis. See Table 4 for list of variables included in the analysis. Open diamonds = unparasitized, closed diamonds = singly parasitized, and closed squares = multiply parasitized.


3
2
1
0
-1
-2
PCA 2 Score
-3
-2
-1
0
1
2
3
PCA 1 Score

male song frequency, the number of visits per hour, and whether the females vocalized. There were no significant differences between unparasitized, singly parasitized, and multiply parasitized nests for any of the three variables, although sample sizes were small and variability among individuals was high (Table 9). Males tended to sing more at multiply parasitized nests. A multivariate approach did not reveal any further trends in the data (Figure 9).

I watched 16 Yellow Warbler nests during the building period, from half cup to complete, unlined cup. Activity at Yellow Warbler nests was also easier to detect because the birds typically travelled well off the ground (> 1m) and nests were often within a single shrub and visible from the blind. I did not use data collected on the variety of angles used on flights to and from the nest, because large variation in the number of visits per hour among nests violates assumptions necessary for second-order two-sample comparison of angular disperson (Batschelet 1981). Of the remaining six variables, only presence/absence of female vocalizations around nests approached significance, although with Bonferroni correction did not (Table 10). Females that vocalized during building tended to be more frequently parasitized than females that did not. A multivariate analysis indicated no trends in the host behaviour data (Figure 10).

Table 9. Comparisons of means for three behaviour variables for Song Sparrows at unparasitized, singly parasitized, and multiply parasitized nests. Test coefficient is for comparison of unparasitized or singly parasitized versus multiply parasitized nests (unparasitized and singly parasitized groups combined).

	Mean ± SE				
Behaviour	Unparasitized (n = 5)	Singly parasitized (n = 8)	Multiply parasitized (n = 10)	U	p
Male song frequency (no./hr)	57.40 ± 16.89	41.38 ± 16.28	87.70 ± 15.81	35.5	0.07
Visits/hour	0.80 ± 0.37	0.75 ± 0.49	2.00 ± 0.82	48.5	0.27
Female vocalizations (no, yes)	3 no, 2 yes	6 no, 2 yes	6 no, 4 yes	n/a[a]	0.31

[a] Fisher's exact test.

Figure 9. Relationship of host behaviour characteristics at 19 Song Sparrow nests in two dimensions, based on a multivariate analysis of three behaviour variables using Principal Components Analysis. Open diamonds = unparasitized, closed diamonds = singly parasitized, and closed squares = multiply parasitized.

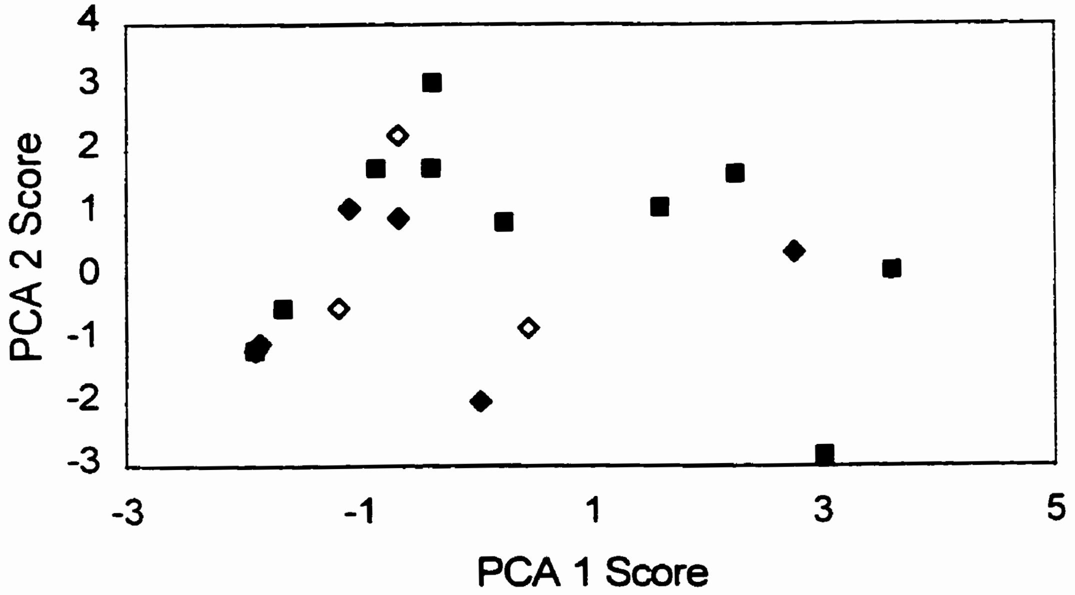
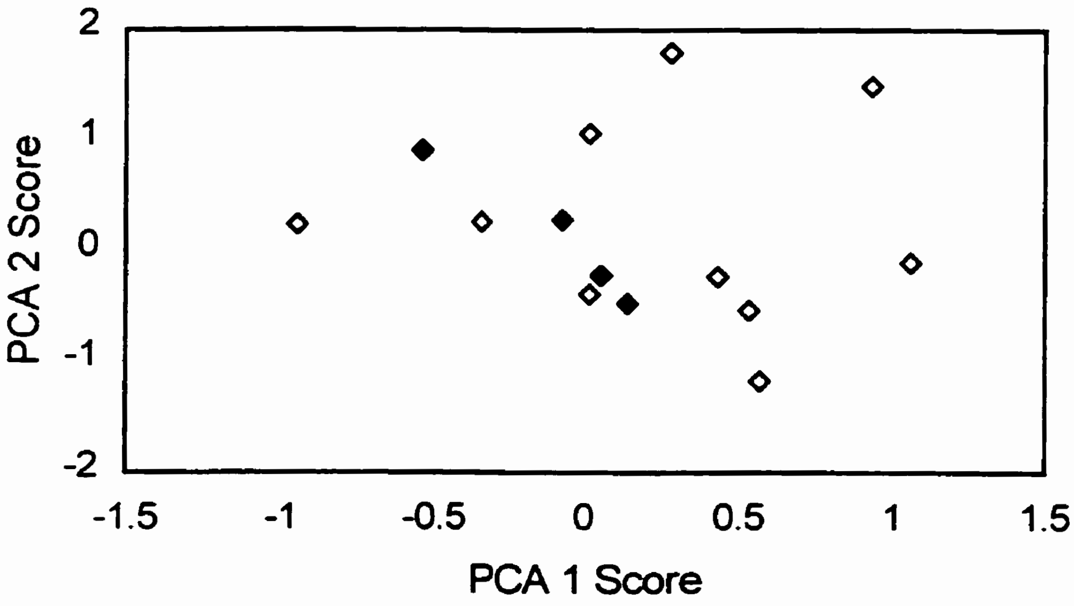

4
3
2
1
0
-1
-2
-3
PCA 2 Score
-3
-1
1
3
5
PCA 1 Score

Table 10. Comparisons of means for six behaviour variables for Yellow Warblers at unparasitized and parasitized nests.

Behaviour	Mean ± SE		U	p
	Unparasitized (n = 11)	Parasitized (n = 4)		
Visits/hr	13.92 ± 2.92[b]	10.50 ± 4.35	19.5	0.58
Female vocalizations	8 no, 4 yes	0 no, 4 yes	n/a[a]	0.04
Male song frequency (no./hr)	40.10 ± 13.65[c]	14.25 ± 8.19	15	0.48
Visit duration (seconds)	37.52 ± 6.09	53.03 ± 7.31	11	0.31
Seconds spent < 15m	905.50 ± 133.87[b]	858.50 ± 113.44	23	0.90
With material?	8 no, 4 yes	3 no, 1 yes	n/a[a]	0.45

[a] Fisher's exact test, [b] n = 12, [c] n = 10.

Figure 10. Relationship of host behaviour characteristics at 13 Yellow Warbler nests in two dimensions, based on a multivariate analysis of six behaviour variables using Principal Components Analysis. Open diamonds = unparasitized, closed diamonds = parasitized.



2
1
0
-1
-2
-1.5
-1
-0.5
0
0.5
1
1.5
PCA 2 Score
PCA 1 Score

Nest mass

Nest mass did not differ among habitat types (F = 0.98, df = 2,50, P = 0.38, Table 11). Nest masses differed, however, among parasitism categories (F = 4.68, df = 3, 49, P = 0.006, Table 11). *Post hoc* comparisons indicated significant differences between unparasitized and singly parasitized, and between unparasitized and each type of multiply parasitized nests (nests multiply parasitized by one female and nests parasitized by multiple females). Although not significant, differences between singly parasitized and multiply parasitized nests, and between the two types of multiply parasitized nests followed the same trend of increasing nest mass with the number of females parasitizing the nest.

DISCUSSION

Multiple parasitism

Multiple parasitism was associated with the most concealed nests in both Song Sparrows and Yellow Warblers. Singly parasitized nests were least concealed and unparasitized nests were in between. This trend from least concealed, singly parasitized nests, to most concealed, multiply parasitized nests, was consistent in both species in both years. Parasitism has been found associated with greater concealment in a few other studies (Buech 1982, Briskie et al. 1990, Davis 1994, Banks 1997, Burhans 1997, Larison et al. 1998, Averill-Murray et al. 1999). However, only one study has examined habitat features associated specifically with multiply parasitized nests (Moskát and Honza in press). In a study of parasitism by the Common

Table 11. Mean mass (g) of Song Sparrow nests by habitat and parasitism category.

	Mean ± SE	n	F	p
Ridge	18.3 ± 0.7	11	0.98	0.38
Interface	18.7 ± 0.9	22		
Marsh	20.0 ± 0.8	20		
Unparasitized	16.2 ± 0.8	14	4.68	0.006
Singly parasitized	19.6 ± 0.7	12		
Multiply parasitized	20.4 ± 0.7	27		
Single female nests	19.9 ± 1.6	7		
Multiple female nests	20.6 ± 0.8	20		

Cuckoo (*Cuculus canorus*) on Great Reed Warblers (*Acrocephalus arundinaceus*), parasitized nests overall were less concealed than unparasitized nests, but there was little difference in cover around singly versus multiply parasitized nests. Considering singly versus multiply parasitized nests separately may be informative because multiple parasitism may be a result of (1) highly susceptible nests (if multiple parasitism involves several females laying in the same nest) or (2) host preference, particularly if multiple parasitism results from one female laying several eggs in the same nest (Martinez et al. 1998a). However, it is not clear why more concealed nests would be more likely to be discovered by cowbirds, because concealment should reduce the ability of cowbirds to locate nests by observing them directly or by observing host activity around nests. At Delta Marsh, approximately half of the multiply parasitized Song Sparrow nests involved more than one female (see Chapter 1, Woolfenden 2000) and, hence, multiply parasitized nests were often those discovered by several cowbirds. One possible explanation is that concealed nests are preferred by the first cowbird parasitizing the nest and that increased activity at the nest associated with cowbird visits is used by other cowbirds to locate the nest. However, concealment of nests parasitized by more than one female compared to nests multiply parasitized by one female did not differ. Alternatively, concealment changes over the season (but see Burhans and Thompson 1998) and might account for the relationship between concealment and multiple parasitism, because multiple parasitism was more frequent at nests initiated later in the season (in Song Sparrows; see Chapter 1). However, this factor was statistically controlled for by using residuals from the regression of each variable against date in the analyses and, hence, this explanation does not explain the pattern.

Discovery versus selection of nests

The relationship between vegetation structure and parasitism probability is further complicated by the contrasting significance of concealment to cowbirds. Parasitism probably involves the discovery of nests and the selection from those of the nest in which to lay an egg (Thompson and Gottfried 1981). If cowbirds rely primarily on active nest searching to locate nests or if cues associated with host activity are also concealed by increased cover around nests, then likelihood of discovery of nests by cowbirds probably would be inversely related to concealment. In contrast, concealed nests are also less likely to be discovered by predators, although this result depends on the predator community and whether predators use visual or olfactory cues (e.g. McLean et al. 1986, Martin 1992). Nonetheless, if these nests are more likely to be successful, cowbirds may preferentially parasitize more concealed nests (see Davis 1994). In addition, more concealed nests may give the cowbird a better chance to lay its egg undetected and unmolested by the host. Because cowbirds take only a few seconds to lay and do so around sunrise when it is getting light (Sealy et al. 1995), the likelihood of discovery by the host depends on whether it is near the nest at the time the cowbird lays its egg (Neudorf and Sealy 1994). Cowbird preference nonetheless predicts a positive relationship between concealment and parasitism. When these opposing selective forces act in concert, the resulting trend may be nonsignificant. My results indicate greatest concealment at nests that are multiply parasitized, which suggests cowbird preference, and least concealment at singly parasitized nests. These patterns may result from the opposing roles of concealment.

Influence of habitat type

Habitat-dependent variation in vegetation may influence patterns of parasitism on Song Sparrows. Multiple parasitism frequencies did not differ significantly among habitats of the marsh, ridge, and interface, but tended to be higher in the marsh and adjoining interface, and multiply parasitized nests in the marsh were almost always the product of more than one female. In these habitats, most ground cover was a dense, even growth of nettles and phragmites, whereas ground cover in the ridge tended to be patches of burdock and nettle. The tendency for multiply parasitized nests to be more concealed, therefore, may be a consequence of higher frequency of multiple parasitism in this habitat that occurs for some other reason. In the marsh, parasitism by more than one female may occur because of a lack of trees and other perch sites that female cowbirds could use for displays involved in territory establishment and maintenance, a behaviour that is seldom observed in this habitat (Woolfenden 2000). Alternatively, females in the marsh may search using a concerted-effort strategy, where two or more females act together (Wiley and Wiley 1980, Mason 1986) or some females may employ a copy-cat strategy, in which they follow the movements of other females (Hahn et al. 1999). In either event, multiple parasitism results because nest-searching costs in this habitat are greater if observation of host activity is limited by the absence of high vantage points. Payne (1973) similarly suggested ground-nesting sparrow nests in marshes may be difficult for single cowbirds to locate.

Variables associated with parasitism differed between Song Sparrow and Yellow Warbler nests. These differences highlight the possibility that vegetation features that explain parasitism may depend on characteristics of the habitat and host species (Hahn and Hatfield 1995, Burhans 1997, Larison et al. 1998, Clotfelter 1998). My results add to a growing body of results that provide contrasting evidence: some studies suggest that concealment is related (e.g. Burhans 1997, Larison et al. 1998), whereas others suggest it is not related (e.g. Grieef 1995, Barber and Martin 1997, Banks 1997, Clotfelter 1998) to parasitism risk. Parasitism on ground- and canopy-nesting hosts may depend on cover, because vegetative structures of ground and canopy habitat usually are dense, complex, and homogeneous. In contrast, parasitism on shrub-nesting hosts may be unrelated to cover because understory shrubbery usually is more open and heterogeneous (Brittingham and Temple 1996, Burhans and Thompson 1998). Actively searching cowbirds can simplify search patterns if there is a single shrub to look within, and hosts carrying nesting material to a single shrub also may be more easily observed (Uyehara and Whitfield 2000). Larison et al. (1998) found that cover in the broad habitat around Song Sparrow nests was negatively related to parasitism, but cover immediately surrounding the nest was unrelated to parasitism. They suggested that cover is important mainly because it conceals host activities. Uyehara and Whitfield (2000) found similar results in the Willow Flycatcher (*Empidonax traillii extimus*), a shrub-nesting species that nests similarly to the Yellow Warbler. In my study, lateral cover both at the nest microhabitat and in the nest habitat did not influence parasitism risk in ground-nesting Song Sparrows, but increased cover in the nest habitat tended to decrease parasitism risk in shrub-nesting Yellow Warblers. In particular, percent cover 1-2 m above ground was lowest around singly parasitized Yellow Warbler nests. This is the height range of most Yellow Warbler nests sampled and flight paths to the nest shrub by nest-building hosts would be through this zone (Briskie et al. 1990).

Perches for observation of host activity

If observation of host activity around nests is important, structural features of the territory that improve cowbirds' ability to observe hosts may increase parasitism probability. The proximity of nests to suitable perches from which cowbirds can observe hosts has been examined with varying results (Anderson and Storer 1976, Gates and Gysel 1978, Gochfeld 1979, Robbins 1979, Freeman et al. 1990, Ekstein et al. 1993, Davis 1994, Romig and Crawford 1995, Brittingham and Temple 1996, Burhans 1997, Clotfelter 1998, Larison et al. 1998, Spautz 1999, Staab and Morrison 1999, Uyehara and Whitfield 2000). I found no support for the prediction that parasitized nests are closer to cowbird perches than unparasitized nests. However, perches were common in both the ridge and interface, and usually the closest perch was no more than 2 m from the nest. In the marsh, my definition of a perch included standing dead phragmites around Song Sparrow nests. Although cowbirds perch on phragmites (pers. obs.), they may not be able to observe host activity from these vantage points, particularly if the ground cover around the perch is dense. Hence, in these habitat types, the definition of a cowbird nest-searching perch is problematic and a comparison of perch proximity may not be appropriate.

In Yellow Warblers, multiply parasitized nests had more dense vegetation 1-2 m above ground throughout the nest habitat, but not necessarily directly at the nest. Larison et al. (1998) suggested dense cover directly over the nest site may provide perches from which cowbirds can more easily observe hosts to locate nests. Similarly, Staab and Morrison (1999) found parasitism was associated with nests in trees with small dbh that may provide perches that larger trees do not. However, most Song Sparrows nest on the ground and Larison et al. (1998) found that in this host, parasitism was associated with denser cover 2-3 m above ground. They suggested that female cowbirds used the vegetation in this zone as a suitable vantage point from which to observe nests. In contrast, Yellow Warbler nests in the present study generally were located 1-2 m above ground, where high foliage density was associated with parasitism. Cowbirds perching in this zone may not be at the best vantage to observe nests (see Spautz 1999), but higher perches may be used to observe host activity in and out of this vegetation zone.

Host behaviour

The importance of observation of host activities on cowbird nest finding has been measured in only a few studies and the results are equivocal (Grieef 1995, Uyehara and Narins 1995, Banks 1997, Gill et al. 1997, Clotfelter 1998). Studies using artificial nests and taxidermic models of hosts to test the importance of host activity have rarely elicited parasitism. Nonetheless, the surreptitiousness of host activity around the nest may be related to parasitism risk. Gochfeld (1979) suggested that lower parasitism frequency in the Pampas Meadowlark (*Sturnella defilippii*) compared to the greater Red-breasted Meadowlark (*S. loyca*) may be because the latter is more obvious during nest building. A positive association between frequency of host vocalizations and likelihood of parasitism in both Song Sparrows and Yellow Warblers suggests that vocalizations are important elements of host behaviour used by cowbirds to locate nests. Frequency of male song in Song Sparrows and female vocalizations in Yellow Warblers appeared to be positively correlated with probability of parasitism. This result is similar to other recent findings in the same and other hosts. Vocalization rates of Willow Flycatchers around the nest were also related to parasitism (Uyehara and Narins 1995). Banks (1997) found several behaviours of hosts at and around their nests, particularly vocalizations, were correlated with probability of parasitism in four host species. In Red-winged Blackbirds (*Agelaius phoeniceus*), nest-associated female vocalizations, but not male songs, when given during the laying period, may provide cues for cowbirds to locate nests at appropriate stages for parasitism (Clotfelter 1998).

Identifying elements of behaviour that provide cues for cowbirds among different host species may be complicated by several factors. Size of a host and its ability to repel an intruding female parasite may affect whether inconspicuous behaviour is the most beneficial response for the host (McLean 1987, Sealy et al. 1998). Territoriality and the size of territories may also influence whether male song can be used effectively by cowbirds as a cue to nest location (Clotfelter 1998). For example, Yellow Warbler males vary their use of song types depending on how far they are from the nest (Weary et al. 1994). Habitat may be an overriding factor that determines which behaviours are conspicuous (Hobson et al. 1988) and whether host behaviour or host nest characteristics are more important in determining susceptibility to discovery by cowbirds. Interactions between behaviour and vegetation variables might occur if host behaviours vary with nest concealment (Hobson et al. 1988), although Banks (1997) found no evidence to support this hypothesis.

Nest mass

To avoid the need to quantify specific behaviours that cowbirds may use to locate nests, a correlate for these behaviours might be used. Uyehara (1996) predicted that nest mass would correlate with nest-building behaviour, assuming that a constant amount of nesting material is brought each trip to the nest and, hence, heavier nests indicate more trips to and from the nest and/or a longer duration of nest-building activities. However, she found no difference in nest mass between parasitized and unparasitized nests in either Song Sparrows or Willow Flycatchers. Nest volume similarly could substitute for nest-building activity, but may not accurately reflect how busy the parents are or the duration of nest-building activity, and does not appear to be related to parasitism risk (Grant 1998, Moskát and Honza in press). In contrast to these studies, parasitized Song Sparrow nests were significantly heavier than unparasitized nests at Delta Marsh. This trend was not related to differences in nest materials or parasitism frequencies in different habitat types, which also might be expected to explain the difference between my study and Uyehara's (1996). It is also unlikely that heavier nests are larger and more conspicuous to cowbirds, because Song Sparrow nests are generally on the ground, embedded in the substrate. An alternative explanation is that nest mass correlates with something else that is not associated with nest building that is preferred by cowbirds. For example, nest size in Magpies (*Pica pica*) is correlated with parasitism by Great Spotted Cuckoos (*Clamator glandarius*), ostensibly because nest size reflects host parental ability (Soler et al. 1995). Preferential selection by cowbirds of superior parents within a species has not been documented conclusively, although there is some indication it may occur (Grant 1998, Hahn et al. 1999, Sedgwick and Iko 1999, but see Smith and Arcese 1994).

SUMMARY

1. Song Sparrow nests initiated earlier in the season were more likely to be parasitized than later nests.
2. Parasitized Song Sparrow nests tended to be initiated earlier than unparasitized nests.
3. Multiple parasitism on Song Sparrow nests earlier in the season may be related to changes in nest availability.
4. Parasitic events in general in Song Sparrow nests were positively correlated with the number of available Song Sparrow nests and not with the number of new nests initiated.
5. Cowbirds did not avoid laying in already-parasitized Song Sparrow nests: the distribution of cowbird eggs per nest differed from a random Poisson and there were more parasitized nests with two cowbird eggs than expected by chance.
6. Thirty percent of cowbird eggs were laid at inappropriate stages in Song Sparrow nests.
7. Multiple parasitism was the result of the same female re-parasitizing a nest almost as often as it was the result of more than one female parasitizing the same nest.
8. Inappropriately laid eggs were laid later in the season and tended to be those laid in nests parasitized by more than one female.
9. Eggs laid in nests parasitized by more than one female were laid throughout the season.
10. Fewer nests were available when eggs were laid into nests parasitized more than once by the same female, which were initiated earlier.

11. Parasitism probability was not significantly related to any of the habitat variables measured around Song Sparrow and Yellow Warbler nests.
12. Parasitism probability was not significantly related to any of the individual behaviours associated with activity around Song Sparrow and Yellow Warbler nests.
13. Nest-building activity as a whole appears to be associated with likelihood of discovery, because heavier Song Sparrow nests were more likely to be parasitized.

LITERATURE CITED

Alderson, G.W., H.L. Gibbs and S.G. Sealy. 1999a. Determining the reproductive behavior of individual Brown-headed Cowbirds using microsatellite DNA markers. Animal Behaviour 58:895-905.

Alderson, G.W., H.L. Gibbs and S.G. Sealy. 1999b. Parentage and kinship studies in an obligate brood parasitic bird, the Brown-headed Cowbird (*Molothrus ater*), using microsatellite DNA markers. Journal of Heredity 90:182-190.

Anderson, W.L. and R.W. Storer. 1976. Factors influencing Kirtland's Warbler nesting success. Jack-Pine Warbler 54:105:115.

Ankney, C.D. and D.M Scott. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97:677-683.

Averill-Murray, A., S. Lynn and M.L. Morrison. 1999. Cowbird parasitism of Arizona Bell's Vireos (*Vireo bellii arizonae*) in a desert riparian landscape: Implications for cowbird management and riparian restoration. Studies in Avian Biology 18:109-120.

Banks, A.J. 1997. Variation among host species in probability of parasitism by brown-headed cowbirds: the role of everyday host activity. M.Sc. thesis, University of Montana, Missoula.

Barber, D.R. and T.E. Martin. 1997. Influence of alternate host densities on Brown-headed Cowbird parasitism rates in Black-capped Vireos. Condor 99:595-604.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, New York, NY.

Berger, A.J. 1951. The cowbird and certain host species in Michigan. Wilson Bulletin 63:26-34.

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.

Brittingham, M.C. and S.A. Temple. 1996. Vegetation around parasitized and non-parasitized nests within deciduous forest. Journal of Field Ornithology 67:406-413.

Buech, R.R. 1982. Nesting ecology and cowbird parasitism of Clay-colored, Chipping, and Field Sparrows in a Christmas tree plantation. Journal of Field Ornithology 53:240-248.

Burhans, D.E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. Condor 99:866-872.

Burhans, D.E. and F.R. Thompson III. 1998. Effects of time and nest-site characteristics on concealment of songbird nests. Condor 100: 663-672.

Carter, M.D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88:11-25.

Clark, K.L. and R.J. Robertson. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator defenses. Behavioral Ecology and Sociobiology 5:359-371.

Clotfelter, E.D. 1998. What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird host nests? Animal Behaviour 55:1181-1189.

Clotfelter, E.D. and K. Yasukawa. 1999a. Impact of brood parasitism by Brown-headed Cowbirds on Red-winged Blackbird reproductive success. Condor 101:105-114.

Clotfelter, E.D. and K. Yasukawa. 1999b. The effect of aggregated nesting on Red-winged Blackbird nest success and brood parasitism by Brown-headed Cowbirds. Condor 101: 729-736.

Darley, J.A. 1983. Territorial behavior of the female Brown-headed Cowbird (*Molothrus ater*). Canadian Journal of Zoology 63:65-69.

Davis, S.K. 1994. Cowbird parasitism, predation and host selection in fragmented grassland of southwestern Manitoba. Master's thesis, University of Manitoba, Winnipeg, Manitoba.

DellaSala, D.A. 1985. The Yellow Warbler in southeastern Michigan: factors affecting its productivity. Jack-Pine Warbler 63:52-60.

Eastzer, D., P.R. Chu and A.P. King. 1980. The young cowbird: average or optimal nestling? Condor 82:417-425.

Ekstein, J.D., K.A. Hansen and S.L. Winter. 1993. Cowbird parasitism of Red-winged Blackbirds in prairie and riparian forest locations. Prairie Naturalist 25:276.

Elliott, P.F. 1977. Adaptive significance of cowbird egg distribution. Auk 94:590-593.

Elliott, P.F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. Auk 95:161-167.

Fleischer, R.C. 1985. A new technique to identify and assess the dispersion of eggs of individual brood parasites. Behavioral Ecology and Sociobiology 17:91-99.

Fleischer, R.C. 1986. Brood parasitism by Brown-headed Cowbirds in a simple host community in eastern Kansas. Bulletin of the Kansas Ornithological Society 37:21-29.

Fleischer, R.C., A.P. Smyth and S.I. Rothstein. 1987. Temporal and age-related variation in the laying rate of the parasitic Brown-headed Cowbird in the eastern Sierra Nevada, California. Canadian Journal of Zoology 65:2724-2730.

Folkers, K.L. and P.E. Lowther. 1985. Responses of Red-winged Blackbirds and Yellow Warblers to Brown-headed Cowbirds. Journal of Field Ornithology 56:175-177.

Freeman, S., D.F. Gori and S. Rohwer. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: some aspects of a host-parasite relationship. Condor 92:336-340.

Fretwell, S. 1977. Is the Dickcissel a threatened species? American Birds 31:923-932.

Friedmann, H. 1929. The cowbirds, a study in the biology of social parasitism. C.C. Thomas, Springfield, Illinois.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. National Museum Bulletin 233.

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.

Friedmann, H. and L.F. Kiff. 1985. The parasitic cowbirds and their hosts. Proceedings of the Western Foundation of Zoology 2:226-304.

Gates, J.E. and L.W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59:871-883.

Gill, S.A., P.M. Grieef, L.M. Staib and S.G. Sealy. 1997. Does nest defense deter or facilitate cowbird parasitism? A test of the nesting-cue hypothesis. Ethology 103:56-71.

Gochfeld, M. 1979. Brood parasite and host coevolution: interactions between Shiny Cowbirds and two species of meadowlarks. American Naturalist 113:855-870.

Goodnight, K., D.C. Queller and T. Poznansky. 1997. Kinship. Version 1.12: http://www.bioc.rice.edu/~kfg/GSoft.html.

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.

Grant, N.D. 1998. Host choice of a generalist brood parasite, The Brown-headed Cowbird (*Molothrus ater*). M.Sc. thesis, Laurentian University. Sudbury, Ontario.

Grieef, P.M. 1995. Cues used by brood parasites and predators to locate nests. M.Sc. thesis, University Of Manitoba. Winnipeg, Manitoba.

Hahn, D.C. and J.S. Hatfield. 1995. Parasitism at the landscape scale: Cowbirds prefer forests. Conservation Biology 9: 1415-1424.

Hahn, D.C. and J.S. Hatfield. 2000. Host selection in the forest interior: cowbirds target ground-nesting species. Pp. 120-127 *in* J.N.M. Smith, T.L. Cook, S.I. Rothstein, S.K. Robinson and S.G. Sealy, eds. Ecology and Management of Cowbirds: Studies in conservation of North American passerine birds. University Of Texas Press, Austin, Texas.

Hahn, D.C., J.A. Sedgwick, I.S. Painter and N.J. Casna. 1999. A spatial and genetic analysis of cowbird host selection. Studies in Avian Biology 18:204-217.

Hann, H.W. 1941. The cowbird at the nest. Wilson Bulletin 53:209-221.

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

Hobson, K.A., M.L. Bouchart and S.G. Sealy. 1988. Responses of naïve Yellow Warblers to a novel nest predator. Animal Behaviour 36:1823-1830.

Holford, K.C. and D.D. Roby. 1993. Factors limiting fecundity of captive Brown-headed Cowbirds. Condor 95:536-545.

Hoover, J.P. and M.C. Brittingham. 1993. Regional variation in cowbird parasitism of Wood Thrushes. Wilson Bulletin 105:228-238.

Hoy, G. and J. Ottow. 1964. Biological and oological studies of the Molothrine cowbirds (Icteridae) of Argentina. Auk 81: 186-203.

James, F.C. and H.H. Shugart. 1970. A quantitative method for habitat description. Audubon Field-Notes 24:727-736.

Kattan, G.H. 1997. Shiny Cowbirds follow the "shotgun" strategy of brood parasitism. Animal Behaviour 53:647-654.

Klaas, E.E. 1975. Cowbird parasitism and nesting success in the Eastern Phoebe. Occasional Papers of the Kansas Museum of Natural History. 41:1-18.

Kozlovic, D.R., R.W. Knapton and J.C. Barlow. 1996. Unsuitability of the House Finch as a host of the Brown-headed Cowbird. Condor 98:253-258.

Larison, B., S.A. Laymon, P.L. Williams and T.B. Smith. 1998. Song Sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. Condor 100:93-101.

Laskey, A.R. 1950. Cowbird behavior. Wilson Bulletin 62:157-174.

Leopold, N.F. Jr. 1924. The Kirtland's Warbler in its summer home. Auk 41:44-58.

Lokemoen, J.T. and R.R. Koford. 1996. Using candlers to determine the incubation stage of passerine eggs. Journal of Field Ornithology 67:660-668.

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

Lowther, P.E. 1979. Nest selection by Brown-headed Cowbirds. Wilson Bulletin 91:118-122.

Lowther, P.E. 1984. Cowbird nest selection. Wilson Bulletin 96:103-107.

Lowther, P.E. 1993. Brown-headed Cowbird (*Molothrus ater*). *In* A. Poole and F. Gill (eds.). The Birds of North America, no. 47. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

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.

Martin, T.E. 1992. Breeding productivity considerations: what are the appropriate features for management? Pp. 455-473 *in* J.M Hagan III and D.W. Johnston, eds. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C.

Martinez, J.G., M. Soler & J.J. Soler. 1996. The effect of Magpie breeding density and synchrony on brood parasitism by Great spotted Cuckoos. Condor 98:272-278.

Martinez, J.G., J.J. Soler, M. Soler and T. Burke. 1998a. Spatial patterns of egg laying and multiple parasitism in a brood parasite: a non-territorial system in the Great Spotted Cuckoo (*Clamator glandarius*). Oecologia 117:286-294.

Martinez, J.G., T. Burke, D. Dawson, J.J. Soler, M. Soler and A.P. Møller. 1998b. Microsatellite typing reveals mating patterns in the brood parasitic Great Spotted Cuckoo (*Clamator glandarius*). Molecular Ecology 7:298-297.

Mason, P. 1986. Brood parasitism in a host generalist, the Shiny Cowbird: II Host selection. Auk 103:61-69.

Mayfield, H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Michigan.

Mayfield, H. 1965. Chance distribution of cowbird eggs. Condor 67:257-263.

McGeen, D.S. and J.J. McGeen. 1968. The cowbirds of Otter Lake. Wilson Bulletin 80:84-93.

McGeen, D.S. 1972. Cowbird-host relationships. Auk 89:360-380.

McLean, I.G. 1987. Response to a dangerous enemy: Should a brood parasite be mobbed? Ethology 75:235-245.

McLean, I.G., J.N.M. Smith and K.G. Stewart. 1986. Mobbing behavior, nest exposure, and breeding success in the American Robin. Behaviour 96:171-186.

McMaster, D.G. and S.G. Sealy. 1998. Short incubation periods of Brown-headed Cowbirds: How do cowbird eggs hatch before Yellow Warbler eggs? Condor 100:102-111.

Mermoz, M.E. and J.C. Reboreda. 1999. Egg-laying behaviour by Shiny Cowbirds parasitizing Brown-and-Yellow Marshbirds. Animal Behaviour 58:873-882.

Middleton, A.L.A. 1977. Effect of cowbird parasitism on American Goldfinch nesting. Auk 94:304-307.

Moskát, C. and M. Honza. In press. Effect of nest and nest site characteristics on the risk of Cuckoo (*Cuculus canorus*) parasitism in the Great Reed Warbler (*Acrocephalus arundinaceus*). Ecography.

Mumford, R.E. 1959. Cowbird parasitizes nest containing young. Auk 76:367-368.

Neudorf, D.L. and S.G. Sealy. 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: Enemy recognition or generalized responses? Behaviour 123:84-105.

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

Nice, M.M. 1937. Studies in the life history of the Song Sparrow. Part I. Transactions of the Linnaean Society of New York 4:1-247.

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.

Ortega, C.P., J.C. Ortega and A. Cruz. 1994. Use of artificial Brown-headed Cowbird eggs as a potential management tool in deterring parasitism. Journal of Wildlife Management 58:488-492.

Payne, R.B. 1965. Clutch size and numbers of eggs laid by Brown-headed Cowbirds. Condor 67:44-60.

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. 1977a. Clutch size, egg size, and the consequences of single vs. multiple parasitism in parasitic finches. Ecology 58:500-513.

Payne, R.B. 1977b. The ecology of brood parasitism in birds. Annual Review of Ecology and Systematics 8:1-28.

Payne, R.B. 1998. Brood parasitism in birds: strangers in the nest. BioScience 48:377-386.

Post, W. and J.W. Wiley. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. Condor 79:176-184.

Queller, D.C. and K.F. Goodnight. 1989. Estimating relatedness using genetic markers. Evolution 43: 258-275.

Ricklefs. R.E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Robbins, C.S. 1979. Effects of forest fragmentation on bird populations. Pp. 198-213 *in* R.M. DeGraaf and K.E. Evans, eds. Management of northcentral and northeastern forests for nongame birds. U.S. Forest Service General Technical Reports NC-51.

Robertson, R.J. and R.F. Norman. 1977. The function and evolution of aggressive behavior towards the Brown-headed Cowbird (*Molothrus ater*). Canadian Journal of Zoology 55:508-518.

Robinson, S.K., S.I. Rothstein, M. Brittingham, L.J. Petit and J.A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pp. 428-

460 *in*: Martin, T.E. and D.M. Finch, eds. Ecology and management of neotropical migratory birds. Oxford University Press, New York.

Romig, G.P. and R.D. Crawford. 1995. Clay-colored Sparrows in North Dakota parasitized by Brown-headed Cowbirds. Prairie Naturalist 27:193-203.

Rothstein, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. American Naturalist 109:161-176.

Rothstein, S.I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. Auk 93:657-691.

Rothstein, S.I. 1990. A model system for co-evolution: Avian brood parasitism. Annual Review of Ecology and Systematics 21:481-508.

Rothstein, S.I. and S.K Robinson. 1998. Parasitic birds and their hosts: studies in coevolution. University of Oxford Press, New York.

Sambrook, J., E.F. Fritsch and T. Maniatis. 1989. Molecular cloning: a laboratory manual. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press.

Scott, D.M. and C.D. Ankney. 1983. The laying cycle of Brown-headed Cowbirds: passerine chickens? Auk 100:583-592.

Scott, D.M. and R.E. Lemon. 1996. Differential reproductive success of Brown-headed Cowbirds with Northern Cardinals and three other hosts. Condor 98:259-271.

Sealy, S.G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. Canadian Field-Naturalist 94:154-158.

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

Sealy, S.G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: An empirical and experimental study. Animal Behaviour 49:877-889.

Sealy, S.G. and R.C. Bazin. 1995. Low frequency of observed cowbird parasitism on Eastern Kingbirds: host rejection, effective nest defense, or parasite avoidance? Behavioral Ecology 6:140-145.

Sealy, S.G., D.L. Neudorf and D.P. Hill. 1995. Rapid laying by Brown-headed Cowbirds *Molothrus ater* and other parasitic birds. Ibis 137:76-84.

Sealy, S.G., D.L. Neudorf, K.A Hobson and S.A. Gill. 1998. Nest defense by potential host of the Brown-headed Cowbird: Methodological approaches, benefits of defense, and coevolution. Pp. 194-211 *in* S.I. Rothstein and S.K. Robinson, eds. Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York.

Sedgwick, J.A. and W.M. Iko. 1999. Costs of Brown-headed Cowbird parasitism to Willow Flycatchers. Studies in Avian Biology 18:167-181.

Sherry, D.M., Forbes, M.R.L., Khurgel, M. 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 Sciences 90: 7839-7843.

Smith, J.N.M and P. Arcese. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: A 16-year study. Condor 94: 916-934.

Smith, J.N.M and I.H. Myers-Smith. 1998. Spatial variation in parasitism of Song Sparrows by Brown-headed Cowbirds. Pp. 296-312 *in* S.I. Rothstein and S.K. Robinson, eds. Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry. W.H. Freeman and Company, New York, NY.

Soler, J.J., M. Soler, A.P. Møller and J.G. Martinez. 1995. Does the Great Spotted Cuckoo choose Magpie hosts according to their parenting ability? Behavioral Ecology and Sociobiology 36:201-206.

Soler, M., J.J. Soler and J.G. Martinez. 1998. Duration of sympatry and coevolution between the Great Spotted Cuckoo (*Clamator glandarius*) and its primary host, the Magpie (*Pica pica*). Pp. 113-128 *in* S.I. Rothstein and S.K. Robinson, eds. Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York.

Southern, W.E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake Region, Michigan. Jack-Pine Warbler 36:105-130.

Southern, W. E. and L.K. Southern. 1980. A summary of incidence of cowbird parasitism in northern Michigan from 1911-1978. Jack-Pine Warbler 58:77-84.

Spautz, H. 1999. Common Yellowthroat brood parasitism and nest success vary with host density and site characteristics. Studies in Avian Biology 18:218-228.

Staab, C.A. and M.L. Morrison. 1999. Managing riparian vegetation to control cowbirds. Studies in Avian Biology 18:18-22.

Strausberger, B.M. 1998. Temporal patterns of host availability, Brown-headed Cowbird brood parasitism, and parasite egg mass. Oecologia 116:267-274.

Thompson, C.F. and B.M. Gottfried. 1976. How do cowbirds find and select nests to parasitize? Wilson Bulletin 88:673-676.

Thompson, C.F. and B.M. Gottfried. 1981. Nest discovery and selection by Brown-headed Cowbirds. Condor 83:268-269.

Trine, C.L. 2000. Effects of multiple parasitism on cowbird and Wood Thrush nesting success. Pp. 135-144 *in* J.N.M. Smith, T.L. Cook, S.I. Rothstein, S.K. Robinson and S.G. Sealy, eds. Ecology and Management of Cowbirds: Studies in conservation of North American passerine birds. University Of Texas Press, Austin, Texas.

Uyehara, J.C. 1996. Correlates and field experiments of nest searching behavior in a brood parasite, the Brown-headed Cowbird. Ph.D. thesis, University of California, Los Angeles.

Uyehara, J.C. and P.M. Narins. 1995. Nest defense by Willow Flycatchers to brood-parasitic intruders. Condor 97:361-368.

Uyehara, J.C. and M.J. Whitfield. 2000. Association of vegetative cover and parasitism in territories of the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). Pp. 204-209 *in* J.N.M. Smith, T.L. Cook, S.I. Rothstein, S.K. Robinson and S.G. Sealy, eds. Ecology and Management of Cowbirds: Studies in conservation of North American passerine birds. University Of Texas Press, Austin, Texas.

Weary, D.M., R.E. Lemon and S. Perreault. 1994. Male Yellow Warblers vary use of song types depending on pairing status and distance from nest. Auk 111:727-729.

Weatherhead, P.J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358-366.

Wiens, J.A. 1963. Aspects of cowbird parasitism in southern Oklahoma. Wilson Bulletin 75: 130-139.

Wiley, J.W. 1988. Host selection by the Shiny Cowbird. Condor 90:289-303.

Wiley, R.H. and M.S. Wiley. 1980. Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments. Ecological Monographs 50:153-178.

Wolf, L. 1987. Host-parasite interactions of Brown-headed Cowbirds and Dark-eyed Juncos in Virginia. Wilson Bulletin 99:338-350.

Woolfenden, B.E. 2000. Demography and breeding behaviour of Brown-headed Cowbirds: An examination of host use, individual mating patterns, and reproductive success using microsatellite DNA markers. Ph.D. thesis, McMaster University, Hamilton, Ontario.

Yahner, R.H. and C.A. DeLong. 1992. Avian predation and parasitism on artificial nests and eggs in two fragmented landscapes. Wilson Bulletin 104: 162-168.

Young, H. 1963. Breeding success of the cowbird. Wilson Bulletin 75:115-122.

Zimmerman, J.L. 1983. Cowbird parasitism of Dickcissels in different habitats and at different nest densities. Wilson Bulletin 95:7-22.

APPENDICES

Appendix 1. Parameters of reproductive performance of Song Sparrows in two years at Delta Marsh, Manitoba. Numbers shown are means ± standard errors.

Reproductive Parameter	1998	1999
Nests studied	60	85
Onset of laying	13-May	18-May
First cowbird egg	17-May	24-May
Proportion of nests parasitized	0.59	0.71
Proportion of nests multiply parasitized	0.60	0.66
Size of unparasitized clutches	4.67 ± 0.16	5.06 ± 0.10
Size of parasitized clutches	4.00 ± 0.19	4.28 ± 0.14
Cowbird eggs per parasitized nest	1.86	1.98
Proportion of nests hatching	0.28	0.33
Proportion of nests succeeding	0.17	0.19
Proportion of nests failing due to predation	0.61	0.46
Sparrows fledged per nest	0.58 ± 0.12	0.46 ± 0.14
Sparrows fledged per successful nest	3.50 ± 0.37	2.43 ± 0.38

Appendix 2. Relatedness coefficients (*r*-values) for pairs of individuals from multiply parasitized nests. Nests 1-17 were found outside the core area, and nests 18-33 were found within the core area. Two-egg nests are listed before three- and four-egg nests in each set (number of eggs for which genetic information was obtained). Nests in which the cowbird eggs were laid by the same female are indicated by SF, nests in which the cowbird eggs were laid by different females by MF, and nests in which some eggs were laid by the same female and one or more by a different female by SF/MF.

1	SF		***Egg numbers***	
		Egg numbers	*C1*	*C11*
		C1	-	0.106
		C11	0.106	-

2	SF		***Egg numbers***	
		Egg numbers	*C4*	*C5*
		C4	-	0.813
		C5	0.813	-

3	MF		***Egg numbers***	
		Egg numbers	*C20*	*C29*
		C20	-	-0.193
		C29	-0.193	-

4	SF		***Egg numbers***	
		Egg numbers	*C8*	*C9*
		C8	-	0.264
		C9	0.264	-

5	SF		***Egg numbers***	
		Egg numbers	*C10*	*C17*
		C10	-	0.391
		C17	0.391	-

6	SF		***Egg numbers***	
		Egg numbers	*C12*	*C14*
		C12	-	0.624
		C14	0.624	-
7	SF		***Egg numbers***	
		Egg numbers	*C21*	*C25*
		C21	-	0.378
		C25	0.378	-
8	MF		***Egg numbers***	
		Egg numbers	*C23*	*C30*
		C23	-	0.097
		C30	0.097	-
9	MF		***Egg numbers***	
		Egg numbers	*C24*	*C36*
		C24	-	0.206
		C36	0.206	-
10	SF		***Egg numbers***	
		Egg numbers	*C31*	*C32*
		C31	-	0.431
		C32	0.431	
11	MF		***Egg numbers***	
		Egg numbers	*C51*	*C52*
		C51	-	0.423
		C52	0.423	
12	MF		***Egg numbers***	
		Egg numbers	*C53*	*C54*
		C53	-	0.029
		C54	0.029	

13	**MF**		***Egg numbers***	
		Egg numbers	*C55*	*C56*
		C55	-	0.148
		C56	0.148	

14	**MF**			***Egg numbers***	
		Egg numbers	*C26*	*C27*	*C39*
		C26	-	0.144	0.002
		C27	0.144	-	0.058
		C39	0.002	0.058	-

15	**SF/MF**			***Egg numbers***	
		Egg numbers	*C45*	*C46*	*C47*
		C45	-	0.008	0.644
		C46	0.008	-	0.464
		C47	0.644	0.464	-

16	**SF/MF**			***Egg numbers***	
		Egg numbers	*C19*	*C28*	*C33*
		C19	-	0.484	-0.078
		C28	0.484	-	-0.154
		C33	-0.078	-0.154	-

17	**SF/MF**			***Egg numbers***	
		Egg numbers	*C6*	*C7*	*C16*
		C6	-	0.722	0.368
		C7	0.722	-	0.176
		C16	0.368	0.176	-

18	**MF**		***Egg numbers***	
		Egg numbers	*1*	*4*
		1	-	0.088
		4	0.088	-

19	**SF**		***Egg numbers***	
		Egg numbers	*21*	*25*
		21	-	0.460
		25	0.460	-
20	**MF**		***Egg numbers***	
		Egg numbers	*23*	*24*
		23	-	0.139
		24	0.139	-
21	**SF**		***Egg***	
		Egg numbers	*26*	*35*
		26	-	0.606
		35	0.606	-
22	**MF**		***Egg numbers***	
		Egg numbers	*27*	*28*
		27	-	-0.101
		28	-0.101	-
23	**MF**		***Egg numbers***	
		Egg numbers	*30*	*40*
		30	-	0.014
		40	0.014	-
24	**MF**		***Egg numbers***	
		Egg numbers	*41*	*56*
		41	-	-0.106
		56	-0.106	-
25	**MF**		***Egg numbers***	
		Egg numbers	*58*	*59*
		58	-	0.062
		59	0.062	-

26	**SF**		***Egg numbers***	
		Egg numbers	*65*	*67*
		65	-	0.524
		67	0.524	-

27	**MF**		***Egg numbers***	
		Egg numbers	*74*	*75*
		74	-	0.419
		75	0.419	-

28	**MF**		***Egg numbers***	
		Egg numbers	*77*	*78*
		77	-	-0.225
		78	-0.225	-

29	**SF**		***Egg numbers***	
		Egg numbers	*80*	*82*
		80	-	0.539
		82	0.539	-

30	**MF**		***Egg numbers***		
		Egg numbers	*5*	*6*	*13*
		5	-	0.174	0.076
		6	0.174	-	0.005
		13	0.076	0.005	-

31	**MF**		***Egg numbers***		
		Egg numbers	*47*	*49*	*51*
		47	-	0.357	0.062
		49	0.357	-	0.092
		51	0.062	0.092	-

32	**SF/MF**		***Egg numbers***			
		Egg numbers	*15*	*16*	*17*	*18*
		15	-	0.198	0.497	-0.052
		16	0.198	-	0.301	0.038
		17	0.497	0.301	-	-0.239
		18	-0.052	0.038	-0.239	-

33	**SF/MF**		***Egg numbers***		
	Egg	***61***	***62***	***63***	***64***
	61	-	-0.073	-0.020	0.441
	62	-0.073	-	0.514	-0.088
	63	-0.020	0.514	-	-0.029
	64	0.441	-0.088	-0.029	-