CANADIAN THESES ON MICROFICHE

THÈSES CANADIENNES SUR MICROFICHE

National Library of Canada
Collections Development Branch

Canadian Theses on
Microfiche Service

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Direction du développement des collections

Service des thèses canadiennes
sur microfiche

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

Canada

NL 339 (r. 86/09)

ABSTRACT

Before the appearance of Brown-headed Cowbirds, Molothrus ater, passerine reproductive strategies in eastern North America, were primarily shaped by competition for limiting resources and predation pressures. The purpose of this study was to examine what adaptations in the reproductive strategy of one host species, the Yellow Warbler, Dendroica petechia, have arisen in response to brood parasitism by the Brown-headed Cowbird in the Ottawa area in the last 150 to 200 years.

I first determined the strength of the selection pressure acting on Yellow Warblers. Then I examined what adaptive responses Yellow Warblers exhibit, first to avoid nest discovery by cowbirds, and second to prevent or reduce the effect of parasitism once the nest has been discovered.

My results indicate that, at present, brood parasitism appears to be as strong a selective pressure as predation, when measured in terms of the reproductive loss to Yellow Warblers. While predation caused a greater reduction in the number of fledglings produced in a season for affected individuals, more than twice as many nests suffered from parasitism than predation. Parasitism accounted for at least 41% of all eggs lost, whereas 35% of the egg loss was attributable to predation. Therefore, the selection pressure from parasitism is acting on Yellow Warblers to favour individuals with traits which help them to avoid being parasitized or lessen the impacts of parasitism.

Results of the analysis of Yellow Warbler nest site quality indicate that those pairs that nested in tall bushes, or farther from high perches were parasitized less frequently. Those pairs that nested after the peak cowbird laying period or exhibited a higher degree of nesting synchrony with other Yellow Warblers were also less likely to be parasitized.

Aggressive responses by Yellow Warblers towards caged intruders placed 1 m from their nest indicate that Yellow Warblers have developed the ability to recognize the specific threat that cowbirds pose. The strongest response to the female cowbird was given during the egg laying and early incubation stage when the nest is most vulnerable to brood parasitism. In contrast, the Yellow Warbler responses to a predator (crow) were strongest during the nestling stage. Furthermore, 5 out of 8 females tested, exhibited an aggressive trait of sitting in a nest in the presence of female cowbird before any eggs have been laid (the "pre-mature incubation response") that probably has no other adaptative value than with respect to brood parasitism. Yellow Warblers respond to the stimulus of a cowbird egg by rejecting it, if they are in the early stage of clutch completion and have enough time left in their breeding season to re-nest. This response was shown to be specific to the cowbird egg, and not due to a secondary disturbance such as: altering clutch size, visiting nests, or placing a female cowbird at nests.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. J. Picman, for his shared enthusiasm, advice and friendship, throughout this project, and for the opportunity to proceed on this undertaking.

I thank my committee members, Dr. P. Weatherhead and Dr. F. Briand for providing constructive criticism in the design of this study and the analysis of results.

Thanks to Jean McAllister, Dave Beedall, and Rob Poole, for assistance in feeding the deer flies and in data collection. I am grateful to Dwayne Moore, and Dr. Roland Thomas for assistance in the analysis of results, and to Marty Leonard for her useful suggestions.

My thanks to Stu Hamil and the National Capital Commission for permission to work at Mer Bleue.

To my parents, Allen and Jean Burgham, my thanks for instilling in me the desire to set and attain my goals.

To my wife, Mary Sean Burgham, I am very grateful for her continued encouragement and financial support.

This study was supported by operating and equipment grants from the Natural Sciences and Engineering Research Council to J. Picman.

TABLE OF CONTENTS

Chapter 1: The Effect of Brood Parasitism on Host Reproduction.

Chapter 2: Adaptations to Avoid Nest Discovery.

Chapter 3: Adaptations to Avoid or Minimize the Effects of Parasitism after Nest Discovery by a Cowbird.

LIST OF TABLES

LIST OF FIGURES

GENERAL INTRODUCTION

Avian reproductive strategies have been shaped by natural selection to maximize an individual's gene representation in future generations. The methods an individual uses are evolutionary and cultural adaptations to pressures in the environment. The more successful an individual is, the greater the representation of it's genes, and thus it's specific traits in the population. Thus reproductive traits which confer an advantage to a nesting individual such as reducing competition or lowering the chance of predation or parasitism will be selected for.

Evolutionary adaptations, which also set the parameters for what can be learned, can only evolve slowly, as selection acts over generations (Ricklefs, 1973, p. 60). The rate of response depends upon the rate of mutations, the amount of variability and the amount of plasticity in the behavioural repertoire (Ricklefs, 1973, p. 69). Consequently, the severity and speed of environmental change will determine how successfully an organism can cope, as change alters the selection pressures acting on the individuals in a population. The strength of a selection pressure will, in turn, influence the speed with which a new trait will spread through a population.

Changes in selection pressures can be a result of sudden natural biotic invasions by species into areas where they were formerly absent, such as: the Tasmanian White-eye (Zosterops lateralis) in New Zealand, the Cattle Egret (Bubulcus ibis) in northern South

America, and the Fieldfare (Turdus pilaris) in southern Greenland (Mayr, 1976, p. 664). However, in the last three hundred years man has altered the biotic structure in many areas of the world, by the introduction of exotic species. The European Starling (Sturnus vulgaris), the House Sparrow (Passer domesticus), the pheasant (Phasianus colchicus) and the Rock Dove (Columba livia) were all successfully introduced in North America, probably causing population declines in meadowlarks (Sturnella magna), some woodpeckers, Eastern Bluebirds (Sialia sialis) and some swallows (Mayr, 1976, p. 660).

The disturbances caused by introductions of exotic species into island communities have been even greater. When the individuals of a population cannot adapt quickly enough to a new pressure such as competition from an exotic introduction, the population falls and the species may become extinct. In the Hawaiian Islands, New Zealand, and the West Indies, the introduction of exotics is believed to have been responsible for the extinction of some endemic species (Long, 1981, p. 17).

Man has also caused sudden new pressures on endemic birds in a more subtle manner. Human-induced changes to the environment (predominantly changes in agricultural methods or implementation of agriculture where it was absent) has often precipitated the spread of species into areas where they were formerly absent, and thus altered the selection pressures acting on endemic species. The Linnet, Carduelis cannabina (Ricklefs, 1973, p. 573), the Collared Dove, Streptopelia decaocto (Mayr, 1976, p. 661), the Shiny Cowbird, Molothrus bonariensis (Friedmann, 1971) and the Brown-headed Cowbird, M. ater (Friedmann, 1963) have all expanded their range as a result of human activities.

While the Linnet and the Collared Dove probably affect endemics through competition for food and nest sites, the two species of cowbirds have a more direct and dramatic, negative effect on some of the endemic species. The Shiny and Brown-headed Cowbirds are brood parasites, laying their eggs in nests of other species. Because these parasites are not specialists (i.e. host specific), the negative impact of parasitism on the population levels of certain host species does not negatively affect the parasite population. Furthermore, the greater the parasite's reproductive output, the greater the damage to the host's reproductive effort (Rothstein, 1975a). Consequently, the negative effect on some host species, and therefore the selective value of some anti-parasite adaptations can be great.

Where the parasites and hosts have been sympatric for thousands of generations, selection favoured parasites that could exploit their hosts to obtain maximum reproductive output, while simultaneously acting on hosts to avoid or minimize the effects of parasitism (Robertson and Norman, 1976). However, when a parasite moves into a new area, the resident species are not adapted to this new pressure. Consequently, nest parasites may cause a sharp decline of host populations. In such a situation, the adaptive value for traits to avoid or minimize the effects of parasitism becomes very high.

The spread of the Shiny Cowbird from South America, into the Carribean since 1950, is thought to be responsible for the decline in the blackbird (Agelaius xanthomus) populations in Puerto Rico, and the near extinction of the Barbadian race of the Yellow Warbler (Dendroica petechia) (Friedmann, 1971). The rapid expansion of the range of the Brown-headed Cowbird into Pacific-western and eastern North America, from the mid-west, has introduced a new and in some cases strong selective pressure on many species (Friedmann, 1971; Mayfield, 1977).

The impact of brood parasitism by the Brown-headed Cowbird on the reproductive success of many host species has been well documented (Friedmann, 1963; Anderson and Storer, 1976; Smith, 1981; Zimmerman, 1983). Host species are limited in the methods available for natural selection to act upon to reduce the effect of brood parasitism on the individual. Many studies (e.g. Hofslund, 1957; Mayfield, 1977; Hatch, 1983) have been published on the reproductive loss imposed on hosts by cowbirds. However, relatively few (Rothstein, 1975b, 1976; Robertson and Norman, 1976, 1977; Scott, 1977; Clark and Robertson, 1981) have looked at what host adaptations have resulted. Each of these studies has usually investigated only one form of defence, and a comprehensive treatment of defensive mechanisms against brood parasitism has not been undertaken.

A study examining all the defensive mechanisms that a host uses should provide better insight into host-parasite interactions and the role of brood parasitism as a selective force. The cowbird-host interaction offers an opportunity which may provide valuable insight into the rate of evolutionary and cultural adaptation in a species recently exposed to brood parasitism. Brood parasitism in the newly inhabited range has altered the adaptive value of some traits associated with the reproductive tactics of heavily parasitized species. Here, I wish to examine whether brood parasitism in the short time of exposure in this area has already selected for traits that will aid individuals to reduce the impact of, or to avoid, parasitism.

The selective pressure from brood parasitism is not constant but changes strength between seasons, depending on the number of cowbirds, the number of hosts and the traits expressed in individuals of both species. The anti-parasite traits that are now exhibited in Yellow Warblers in this area need not be a result of the strength of the current selective pressure, but may be a consequence of past selective pressures from brood parasitism over the last 150 to 200 years. However, because it is impossible to measure past selective pressures directly, I determined how strong the selective pressure from brood parasitism is on Yellow Warblers in south-eastern Ontario. I then examined what traits are now exhibited by Yellow Warblers which are effective in reducing the effects of brood parasitism by Brown-headed Cowbirds.

To gain an understanding of the current strength of the selection pressure acting on Yellow Warblers in my study area, I determined the degree and frequency of parasitism and compared the amount of reproductive loss from brood parasitism to the loss from nest predation (chapter 1). The impact of brood parasitism on the breeding success of Yellow Warblers over the past 150 to 200 years, should in turn, be reflected in the reproductive strategy of a host species. Therefore, I examined what traits Yellow Warblers exhibit to avoid having their nest located by a female cowbird (chapter 2), or to avoid being parasitized or at least lessen the impact of parasitism once their nest was discovered by a female cowbird (chapter 3). Finally, I conclude with a general discussion on what tactics have and have not appeared in the short time of exposure of eastern Yellow Warblers to brood parasitism, and discuss what needs to be done to further the study of the impact of brood parasitism in new areas of cowbird expansion.

CHAPTER 1

The Effect of Brood Parasitism on Host Reproduction

INTRODUCTION

Cowbird Range Expansion

The Brown-Headed Cowbird was once restricted to the short grass prairie in the centre of the continent where it fed in disturbed pasture left by grazing herds of Bison (Bison bison). It developed a nomadic lifestyle during the breeding season in response to the unpredictable and patchy food availability (Hill, 1976). This brood parasite has extended its range eastward within the last two hundred years as the eastern forests of North America were cleared to make way for agriculture (Van Velzen, 1972). More recently, its spread has continued in the western mountaneous regions as man opened these areas for recreational use (Verner and Ritter, 1983). In southwest British Columbia the earliest breeding records for cowbirds are from the 1920's; and cowbirds have bred in some of the gulf islands of British Columbia only since the late 1960's (Smith, 1981).

The expansion of the cowbird range has also continued to the east and north in this century. In Ontario, the species' limit has moved northward at least two hundred miles in the first half of this century (Snyder, 1959 in Friedmann, 1963). This recent expansion of the cowbird's range from its origin in the mid-west is summarized in VanVelzen (1972; Fig. 1), and encompasses my study area.

Figure 1 The abundance and distribution of the Brown-headed Cowbird in North America (from Van Velzen, 1972).

density (birds/route)

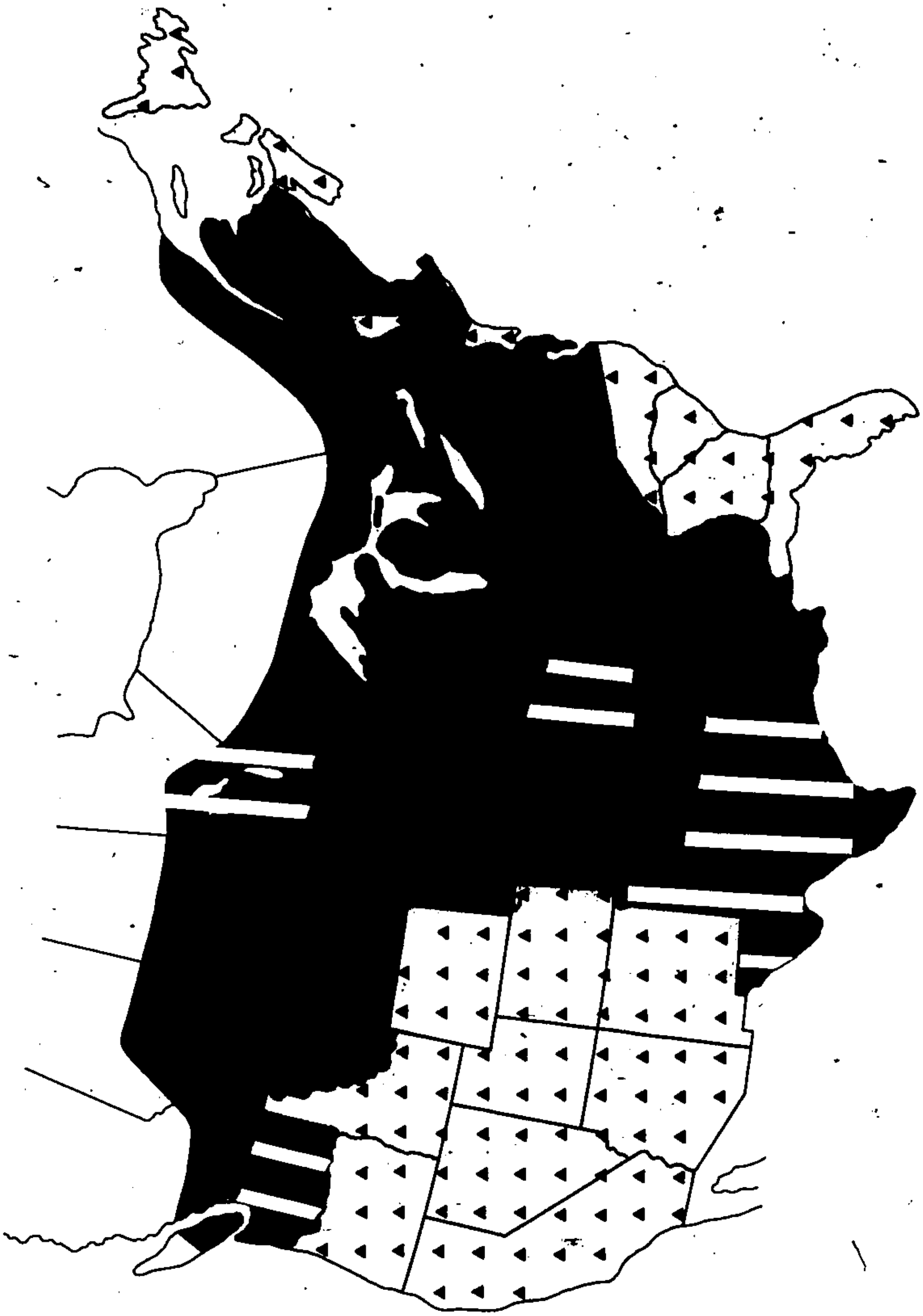
☐ **absent or unknown**

▲ ▲ 1 - 5

■ 6 - 19

▥ 20 - 29

■ 30 - 50



Changing Habits

Cowbird range expansion has exposed this species to new habitat types. Cowbirds have also come into contact with many new potential host populations which have had no prior experience with brood parasitism, and thus may be more susceptible to cowbirds. The cowbird behavioural pattern has been altered from a nomadic pattern in the mid-west (Lowther and Johnston, 1977) to a more sedentary pattern (Laskey, 1950; Darley, 1978, 1982) in the east. This is due primarily to the change in habitat structure (Dufty, 1982) and food availability (i.e. less arid conditions in the east increase diversity and predictablity of food). The change in the behavioural pattern may also be due in part to the greater availability of hosts (Dufty, 1982) and the greater vulnerability of host nests in eastern North America.

The newly exposed hosts may also be changing their behaviour. Hosts newly exposed to the pressure from cowbirds should be more susceptible to brood parasitism than those who have been sympatric with cowbirds for thousands of years. Different patterns of brood parasitism between eastern North America and the original mid-western range (Friedmann, 1963; Hanka, 1979) may reflect this. In 869 nests of 21 species occurring in a mid-western study, 91% of the 76 cases of parasitism belonged to Red-winged and Brewer's Blackbirds (Agelaius phoeniceus and Euphagus cyanocephalus) Hanka (1979). In contrast, eastern icterids are infrequently parasitized, while Parulidae and Fringillidae receive more attention from cowbirds (Ontario Nest Records Scheme, 1956-80), than they do in the mid-west (Friedmann et al., 1977).

Hanka's (1979) explanation for the different frequencies of brood parasitism is based on the differences in the availability of water between the two different regions and its effect on food availability. However, more solitary nesting by Icteridae in the mid-west may also explain the differences in the pattern of parasitism, as coloniality is an effective defence. While these explanations are reasonable, the obvious differences in sympatry that existed for thousands of years, which have allowed mid-western host species to adapt to the pressure of parasitism, should be considered. The vulnerability of eastern Parulidae and Fringillidae may explain their high rates of parasitism.

The Severity of the Threat

For species where another pressure has combined with parasitism, an inability to adapt quickly may result in extinction. The Dickcissel (Spiza americana) has long been sympatric with cowbirds, yet the increasing loss of female Dickcissels in their winter~~ing~~ range has caused a decrease in nest density, resulting in an increased pressure from cowbird parasitism. This combination of factors appears to be leading the Dickcissel to extinction (Fretwell, 1977).

The potential threat to host species in the east may be more acute. Eastern cowbird hosts have been quickly exposed to this new pressure. This pressure may destabilize the population so that it is unable to contend with other disruptions. The Kirtland's Warbler (Dendroica kirtlandii) was near extinction before control measures directed against cowbirds reduced parasitism from 65 to 21%. This species was vulnerable to the severe reproductive loss imposed on them by cowbird parasitism because of its small gene pool and a lack of defence mechanisms (Anderson and Storer, 1976). Mayfield (1977) noted that if the rate of parasitism exceeds 30% single brooded small species may be susceptible, and become extinct. Unlike specialized parasites, whose populations fluctuate with the host population, cowbirds are generalists known to have parasitized 216 species in North America (Friedmann et al., 1977). Thus the size of the cowbird population is not dependent on one host, and severe declines in host populations are possible without adversely affecting the parasites population size.

Yellow Warblers are a widely distributed host species occurring in the original and newly invaded cowbird range. Higher frequencies of parasitism in the east (Ontario Nest Records Scheme) than in the mid-west (Friedmann et al., 1977) may be a result of eastern Yellow Warblers being less well adapted, because of less time of exposure to cowbirds. Because Yellow Warblers raise only 1 brood per season at this latitude (Friedmann, 1963), they may be more susceptible to reproductive losses from cowbirds than some other hosts. These characteristics make Yellow Warblers an interesting species to study to determine how brood parasitism has affected them. To determine the strength of the selection pressure from brood parasitism acting upon Yellow Warblers in this area of cowbird range expansion, I measured: 1) the frequency of parasitism; 2) the degree of parasitism (number of cases of single or multiple parasitism); 3) the reproductive loss from parasitism, compared to the loss from predation; 4) the success cowbirds had with this host.

METHODS

The Study Area

This study was undertaken from April to August 1984, at the Mer Bleue Bog, 5 km east of Ottawa, Ontario. The western portions of this area are old field and marsh habitats lying between valley moraines. The 24 ha of old field habitat was wet throughout May because of poor drainage, but dried by early June. The dominant shrubs were meadow sweet (Spirea spp.), and willow (Salix spp.) with occasional trees of which birch (Betula spp.) was the most common. Yellow Warblers, Common Yellowthroats (Geothlypis trichas), Song Sparrows (Melospiza melodia), Swamp Sparrows (Melospiza georgiana) and Goldfinches (Spinus tristis) were the common nesting inhabitants in this area.

The Study Species

I chose Yellow Warblers as the main study species because of their high abundance in the area, high rates of parasitism of this species by cowbirds, their bright colouration for better visibility and the relative ease of locating their nests.

I observed the birds using 8 X 30 binoculars. Their behaviour and area of activity were noted. Nest searches began in mid May, by systematically searching the vegetation where Yellow Warblers were active. Nests were also found by following Yellow Warblers carrying nest material. Nests were labelled using numbered nest tags and flagging tape two metres north of the nest site to avoid drawing attention to the nest, and the nest positions were recorded on a map. Morning nest checks were carried out at least once every 2 days, except when heavy rain intervened.

Because predation is usually thought of as one of the major selective forces directing natural selection, the incidence of parasitism and predation was recorded to get a relative indication of the frequency of these two disturbances in the reproductive cycle of Yellow Warblers. The percentage of multiple parasitism (being parasitized more than once) in relation to the total number of cowbird eggs laid (intensity of parasitism) was recorded for calculating McGeen's (1972) pressure index. This pressure index was designed to determine the pressure on a host species from cowbird parasitism. In addition, the reproductive cost to the host, in terms of lost eggs and young resulting from brood parasitism and predation was recorded, to further gauge the impact of parasitism on Yellow Warblers.

The effect of a cowbird chick on Yellow Warbler nestlings was determined by measuring the following parameters of growth: 1) tarsus length; 2) distance between the nares; 3) bill length (from the nares to the tip); 4) wing length; and 5) weight. All measurements were taken on Yellow Warbler nestlings at 6 days of age, from nests with and without cowbird chicks.

Cowbird success with this host species was determined by examining the fate of each cowbird egg.

RESULTS

Frequency of Parasitism

The majority of Yellow Warbler nests were found during the nest-building stage, in the last week of May and first week of June by following Yellow Warblers carrying nesting material. Of the 37 original nests found, 30% (Table 1) were parasitized, while only 14% were preyed upon. It is likely that these were all first nest attempts, since all but 9 were initiated before June 1st. Nests initiated before this date are unlikely to be re-nests as the earliest clutch initiation date for Yellow Warblers in this area was May 29th. The 9 nests initiated on or after June 1st were also likely first nests, as no other Yellow Warbler nests were found when the surrounding scrub was searched, whereas in the 3 known re-nesting attempts, the distance of the new nest was at most 25 m from the original nest site.

In every category (Table 1) parasitism was at least twice as frequent as predation. Although there were only 3 re-nests in new locations, 2 of these nests were parasitized. This was a significantly ($P<0.05$, Fisher Exact Test) higher rate of parasitism than the rate for the 9 re-lined nests, of which only 2 were subsequently parasitized.

Reproductive Cost To Yellow Warblers

Egg loss (eggs that failed to hatch) is one measure of the reproductive cost to Yellow Warblers. The egg loss per depredated nest was higher than the egg loss per parasitized nest. However, 41%

Table 1 Yellow Warbler nest success and the frequency of parasitism and depredation for different nest types.

	Total # of nests	# (%) of nests parasitized	# (%) of nests depredated	# (%) of nests successful
# of original nests found	37	11 (30)	5 (14)	21 (56)
# of re-nests in new location	3	2 (67)	1 (33)	0 (0)
# of re-nests in old cup	9	2 (22)	0 (0)	7 (78)
Total # of nests	49	15 (31)	6 (12)	28 (57)

of the total egg loss was due to cowbird activity while 35% of the egg loss was due to predators (Table 2). Moreover, the estimate of 41% egg loss due to cowbird activity is conservative. It is probable that more host eggs were ejected by cowbirds and replaced by the host depositing a new egg, than I was aware of. To determine this, I compared the initial clutch size between parasitized and unparasitized nests (see Mayfield, 1961). But, because Yellow Warblers frequently reject cowbird eggs and re-nest or re-line the existing nest, I had to make this comparison for two other accepter species abundant in my study area, the Common Yellowthroat and Swamp Sparrow (Table 3). The average number of host eggs remaining in parasitized nests was less than the average number in unparasitized nests for both species. However, this was not significant (Mann Whitney U test), because of small sample sizes. When the data is combined for both accepter species the difference becomes statistically significant (Table 3). This indicates that cowbirds frequently remove an egg from the nest and probably cause more egg loss than indicated by my data.

Of the Yellow Warbler eggs lost because of cowbird activity (Table 4), 61% and 28% were due to re-lining (burial of the original clutch) and re-nesting (nest desertion), respectively. This means that 89% of all the Yellow Warbler eggs lost due to cowbirds, were lost because of rejection by Yellow Warblers of the parasitized clutch.

Pairs that had no disturbance from parasitism or predation fledged significantly more young (3.76/nest) than those that were parasitized (2.67/nest) and accepted the cowbird egg, or initiated a new clutch

Table 2 Yellow Warbler egg loss from all sources.

	N	% of total eggs	% of eggs lost	# of nests	egg lost/nest
Host eggs laid	159	100	------		
eggs depredated	15	9	35	4	3.8±1.3
eggs infertile	7	4	16	7	1.0±0.0
eggs lost to abandonment	4	3	9	2	2.0±1.4
egg loss from cowbird activity	18	11	41	15	1.2±0.9

Table 3 Comparison of clutch size for parasitized and unparasitized nests of 2 accepter species.

		n	$\overline{X} \pm$ S.D.	P*
YELLOWTHROAT	parasitized	3	2.67±1.15	>0.05
	unparasitized	6	3.67±0.52	
SWAMP SPARROW	parasitized	2	1.50±0.71	>0.05
	unparasitized	6	4.70±0.52	
BOTH ACCEPTER SPECIES	parasitized	5	2.20±1.10	<0.01
	unparasitized	12	4.17±0.72	

* Mann Whitney U Test

Table 4 Yellow Warbler egg loss due to cowbird activity.

	N (%)	% of all eggs lost	% of eggs laid
eggs lost due to cowbird removal	2 (12)	5	1
eggs lost through desertion	5 (28)	12	3
eggs lost through burial	11 (61)	24	7
total egg loss to cowbird activity	18 (100)	41	11

after rejection (Table 5). However, predation may have had an even larger impact than parasitism on those pairs that suffered nest predation. The pairs that suffered from nest predation did not appear to re-nest and therefore fledged no young during this breeding season. I did not include the data for those nests that were parasitized or depredated early in the breeding season, and for which I did not find a new nest, since in these cases new nests may have been built elsewhere and successfully produced fledglings.

Cowbird Success

Cowbird success with this population of Yellow Warblers was low (Table 6). Of 15 cowbird eggs laid, 67% were lost to egg burial and 20% to nest desertion giving a total of 87% (13) rejected by Yellow Warblers. Only 1 of the 15 cowbird eggs laid hatched, and that chick was preyed upon at seven days of age. The predator was probably a small mammal, as the 2 Yellow Warbler chicks were eaten, but the cowbird chick was only partially consumed.

Multiple Parasitism

The number of cases of multiple parasitism was low. Of the original 37 Yellow Warbler pairs, 10 were parasitized once, one was parasitized twice and one was parasitized three times. The resulting cowbird pressure index on Yellow Warblers was 31.7, which is similar to the pressure index determined for other studies (Table 7). While the pressure index is useful for comparing parasitism pressure on Yellow Warblers in different studies, it is inadequate for comparison with pressure on accepter species. Yellow Warblers often reject cowbird

Table 5 Differences in the seasonal fledging success between nests effected by predation or parasitism and those that were not.

GROUP	n	# OF YOUNG FLEDGED X±S.D.	P*
untouched	21	3.76±0.77	---
parasitized	9	2.67±1.12	<0.05
depredated	5	0.00±0.00	<0.001

*P – the probability was calculated using a Mann Whitney U test between the untouched and parasitized group, and then between the untouched and depredated group.

Table 6 Cowbird success with Yellow Warblers.

	N (%)
cowbird eggs laid	15 (100)
cowbird eggs lost to burial	10 (67)
cowbird eggs lost to desertion	3 (20)
cowbird eggs depredated	1 (7)
total # of cowbird eggs lost	14 (93)
# of cowbird chicks hatched	1 (7)
cowbirds chicks depredated	1 (7)
cowbirds fledged	0 (0)

Table 7 Cowbird pressure on Yellow Warblers from 7 studies determined by McGeen's (1972) method.

Total Nests	Nests Parasitized #	Nests Parasitized %	Cowbird Eggs Total	Cowbird Eggs Multiple #	Cowbird Eggs Multiple %	Successful #	Successful %	Pressure Index *	Source
262	84	32.0	98	21	21.4	16	16.3	26.7	McGeen (1972)
41	12	29.2	15	4	26.7	1	6.7	28.0	Schrantz (1943)
20	9	45.0	10	2	20.0	2	20.0	32.5	Batts (1961)
44	18	41.0	33	24	72.0	2	6.0	56.0	Berger (1951)
21	12	57.0	17	9	53.0	1	6.0	55.0	Young (1963)
109	45	41.0	59	18	30.5	6	10.1	35.7	Clark & Robertson (1981)
37	11	30.0	15	5	33.3	0	0.0	31.7	(this study)

* Pressure index = (% parasitized + % multiple parasitism)/2

eggs and re-line the nest or re-nest, thus cowbirds in the multiple parasitism cases are not placing a cowbird egg in a nest with another cowbird egg as would occur with accepter species. A re-lined or new nest induced by parasitism may be seen by the cowbird as another opportunity equal to any other unparasitized nest, and therefore the probability that this nest or host pair will be parasitized again differs from that of a parasitized accepter species.

Impact From Parasitism

In an attempt to determine more accurately the impact that parasitism has on the reproductive efforts of their hosts, the final clutch size of re-initiated nests of those birds that suffered reproductive loss was compared to the clutch size of those who had not suffered any loss. There was no significant difference between these 2 groups (Table 8). When the final clutch size of re-initiated nests of only those that had suffered a more substantial loss (a minimum of 3 eggs), was compared to the clutch size of the undisturbed pairs, the difference was highly significant (Table 8).

There were no significant differences (Table 9) for any of the measures of growth that were used to determine whether sharing a nest with a cowbird nestling was detrimental to Yellow Warbler nestlings.

Table 8 Differences in clutch size between those Yellow Warblers with no reproductive loss and those who laid a replacement clutch following cowbird parasitism.

# of eggs lost due to parasitism	n	CLUTCH SIZE $\bar{X} \pm$ S.D.	P*
0 (unparasitized)	25	4.13 ± 0.83	
1 - 2	9	4.00 ± 1.15	0.682
> 2	3	2.33 ± 0.58	<0.01

* Mann Whitney U test

Table 9 Differences in Yellow Warbler nestling growth (at 6 days of age) for young raised with and without a cowbird chick.

		tarsus length	across nares	beak length	wing length	weight
with cowbird chick	n	2	2	2	2	2
	$\bar{X} \pm$ S.D.	16.6±0.3	2.2±0.1	4.3±0.3	33.5±2.1	9.1±0.9
without cowbird chick	n	19	19	19	19	19
	$\bar{X} \pm$ S.D.	16.2±0.3	2.2±0.1	4.7±0.3	34.0±1.2	9.4±0.4
P*		>0.05	>0.05	>0.05	>0.05	>0.05

* Mann Whitney U Test

DISCUSSION

Parasitism Versus Predation

Predation is considered one of the most important selective pressures acting on animal species, affecting both prey species morphology and behaviour (Wittenberger, 1981). The greatest threat from predators to small altricial passerines, such as Yellow Warblers, occurs during the nesting stage when their progeny are sessile. The vulnerability at this stage and the heavy reliance on parental care has resulted in many anti-predator strategies concerned with defence and concealment of nests and their contents. In my study the frequency of nest predation was 12% overall, and never more than half as frequent as brood parasitism in each category (Table 1). Nest predation has been a constant selective pressure acting on Yellow Warblers in eastern North America, whereas cowbird parasitism presents a new selective force. The evolved anti-predator adaptations resulting from longer sympatry with predators may be responsible for the frequency of predation being lower than brood parasitism.

Other studies have found the frequency of brood parasitism of Yellow Warblers of similar magnitude or higher. In Michigan, Berger (1951) had 40.9% (n=44) parasitism, while in Ohio, Hicks (1934) found 42% (n=146). G. Peck's (pers. comm.) findings in the most recent Ontario Nest Records Scheme (1956-1980) provided the largest sample and yielded similar figures to my study of 27.4% (n=1439). These findings are consistently higher than the frequency of parasitism of Yellow Warblers in the mid-west. The Prairie Nest Records Scheme, and the

Western Foundation of Vertebrate Zoology (Friedmann et al., 1977) found that the rate of parasitism of Yellow Warblers was 20.6% (n=102), and 8% (n=348) respectively. The difference in the frequency of parasitism between this recently invaded eastern host, and it's mid-western counterpart which has existed sympatrically with cowbirds for thousands of years, is common in many of the species found in both eastern and western North America (Friedmann et al., 1977). The higher rates of parasitism for Yellow Warblers in the east may be partially explained by eastern birds being less well adapted, compared to those which have been sympatric with cowbirds for much longer.

Re-lining Versus Re-nesting

Although the sample size was small, the difference in frequency of parasitism and predation between re-nests in new locations and re-linings (Table 1) may indicate a greater danger of being parasitized or depredated when building a new nest, instead of simply re-lining a nest. It is widely reported (e.g. Friedmann, 1963; Hann, 1941; Payne, 1973) that cowbirds observe nest building activity to locate active host nests. Birds re-building nests in new locations must make more trips to and from a new nest site, than those that are re-lining an existing nest. This activity may also increase the chance of being noticed by a predator. As well, re-lined nests, being in the same location, may not be parasitized again by a cowbird, if there are other suitable nests to parasitize, whereas a conspicuous, new re-nest may be regarded by the cowbird as a new, active nest. Re-nesting requires more time than re-lining a nest and consequently the clutch initiation dates for re-nesting attempts tended to be later. However, this later clutch initiation does not provide a good explanation for higher rates of parasitism, since generally the later Yellow Warbler nests had less chance of being parasitized (Table 12, chapter 2), and the later re-lined nests were not parasitized.

Re-lined Yellow Warbler nests were no more susceptible to cowbird parasitism than original nests (Table 1). Clark and Robertson (1981) found that since egg burial required only a small energy expenditure, Yellow Warblers seemed to be physiologically capable of replacing the buried eggs. They found no difference in clutch size between re-lined and original nests. If the risk from parasitism was greater in re-nests, then selection should favour re-lining over re-nesting in Yellow Warblers. Although not statistically significant, (X^2=1.60, P>0.05) the results (Table 1) indicate a trend. Of 12 subsequent attempts to initiate a new clutch, 9 were re-linings of original nests, while only 3 were re-nests in new locations. However, re-nests may still occur if the original nest is not stable enough to support another attempt (Clark and Robertson, 1981).

Egg Loss

The available evidence suggests that the figure of 41% egg loss attributable to parasitism is an underestimate. Of 15 cases of parasitism of Yellow Warblers, there were only 2 cases of egg removal (Table 4). However, Table 3 provides evidence from 2 other accepter species in the same area that cowbirds remove eggs from parasitized nests more frequently. Hann (1937) found that cowbirds removed a host egg from 85% of the nests they parasitized, while Zimmerman (1983) noted 1.65 eggs removed by cowbirds per parasitized nest. Despite the tendency of cowbirds to parasitize more experienced Song Sparrows (<u>Melospiza</u> <u>melodia</u>), which tend to lay larger clutches, Smith (1981) found that the clutch size in 98 parasitized nests was 2.61 host eggs versus 3.25 eggs in 115 unparasitized nests. This highly significant difference suggests that cowbirds are removing Song Sparrow eggs from a over half of the parasitized nests. Mayfield's (1961) study of the Kirtland's Warbler found even larger differences between the number of host eggs in parasitized and unparasitized nests, (2.73 and 4.63 respectively). Clark and Robertson (1981) suggested that cowbirds were removing a host egg from about 50% of the parasitized Yellow Warblers. Results from these other studies and Table 3 indicate that host egg removal by cowbirds is common and that 41% of the egg loss attributed to parasitism is an underestimate.

Eighty-eight percent (Table 4) of the total eggs lost due to cowbird parasitism was lost due to rejection of the parasitized clutches by the hosts themselves. Berger (1951) and Clark and Robertson (1981) reported 100% and 71% rejection, respectively, for Yellow Warblers that had been parasitized. Norris (1947) and Berger (1951) both found that for each cowbird reared, one host young on average, did not survive. However P. Harrington (Bent, 1958) estimated a loss of 3.33 host young per cowbird reared in one hundred parasitized passerine nests near Toronto. Terrill (1961) stated that the fledging of even one host young in a parasitized nest was notable and more often there were no survivors. In an attempt to provide a reason for the variability in host losses reported, Friedmann (1971) felt that small host species or those hosts with relatively slow incubation and nestling development rates were very susceptible to parasitism and have low nest success, while larger, or faster developing host species were not as affected. The impact of parasitism on Yellow Warblers is clearly sufficient to warrant the desertion or burial of viable Yellow Warbler eggs accounting for 35% of all eggs lost.

Parasitism usually occurred early in the breeding season and thus Yellow Warblers that were parasitized and rejected the cowbird egg by nest desertion or egg burial were able to initiate a new clutch. As a result even parasitized Yellow Warblers were still able to fledge 2.67 young/nest. However, this is significantly less than the 3.76 young/nest fledged from nests which have no predation or parasitism (Table 5). Because predation tended to occur later in the breeding season, it was unlikely that re-nesting attempts were initiated and thus no fledglings were raised (Table 5).

Predation caused higher egg loss per depredated nest because nests in the egg laying or incubation stages are vulnerable and predators usually eat all eggs in a nest. Cowbirds prefer to parasitize the nest early in the egg-laying period, thus fewer eggs are likely to be lost per parasitized nest, and the pair has a greater chance of re-initiating a clutch. While the overall reduction in the number of fledglings produced/pair in a breeding season was greater from predation than parasitism, the overall egg loss was still slightly greater from parasitism than predation, and parasitism was twice as frequent. Therefore, at present cowbirds may exert at least as great a selective pressure on Yellow Warblers as the local nest predators.

Cowbird Success

The lack of cowbird success with Yellow Warblers (Table 6), (Berger, 1951; Clark and Robertson, 1981) is attributable to their habit of rejection by nest desertion or egg burial. While cowbirds suffer from low success with Yellow Warblers and all rejecter species, the benefits from laying up to 40 eggs (Scott and Ankney, 1983), and the ability to parasitize a greater number of hosts compensates for this. Hence, the lack of success with Yellow Warblers does not appear to cause a selective pressure on cowbirds to avoid parasitizing this host.

Degree of Parasitism

Multiple parasitism occurred in 33% of all cases of parasitism, which yielded a pressure index of 31.7 (Table 7). This pressure index is comparable to other studies on this species in eastern North America, with the exception of Berger (1951) and Young (1963) who had pressure indexes of 56 and 55, respectively. Unfortunately the pressure index cannot be calculated for Yellow Warblers in the mid-west since information regarding the percentage of multiple parasitism is lacking. However, since the frequency of parasitism is low in the mid-west, the pressure index is likely to be significantly lower in the mid-west than in eastern North America.

Disadvantages to Hosts

As shown in Table 8, and by Clark and Robertson (1981), there was no significant difference in the final clutch size between those Yellow Warblers that suffered no reproductive loss and those that re-initiated a nest after suffering moderate losses. However, I found that there was a significant difference in final clutch size between the "no reproductive loss" group and those that re-initiated a nest after suffering higher reproductive losses (Table 8). This indicates that those Yellow Warblers that had already invested their energy in at least 3 eggs and had been forced to start again, could not subsequently invest to the same degree.

The effects of parasitism on host reproduction can last beyond the nesting stage. Larger reproductive costs may reduce subsequent adult survival (Askenmo, 1979; Bryant, 1979). The effect on offspring having to compete for food resources with a much larger nest mate, with a larger mouth and louder begging calls may slow their growth and result in less fit fledglings with lower survivability. Sharing nests with cowbirds did have significant effects on Song Sparrow young at six days of age, although it did not cause differences in survival at 4 weeks of age (Smith, 1981).

Sharing a nest with a cowbird chick was not detrimental to the growth of the Yellow Warbler chicks (Table 9). However, in the only nest where this situation occurred, only 1 cowbird and 2 Yellow-Warbler chicks had to be fed. The effect of a growing cowbird chick competing for food with more host chicks could become much more severe.

Hann (1937) and Zimmerman (1983) found no differences in growth rates between chicks in parasitized and unparasitized nests for Ovenbirds and Dickcissels, respectively. However, there were significant differences when 2 cowbirds were being raised in the same nest (Hann, 1937). Hann felt that while having 1 cowbird chick present in a nest with host chicks did significantly increase the demand for food, the parents were capable of increasing the food supply.

The only cowbird chick that hatched in my study was subsequently preyed upon at 7 days of age (Table 6). Smith (1981) had very high losses for fledgling cowbirds which he attributed, in part, to loud begging and subsequent predation by crows. The loud begging of the lone cowbird chick in my study may have contributed to the location of the nest by a predator, and this may be another disadvantage to Yellow Warblers in accepting a cowbird egg.

Brood parasitism may reduce adult reproductive fitness by the stress and energy involved in either rejecting a foreign egg and re-building or re-lining a nest, or accepting a foreign egg and providing more food for the resulting chick with lower success and a greater chance of nest predation due to loud begging calls by the cowbird chick.

To conclude, my data suggests that cowbird parasitism is an important factor in reducing reproductive success of Yellow Warblers in this area. Therefore, cowbird parasitism is an important selective force that should maintain the evolved behavioural traits that aid individuals to avoid or lessen the impact of brood parasitism.

CHAPTER 2

Adaptations to Avoid Nest Discovery

INTRODUCTION

Many studies have investigated some of the possible defences that hosts can employ once a nest has been discovered by a cowbird (e.g. Rothstein, 1976; Robertson and Norman, 1977; Scott, 1977; Finch, 1982). These methods will be examined in chapter 3. However, before cowbirds can successfully parasitize a nest, they must first find one that is suitable. While some studies (e.g. King, 1973; Norman and Robertson, 1975; Lowther, 1979, 1984; Thompson and Gottfried, 1981) have investigated how cowbirds search for and select a nest, I know of no study, with the exception of Clark and Robertson (1979), that approaches the subject from the host's viewpoint. If hosts are undergoing a lot of pressure from brood parasitism, individuals who can reduce their chances of being parasitized by lowering the cowbird's chances of discovering their nests, should be at a selective advantage. In a population undergoing strong selection pressure by cowbirds, those individuals that are better able to avoid nest detection by cowbirds should have greater reproductive success. I examined four possible strategies that may already be exhibited by Yellow Warblers to avoid nest detection by cowbirds. These strategies are: 1) male avoidance of the nest during vulnerable nest stages; 2) temporary abandonment of the nest site in the presence of a female cowbird; 3) reduction of nest visibility; 4) adjustment of the timing of host breeding activities.

Many references (e.g. Hann, 1937; Payne, 1973; Norman and Robertson, 1975; Lowther, 1979) have been made to the importance of observation of nesting birds to the nest search strategy employed by female cowbirds. Hann (1937) speculated that the observations by female cowbirds of host nest building, stimulates the ovulation and egg development in cowbirds, and accounts for the high degree of synchrony between host and parasite egg laying. Because of the importance of observation of host activity to cowbirds, a strategy that minimizes the activity around the nest area could be effective in reducing the chance of nest discovery. The first two proposed strategies would reduce host activity in the nest area.

Male Avoidance

Biedenweg (1983) found that male Mockingbirds (*Mimus polyglottos*), spent a large percentage of time perching or "loafing". He felt this was a response to predation pressures and that the male while "loafing" was keeping watch for predators. However, it is also possible that the male was maintaining a low profile so as not to attract predators to the nest. In the Abert's Towhee (*Pipilo aberti*), the male, while accompanying the female during foraging, does not visit the nest area during the egg laying phase, but perches alone in shrubs. While Finch (1984) felt this was to minimize the expenditure of energy, it may also reduce the chance of nest location by predators or parasites.

Yellow Warbler males are more conspicuous than females, because of their slightly brighter colouration, vocalizations, and territorial behaviour. They also make only a minor contribution to nest construction (pers. observ.; Schrantz, 1943). Natural selection could favour avoidance of the nest area by males during the early stages of nesting when the nest is more vulnerable to parasitism. Most of the attention to nests by female cowbirds is during nest construction and the egg laying period (Mayfield, 1961). This hypothesis would predict that if male avoidance is observed and is a result of parasitism, the male should reduce his presence near the nest during the nest building and egg laying stages, since at these stages the nest is vulnerable to discovery and subsequent parasitism. Male avoidance could also be a result of predation pressure. However, if predation was the cause, avoidance should increase or remain high throughout the nest stages tested. Alternatively, predation may cause males to keep close to the nest to warn the mate or to defend the nest against predators or brood parasites, or to keep intruder males from their mate in the early stages of nesting.

Temporary Abandonment

A premature alert and aggressive stance against a cowbird may actually aid the cowbird in finding the nest (Smith, 1981). Hence, temporary abandonment of the vicinity of the nest by Yellow Warblers when a cowbird is nearby, may also reduce the chance of nest location. If Yellow Warblers use this strategy and this is a specific response to parasitism, then they should abandon the nest area temporarily when a female cowbird is placed within the vicinity of the nest area during the most susceptible nest stages (nest construction and egg laying). The response would be expected to decrease in early incubation and be absent in the nestling stage when cowbirds are no longer a threat. However, if this strategy has developed as a generalized response to any threat, then the same response should be seen both with the cowbird and a nest predator, and should be exhibited throughout the nest cycle.

Active Searching by Cowbirds

In addition to the silent, sessile observation technique, Norman and Robertson (1975) described two other active techniques that female cowbirds may use to locate nests. These are: walking through scrub and forested habitat, watching other birds, and looking up into the overhead vegetation; and hopping, wing flapping and calling in a non-random pattern along hedge-rows, in an attempt to flush nesting birds. By these methods, cowbirds presumably can locate nests without observing host activity (Lowther, 1979). Therefore, the following 2 methods of avoiding detection by cowbirds should take on added importance.

Choice of an Appropriate Nest Site

Nice (1937, in Friedmann, 1963) felt that cowbirds and predators could not find well concealed nests as easily as nests that were poorly concealed. If a nest can be made more difficult for a cowbird to find by its location, selection should favour those host individuals that choose nest locations with these favourable characteristics.

Timing of Breeding Activities

The relationship between cowbird and host breeding seasons is a major contributing factor to the degree of parasitism imposed upon a species (Berger, 1951). In areas where the vegetation begins to leaf in late April and early May (such as southern Ontario, Michigan, and Indiana) the peak of cowbird laying period is concentrated in mid to late May (Hann, 1937; Berger, 1951; Nolan, 1963). The peak of cowbird egg laying corresponds with when most hosts are nesting. In northern Michigan where leafing of vegetation is delayed until mid May, the peak cowbird laying period is in early June (Payne, 1965). When birds are able to nest before the peak period of cowbird egg laying, the nest success is much higher, as many more individuals avoid parasitism or multi-parasitism (Verner and Ritter, 1983). Finch (1983) felt that heavy cowbird parasitism may be a selective factor for early breeding of Abert's Towhees. In the lower Colorado River valley, towhees can start breeding earlier, since they are permanent residents. Because the probability of producing fledglings is very low after cowbirds begin breeding, early breeding is favoured. In my study area, Yellow Warblers cannot begin nesting earlier than the cowbird breeding season, as they must wait for the onset of foliage and insect emergence.

There are 2 temporal strategies that could be effective for Yellow Warblers to avoid the high cowbird parasitism pressure. High nest density and synchrony of nesting activities should lower the frequency of parasitism (Clark and Robertson, 1979), because of a swamping effect. However, if nest density is low, the strategy of nesting in synchrony may not be as effective as female cowbirds would presumably adjust their territory to take advantage of suitable nests becoming available.

The strategy of later nesting could also be effective in reducing the rate of parasitism. The peak cowbird laying period is usually in mid to late May and declines throughout June (Hann, 1937; Nolan, 1963; McGeen and McGeen, 1968). Those individuals that breed later than the peak cowbird laying period are more likely to avoid being parasitized. Thus, selection may favour later breeding in Yellow Warblers. However, the disadvantages of being out of phase with the optimal food supply (Immelmann, 1971 in Rothstein, 1975a) and possible higher predation pressures, may outweigh this advantage, hence, setting limits as to how late these birds can breed.

The purpose of this chapter is to determine whether Yellow Warblers exhibit male avoidance, temporary abandonment, choice of certain nest site qualities or whether they adjust the timing of their breeding activities to avoid having their nest located and subsequently parasitized by Brown-headed Cowbirds. A summary of the hypotheses, predictions and their tests is presented in Table 10.

Table 10 Hypotheses, predictions and tests for strategies to avoid nest discovery by cowbirds.

#	HYPOTHESIS	PREDICTIONS	TESTS
1	MALE AVOIDANCE	-the male Yellow Warbler presence near the nest should be significantly lower than the female during the nest stages most vulnerable to parasitism.	-comparison between the time males and females spent within 10 m of the nest during different nest stages.
2	TEMPORARY ABANDONMENT	-the male and female should temporarily abandon the nest when a female cowbird is near during the most susceptible stages, and they should show a weaker response to the other stimuli.	-compared responses to 4 different intruders during different nest stages.
3	NEST SITE QUALITY	-nests less exposed, should be parasitized less frequently.	-measured 5 different nest nest variables for parasitized and non-parasitized nests.
4	TIMING OF BREEDING ACTIVITIES	-nests initiated before or after the peak cowbird laying period should be less frequently parasitized. -when many nests are initiated together, they are less likely to be parasitized.	-recorded the nest initiation dates for parasitized and non-parasitized nests. -compare the frequency of parasitism between synchronous and asynchronous nests.

METHODS

All data were collected on the same 49 Yellow Warbler nests mentioned in the methods of chapter 1 to determine whether the hypotheses should be accepted or rejected on the basis of the predictions made.

Male Avoidance

To determine whether males avoid the nest area (Hypothesis 1, Table 10), I recorded (from a minimum of 15 m) and compared the time the male spent within 10 m of the nest to the time spent in this area by the female, during nest construction, the egg laying period, early incubation and late incubation. Each of five nesting pairs was examined between 6 a.m. and 10 a.m., during the stages of nest construction, egg laying, early and late incubation, for a 2 hour period at each nest stage.

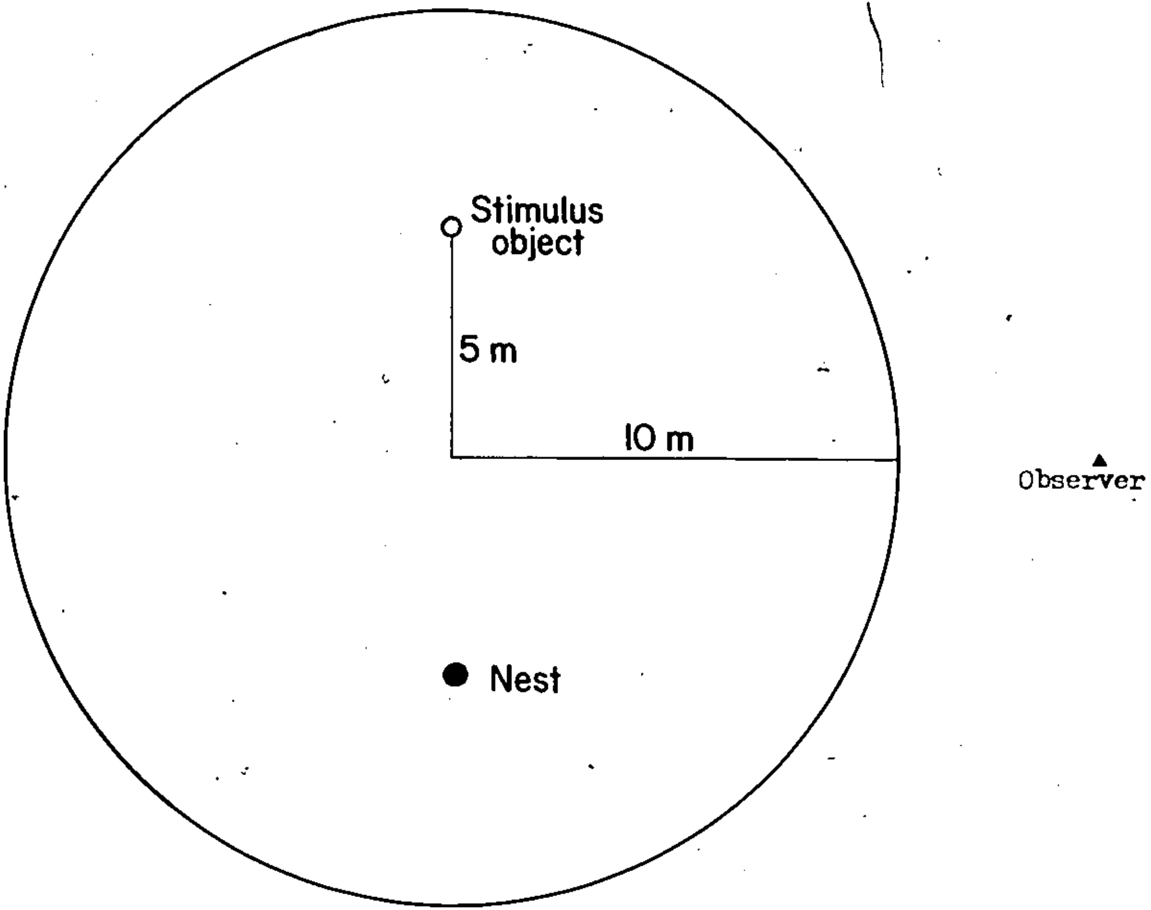
Temporary Abandonment

To test the hypothesis of temporary avoidance (Hypothesis 2, Table 10), I placed 4 different stimulus objects 10 m from each of 5 nests. I used a distance of 10 m, because at farther distances (15 m), the stimulus objects were ignored and at closer distances (5 m) the hosts generally responded more aggressively to most stimuli. All stimulus objects were caged and included: female cowbird; male cowbird; crow; and a female House Sparrow (as a control). These different stimulus objects were used because they each represented a different level of danger to the Yellow Warblers. These trials were conducted during nest construction, egg laying, early incubation and the nestling stage. I recorded the time that the warblers spent within a circle with a radius of 10 m, centered on a point half-way between the nest and the stimulus object (Fig. 2). I placed the caged bird 10 m from each nest, and the response was examined for a 5 minute period from a minimum of 15 m from the centre point.

Nest Site Quality

To determine whether any of the nest site characteristics were important in making the nest less vulnerable to cowbirds (Hypothesis 3, Table 10), I measured 5 nest site characteristics for all nests, and whether each nest was parasitized, depredated or undisturbed. A larger number of variables were recorded for nest site quality, instead of only one measure, as it is unknown whether human discrimination is comparable to discrimination by cowbirds. The nest cover was measured by placing an 18 by 22 cm grid consisting of 30 red dots, 3 cm apart, in front of the nest. The number of complete dots seen from 3 m was recorded. The procedure was then repeated until readings from 4 sides of the nest were recorded, giving a maximum of 120 dots for a completely exposed nest. The height of the vegetation the nest was in and the distance from the ground to the lip of the nest were measured. The distance between the nest and the nearest common song perch the male Yellow Warbler used was measured along with the distance between the nest and the nearest tall perch. The nearest tall perch was any bush or tree that was higher than the surrounding bushes where the nest was located (>2.5m). I measured these characteristics for all but two nests between June sixth and ninth.

Figure 2 The experimental area used for the trials to test for temporary abandonment.



Timing of Breeding Activities

To determine whether early or late nesting pairs, or pairs that initiate their nests asynchronously, were more vulnerable to brood parasitism by cowbirds (Hypothesis 4, Table 10) I compared the dates of nest initiation between parasitized and unparasitized Yellow Warblers, and I compared the frequency of parasitism between nests exhibiting a higher degree of synchrony (11-30 nests initiated/week) and those exhibiting a higher degree of asynchrony (1-10 nests initiated/week).

RESULTS

Male Avoidance

No significant differences ($X^2=4.01$, $P>0.10$, Kruskal-Wallis test) were seen between male presence within 10m of the nest at the different nest stages (Fig. 3). The slight increase in male absence from this area during the egg laying stage reflects the slight increase in female absence during this stage ($U=4.0$, $P>0.05$, Mann Whitney U test) from the nest construction stage and may indicate that mate guarding is occurring. Because the female was observed to incubate most of the time, her presence rose greatly during the early and late incubation stages while the male's presence did not increase significantly. The male did not show any greater avoidance of the nest area than the female during the vulnerable stages of nest construction ($U=6.5$, $P>0.10$, Mann Whitney U test) and egg laying ($U=8.0$, $P>0.10$, Mann Whitney U test; Fig. 3). Hence, I conclude that these results do not support the male avoidance hypothesis (Table 10).

Temporary Abandonment

Male and female Yellow Warblers did not tend to abandon the nest area significantly more for the crow, female cowbird and male cowbird than for the control (House Sparrow) during any of the nest stages. The adult Yellow Warblers showed no trends to abandon the nest area more readily during the stages most vulnerable to cowbird parasitism (nest construction and egg laying) in response to the female cowbird (Fig. 4). Abandoning did not increase with parental investment (older nest stage) in response to the predatory threat from the crow. In fact,

Figure 3 The average time (in percent) female (open) and male (shaded) Yellow Warblers spent within 10 m of the nest, over a 2 hour period, during 4 different nest stages.

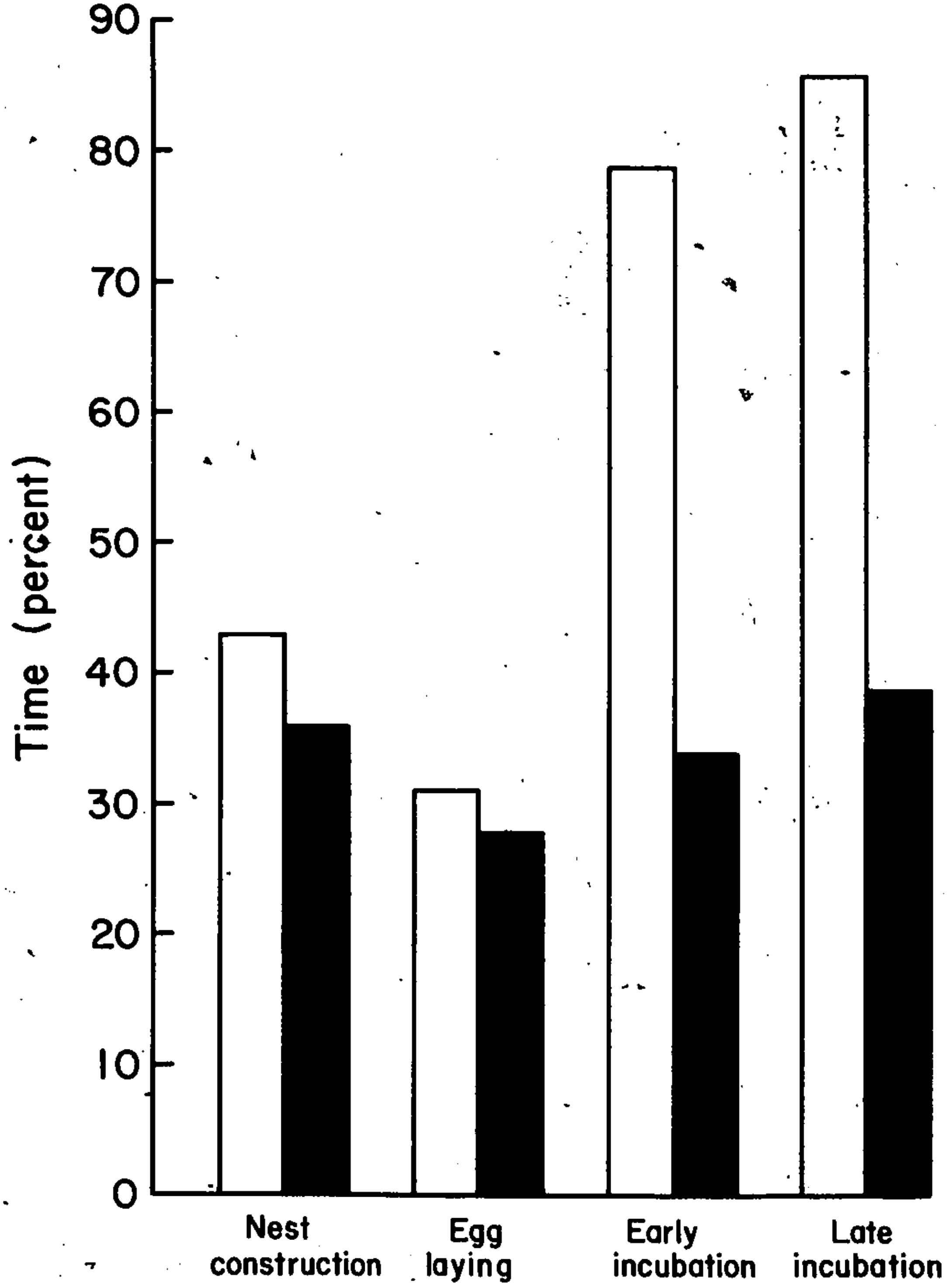
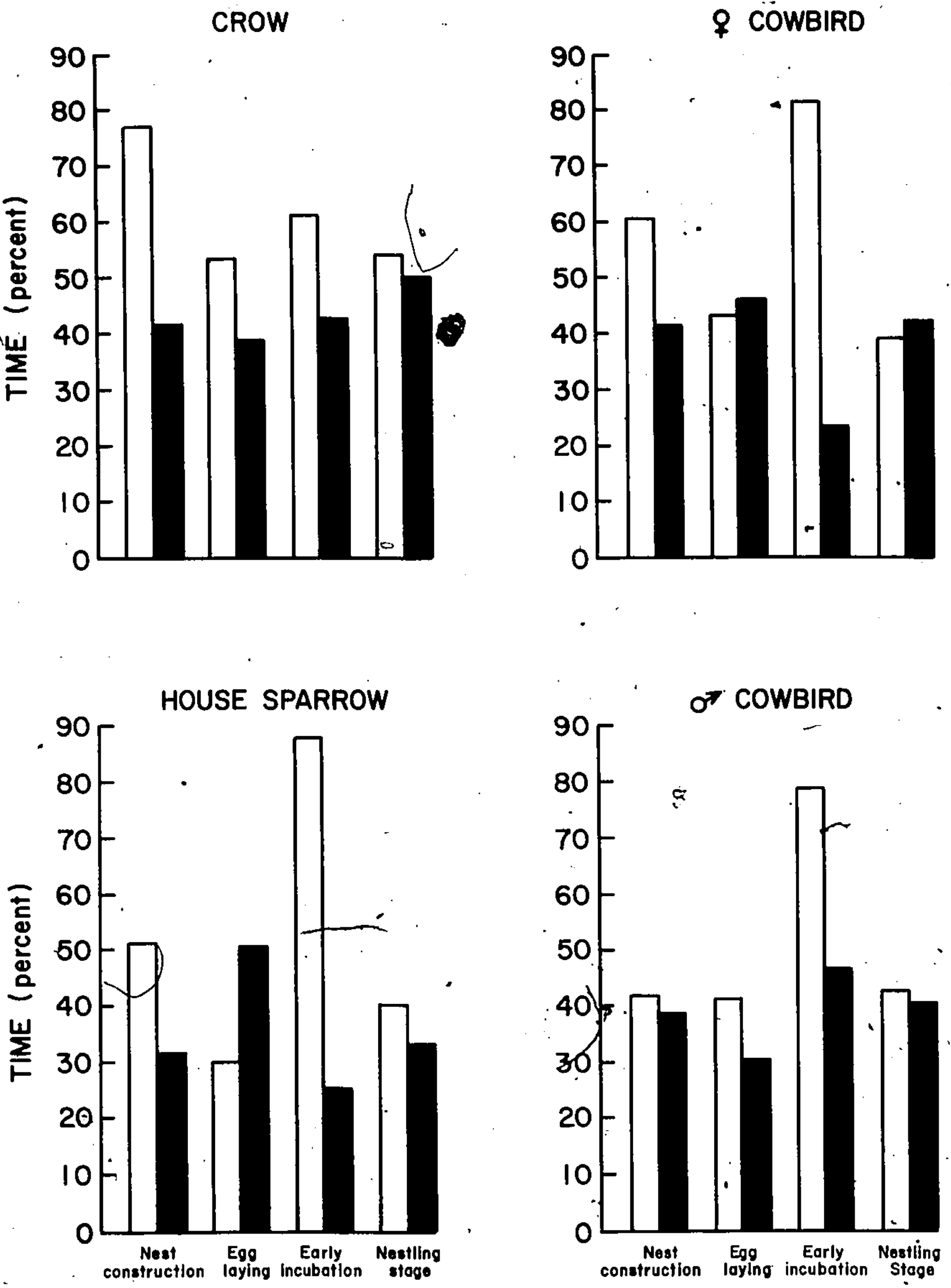

Time (percent)
90
80
70
60
50
40
30
20
10
0
Nest construction
Egg laying
Early incubation
Late incubation

Figure 4 The average time (in percent) female (open) and male (shaded) Yellow Warblers spent in the designated area (Fig. 2), over a 5 minute trial, during 4 nest stages, using 4 different stimulus objects.


CROW
♀ COWBIRD
HOUSE SPARROW
♂ COWBIRD
TIME (percent)
TIME (percent)
0
10
20
30
40
50
60
70
80
90
Nest construction
Egg laying
Early incubation
Nestling stage
Nest construction
Egg laying
Early incubation
Nestling Stage

contrary to the predictions, the higher values of male and female presence tended to be for the stimuli that were threats: the crow and the female cowbird. The results of this test do not support the temporary avoidance hypothesis (Table 10).

Nest Site Quality

Using Hotelling's Multivariate Test of Significance (Burns and Wang, 1981), nest site characteristics were compared between nests found by cowbirds (parasitized) and those that I assume were not found by cowbirds (since they were never parasitized). The nest parameters used were able to significantly (P=0.05) discriminate between the two groups (Table 11). However when the variables were tested independently, only the vegetation height and the distance to the nearest perch differed significantly (P=0.03 and P=0.01 respectively) between the parasitized and unparasitized groups (Table 11). These results support the nest site quality hypothesis (Table 10).

Timing of Breeding Activities

Only 14 nests were initiated in May, compared to 35 nests initiated in June. Nests initiated in May had a significantly ($P<0.05$) greater chance of being parasitized than nests initiated later in the season (Table 12). Nests initiated synchronously (with 11-30 other nests/week) were highly significantly ($P<0.01$) less likely to be parasitized than those initiated asynchronously (with 1-10 other nests/week) (Table 13). Hence, the timing of breeding activities, both with initiating nests later and in synchrony with other nests, appears to be important (Table 10).

Table 11 The importance of 5 nest parameters in determining whether nest concealment is effective in avoiding brood parasitism.

	unparasitized	parasitized	P(F-test)	P(Bartletts)	P(Boxs M)	P(Hotellings)
N	28	12				
NEST COVER	12.64±15.34	11.58±17.40	0.94	0.95		
NEST HEIGHT	107.89±13.63	104.08±16.85	0.48	0.77		
VEGETATION HT	171.89±20.37	155.50±18.84	0.03	0.76	0.14	0.05
PERCH DISTANCE	7.18±6.46	2.92±1.16	0.01	0.25		
SONG PERCH DIST	6.32±3.03	4.42±1.31	0.24	0.15		

Table 12 1-tailed X^2 test* for the frequency of parasitism for early and late nesting Yellow Warblers.

	# of nests				
	unparasitized	parasitized	total	X^2	P
MAY	6	8	14	4.86	<0.05
JUNE	28	7	35		

* with Yates correction for continuity.

Table 13 1-tailed X^2 test* to compare the frequency of parasitism for nests initiated synchronously and asynchronously.

# OF NESTS INITIATED/WEEK	# OF NESTS				
	PARASITIZED	UNPARASITIZED	TOTAL	X^2	P
1-10 (asynchronous)	8	3	11	9.43	<0.01
11-30 (synchronous)	7	31	38		

* with Yates correction for continuity.

DISCUSSION

Male Avoidance

Male Yellow Warblers did not tend to stay away from their nest site any more than females during the 2 early nest stages (Figure 3). Since females are mainly responsible for egg incubation, their presence around the nest increased dramatically during the early and late incubation stages, while the males' did not significantly change. The males' presence near the nest tended to reflect the females' presence during the nest construction and egg laying stages, and this may have been due to mate guarding. While males infrequently brooded the eggs during incubation, they still made visits to their nest to feed the female and no avoidance of the nest area was seen during this stage. The interest by the male towards the female in the form of mate guarding during early nest stages and feeding of the incubating female would appear to override any selection for male avoidance. M. Studd (pers. comm.) found that males decrease the length of their visits to the nest after the middle of the incubation period. He speculated that this might be to minimize the disturbance at the nest during hatching of the eggs and decrease the risk of predation. However, frequency rather than duration of visits to a nest should be the criterion for attracting predators attention to a nest, and I saw no decrease in the frequency of visits.

Temporary Abandonment

The responses by both male and female Yellow Warblers to the intruders were contrary to the predictions for temporary abandonment. With the possible exception of the crow, the females tended to ignore the other stimuli during the early incubation stage and continued to incubate. The females' response to the crow would be better described as watchfulness than abandonment. The Yellow Warblers tended to show more curiosity towards all stimulus objects. This curosity may be part of a strategy to be vigilant when an intruder is in the nest area, and may have developed as a response towards conspecific intruders or predators. Alternatively, the curiosity shown may reflect the unusual nature of the caged stimuli.

Although deserted nests have been known to have been parasitized (Berger, 1951), the rate of parasitism for inactive nests with eggs is much lower than the rate for active nests, indicating the importance of host-activity (Lowther, 1979). Therefore, host activity may aid female cowbirds in nest location by attracting attention to active nests (Lowther, 1979). However, the attention span of cowbirds is longer than would be required for nest location (Mayfield, 1961). Host activity may provide other advantages for female cowbirds, such as: 1) avoiding parasitism of poor hosts (Thompson & Gottfried, 1981); 2) identifying the nest stage to achieve synchrony in egg laying (Lowther, 1979); and, 3) stimulating egg development by observation of nest building (Hann, 1937). Thus the response by Yellow Warblers to a female cowbird 10 m from the nest may be maladaptive and be partially responsible for the high rate of parasitism of Yellow Warblers.

Nest Site Quality

Due to the different techniques employed by cowbirds to find host nests (Norman and Robertson, 1975), a particular nest site characteristic which is effective in avoiding detection by cowbirds using one method may not be effective against another method. This, overall, may give the impression that a particular nest characteristic is not effective in lowering chances of nest location by cowbirds; ~~and~~ only those characteristics which strongly reduce the chance of nest location may show up significantly.

In Nice's (1937, in Smith, 1981) study of Song Sparrows, nest cover was correlated with parasitism. Those nests that were more exposed had a higher risk of being parasitized. However, two more recent studies show no significant relationship between nest cover and avoidance of parasitism. Smith (1981) indicated that while there was no significant relationship in his study on Song Sparrows a trend did appear to back up the assertion by Nice (1937, in Smith, 1981). Anderson and Storer (1976) found no significant relationship while looking at the heavily parasitized Kirtland's Warbler. The Yellow Warblers in this study did not show any trend towards the nest cover - parasitism avoidance relationship (Table 11). The variability in results in different studies of this nest characteristic may reflect the different sampling techniques or the habitat differences associated with different species.

The variablity of results from studies of different species is again seen when examining whether the height of nests is an important determinant in being parasitized. Lowther (1980) found that the only catbird nests in his study to be parasitized were those high up in the bushes. Nolan (1963) examined 14 passerine species in Indiana, and found a trend (although not significant) that cowbirds more frequently parasitize elevated nests than ground nests. Yet Newman (1970) felt that the nests of the Lark Sparrow, Chondestes grammacus, that were located on the ground were "more accessible" to cowbirds than those higher up in the bushes.

In this study, the lack of any significant difference for nest height may have been expected since the range of heights from the ground of Yellow Warbler nests was small (81-130cm.) No significant difference was found between the heights of parasitized and unparasitized nests. This finding agrees with Smith's (1981) study on Song Sparrows, who also found no significant differences. While King (1973) was not investigating the nest characteristics in terms of nest location, he failed to demonstrate any significant preference by cowbirds for high or low nests. Cowbirds appear to be able to exploit nests at any height, and the different results may reflect different local search strategies that, in turn, reflect the local species composition, nest density and distributions.

Anderson and Storer (1976) found no significant relationship between the height of the vegetation supporting the nest and the occurrence of parasitism of Kirtland's Warblers. In my study, the significant relationship may be due to the fact that the surrounding vegetation (usually Spirea spp.) did not vary in height and from a perch a female cowbird could more easily locate Yellow Warbler nests when the vegetation was lower, and hence nests were less concealed. Also the activity and approach of the breeding pair to the nest may be more conspicuous when the vegetation is low, and this may aid cowbirds in locating the nest.

It has been observed (Berger, 1951) that cowbirds most often search for suitable nests from a perch in a tree or tall bush. This explains why the distance to the nearest high perch was the most significant nest characteristic for determining whether a nest would be parasitized. I often observed female cowbirds during the mornings of May and June perched high up in trees (10 - 15 m). Berger (1951) also found that parasitized nests of old field species, were generally closer to higher thickets and trees which provide perches and cover for observation by female cowbirds. Anderson and Storer (1976) found that Kirtland's Warblers' nests within 25 feet of high perches had a greater parasitism pressure than those farther away, and nests were more successful in the absence of large trees. A multi-species study on field-forest habitat found that cowbird parasitism was 15 - 25% near the edge of the forest, but dropped to 0 - 5% when farther from this interface of forest and field (Gates and Gysel, 1978). The authors of this study seldom saw cowbirds in the forest or field interiors, and they speculated that cowbirds may find it more difficult to locate nests in areas where their view is obscured by foliage. This view is supported by Payne's (1973) findings; cowbirds failed to parasitize 2 types of salt marsh sparrows in California and he felt this was due to the difficulty of finding nests in low extensive marsh which did not afford any higher vantage points for observation by female cowbirds. However, an alternative explanation may be, that if colonial blackbirds are nesting nearby they may deter the cowbirds from parasitizing nests in this area (Clark and Robertson, 1979).

The distance from each nest to the nearest male singing perch that a male warbler used did not have any bearing on whether a nest would be parasitized or not. A female cowbird may initially be attentive to a singing male warbler as an indication of possible nesting. However as a male sings throughout the territory, but most often near the territory boundaries, it is unlikely that a female cowbird would locate nests by following male singing activities.

Timing of Breeding Activities

Cowbirds appear to synchronize their peak breeding period with the time when most hosts begin nesting. The synchronization of cowbird egg laying with host laying appears to be very important in assuring the cowbird egg hatches first. Berger (1951) found that hatching first is correlated with fledging success. When parasitizing Yellow Warblers, the synchroniztion of cowbird egg laying appears to take greater importance. McGeen and McGeen (1968) found that 86.5% of asynchronized (out of phase with host laying) cowbird eggs were covered or deserted, but this only happened to 22.5% of well synchronized cowbird eggs. They found the peak of cowbird egg laying correlates with the beginning of the Yellow Warbler nesting cycle in mid to late May. My findings also showed that early Yellow Warbler nests (initiated in May) were parasitized significantly more than later nests (initiated in June) (Table 12). The incidence of cowbird parasitism did decline throughout the Yellow Warbler nesting period, even when more Yellow Warbler nests became available to parasitize. This agrees with other studies on Ovenbirds (Hann, 1941), Lark Sparrows (Newman, 1970), Yellowthroats (Hofslund, 1957), and the Acadian Flycatcher (Empidonax virescens; Walkinshaw, 1961). However, the most significant contribution to the avoidance of parasitism with regard to timing of nests initiation is synchrony with conspecifics. Nests initiated more synchronously with other Yellow Warbler nests, were less likely to be parasitized than those nests initiated asynchronously, despite the low density (less than 5 nests/ha) (Table 13).

As soon as nest construction is initiated, the nest is in danger of being discovered by cowbirds. Perhaps due to competing demands, male warblers did not avoid the nest area during the early nest stages, and the warbler pairs did not exhibit temporary abandonment of the nest site when a female cowbird was near (10 m). However, individuals who nested in higher bushes, farther from high perches, later in the breeding season or synchronously with other Yellow Warblers were more likely to avoid nest detection by cowbirds. Hence, with regard to cowbird nest parasitism, natural selection should favour Yellow Warbler individuals exhibiting these behavioural traits.

CHAPTER 3

Adaptations to Avoid or Minimize the Effects of Parasitism After Nest Discovery

INTRODUCTION

Once a cowbird locates a suitable nest it may require one or more pre-laying visits (Scott, 1977) and enough time to deposit its egg and sometimes remove a host egg. I examined 3 possible strategies that Yellow Warblers could use to reduce the threat posed by cowbirds, once a nest has been discovered. These are: 1) coordination of movements by potential hosts to minimize the time that both individuals are away from the nest (nest guarding); 2) aggressive exclusion of a female cowbird by the nest owner; 3) rejection of a cowbird egg.

Nest Guarding

Ricklefs (1969) suggested that increased site tenacity to the nest during the egg laying stage, may be an adaptive strategy against brood parasitism. Once a cowbird has discovered the location of a nest it may attempt to visit the nest prior to actually parasitizing it (Mengel and Jenkinson, 1970; Hann, 1941). Nest guarding is a strategy to ensure that at least one of the individuals from the breeding pair is near the nest most of the time. Nest guarding may deter a cowbird from a pre-laying visit or from parasitizing the nest (Scott, 1977). Putnam (1949) thought that the high nest success of Cedar Waxwings (Bombycilla cedrorum) was due, in part, to nest guarding. Nest guarding in the Gray Catbird (Dumetella carolinensis) was probably at least partially responsible for the low incidence of parasitism (Slack, 1976; Scott, 1977). Scott (1977) felt that the relatively low incidence of parasitism in catbirds is due to the inability of some cowbirds to get pre-laying visits or to get to the nest for uninterrupted laying. Slack (1976) observed nest guarding by catbirds during the egg laying stage, when it would be most effective against cowbirds. Both authors saw catbirds in pursuit of female cowbirds.

Slack (1976) found no significant difference in catbird nest guarding behaviour between the 3 different time periods he sampled. Therefore, although female cowbirds usually parasitize nests before 6 to 9 a.m. (the period for which I examined Yellow Warblers for evidence of nest guarding), I assumed that nest guarding, if present, would be seen during both periods. If nest guarding was present in Yellow Warblers it should have been observed during this early morning period as female cowbirds appear to require pre-laying visits to the nest (Hann, 1941; Scott, 1977), and this interest in nests by cowbirds occurs throughout the morning (Hann, 1941; Mengel and Jenkinson, 1970).

If Yellow Warblers nest guard, the male should coordinate his movements with the female and be near the nest more often in the absence of the female, to minimize the amount of time when a nest is left unguarded. If nest guarding occurred, I wanted to see at which nest stage or stages it was most pronounced. The presence of a behaviour at a particular nest stage may indicate which selective force has favoured that adaptation. If nest guarding occurred approximately equally throughout nesting, it probably represents a response to predation pressures. If the hypothesis that Yellow Warblers exhibit nest guarding as a response specifically to parasitism is correct, nest guarding should be observed most during the egg laying and early incubation stages. Alternatively, if the male is near the nest more often in the presence of the female, this may indicate mate guarding is occurring. If this trend persists into the incubation stage, it may indicate an anti-predator behaviour where the male watches for predators in the presence of the female.

Aggression

Often a threat to the survival of the young in a nest may elicit an aggressive response by the parents towards the threatening intruder. Aggressive nest defence can prevent nest predation (Robertson and Blancher, 1982) and increase nest success (Gottfried, 1979). This behaviour can also be effective in dettering cowbirds, thus avoiding nest parasitism (Slack, 1976). To mount an effective defence, the parent must first recognize the nature of the threat both to its offspring and itself, and its aggressive action must be disturbing, confusing or threatening enough to deter the intruder.

Aggression towards cowbirds has been observed in Northern Orioles (*Icterus galbula*) (Robertson and Norman, 1976) and Gray Catbirds (Scott, 1977; Slack, 1976). In these species it was found to be effective in driving away cowbirds. However, these birds are as large, or larger than cowbirds. Aggression by smaller birds when they are on their own, may be ineffective against cowbirds. Scott (1977) observed a pair of Song Sparrows and Yellow Warblers on 2 separate occasions, showing alarm and aggression in response to a cowbird that was parasitizing them. On both occasions witnessed by Scott (1977), and on another seen by Hann (1937) with Ovenbirds, aggression did not deter the cowbird from parasitizing the nest. In fact, in low density host situations, cowbirds may be using aggression to find host nests (Robertson and Norman, 1977). This may explain why both Smith (1981) and Anderson and Storer (1976) observed higher frequencies of parasitism for the older, more experienced females than the naive female Song Sparrows and Kirtland's Warblers, respectively.

Host nest density has been shown to be a significant determinant for the effectiveness of aggression towards cowbirds. Interspecific group mobbing has been demonstrated to result in the reduction of parasitism (Robertson and Norman, 1977). Therefore, although aggression in low density situations may be maladaptive, it is probably advantageous in high inter- or intraspecific nest density situations. Since high nest density individuals are more successful than low nest density individuals, selection should favour increased aggression to cowbirds overall in a population (Robertson and Norman, 1977).

Willingness for parents to defend (invest in) offspring should increase as nesting proceeds from eggs to young due to the decreasing future investment needed to successfully produce offspring (Dawkins and Carlisle, 1976). This would lead to the prediction that with an increase in either the number of young or the age of the young (which are both measures of "reproductive value" of a nest) there should be a corresponding increase in the response by a breeding pair to a threat to their nest. However, selection should favour maximum gene representation of the defending individual in the future. Therefore, a level of defence that compromises between the security of the parent and offspring should be favoured (Andersson et al., 1980).

However, another important factor in the level of aggressive response to an intruder which has often been neglected, is the type of intruder. Natural selection should favour individuals who respond appropriately to biologically relevant stimuli (Patterson et al., 1980). Gottfried (1979) found the response of birds nesting in an old field habitat to a snake and a Blue Jay was determined by whether the predator tended to prey on eggs or nestlings and during which nest stage the trial was conducted. Verbeek (1972, in Buitron, 1983), Beidenweg (1983) and Buitron (1983) found that differential responses to different predators were determined by nest stage for Yellow-Billed Magpies (Pica nuttalli), Northern Mockingbirds (Mimus polyglottos) and Black-Billed Magpies (Pica pica), respectively.

Patterson et al. (1980), while reporting similar results using White-Crowned Sparrows (Zonotrichia leucophrys) as the nesting species, developed an argument for the interaction of what they termed the reproductive value (RV) and stimulus value (SV). The models developed by Patterson et al. (1980) gave equal weighting to the RV (the mean amount of future reproductive success of a given age and sex) and the SV (the amount of loss or gain in reproductive success as a function of responding to a particular stimulus). While only a rough approximation, their results demonstrated that this approach provides a more accurate explanation of why mature nesting White-crowned Sparrows will give differential responses to different nest predators through the nesting cycle.

The theoretical SV-RV model presented for each stimulus may have several sources of error: 1) the RV may not increase in a linear manner since before eggs hatch it is possible that they are infertile, but after hatching this possibility is eliminated and there may be a corresponding jump in the level of RV (Andersson et al., 1980); 2) the effect of age or experience may influence a pairs' determination of the SV of an intruder; 3) environmental quality may influence the amount of parental care and thus the RV; 4) the SV values of maximum, intermediate and minimum are only approximations; 5) the SV-RV predictions were based on an average of the 2 values, yet one value could be more important in a particular situation (Patterson et al., 1980). Therefore, the predictions based on this model are semi-quantitative and their test is based on relative rather than absolute changes in behavioural responses. This approach has not been used before to explain the level of aggression by potential hosts towards the Brown-headed Cowbird.

The RV-SV hypothesis leads to the following predictions:

1) The aggressive response towards female cowbirds should be strongest during the early incubation stage when the female cowbird is a strong threat to the clutch. The response in the early stage of nesting should be moderate as the RV of the nest

is low, while the SV is high. The response in the nestling stage should also be moderate as now the RV is high, but the SV is low.

2) The aggressive response towards the crow should increase steadily throughout nesting, as the SV remains at a maximum and the RV increases steadily.

3) The aggressive response to the male cowbird should increase with the increasing RV as the SV remains at a moderate level during the first 2 nest stages. Because the RV continues to substantially increase while the SV decreases in the nestling stage, the response should still show a slight increase.

4) The SV of the House Sparrow (the control) remains at a minimum throughout nesting, as the RV increases. Therefore, the response to the House Sparrow should be very weak and increase only slightly as nesting progresses.

By examining responses to intruders representing different levels of danger to breeding Yellow Warblers, I tested the predictions of the RV-SV hypothesis. The predictions made from this hypothesis are also presented later in graphical form (the thick, solid lines) in Fig. 6.

Egg Stimulus

Rothstein (1975a) stated that the most common form of adaptations specific to cowbirds is rejection of foreign eggs. The 2 factors which must be considered to calculate the reproductive loss due to parasitism and thus the adaptive value of rejection are the probability of parasitism, and the amount of reproductive loss that will occur if the cowbird egg is accepted (Rothstein, 1975b).

The manner of rejection by the "rejecter" species makes it difficult to ascertain the current level of parasitism since many, if not most, of the cases of parasitism will go unrecorded. The method of rejection that Yellow Warblers use is ideally suited for a study of the adaptive value of the rejection response. Their response of egg burial or nest desertion retains the evidence of parasitism and thus no bias of its frequency is introduced (Friedmann et al., 1977).

Rothstein (1975a) doubted, however, that egg burial or nest desertion were anti-parasite adaptations but rather that they resulted from: 1) human disturbance; 2) the alteration of total clutch size; or 3) the appearance of an intruder (the cowbird) at the nest. He feels that the only convincing evidence that egg burial is a direct response to a cowbird egg is if cowbird eggs are buried when layed after one or more host eggs are present and if unparasitized nests in the same area and during the same time have no egg burial.

Rothstein (1978) found that while egg rejection is learned, the basis of rejection behaviour is genetic. He found that Northern Orioles are genetically programmed to weigh certain egg parameters more heavily than others in determining whether an egg is "foreign" and whether it should be rejected. Rothstein (1975b) determined that the approximate time for the spread of rejection behaviour was 50 - 100 years for the Eastern Phoebe with a low selection coefficient and 29 - 58 years for the Kirtland's Warbler which has a higher selection coefficient, similar to that of the Yellow Warbler. This would explain why a species with intermediate levels of rejection are not common, since the rate of spread of this trait is fast.

Clark and Robertson (1981) demonstrated with natural cases of parasitism that eastern Yellow Warblers show an indeterminant level of rejection, accepting or rejecting cowbird eggs depending on the stage and timing of the nest. Their study provided the evidence that Rothstein (1975a) desired to demonstrate that egg burial is a direct response to a cowbird egg. Yet Friedmann et al. (1977) felt that only experimentation can elucidate the nature of any species showing an intermediate level of rejection. If rejection is a response to the cowbird egg specificly, then unparasitized clutches that have human disturbance, altered clutch size or have a female cowbird placed at the nest during trials, should not be rejected. In contrast, clutches that are naturally and artificially parasitized during the early egg laying stage should be rejected.

Once their nest has been discovered Yellow Warblers may exhibit several traits to reduce the threat to their reproductive fitness from cowbirds. The purpose of this chapter is to determine whether Yellow Warblers employ nest guarding, whether the aggression shown is a result of the RV and SV, and whether egg rejection is a specific response to a cowbird egg. A summary of the hypotheses, predictions and their tests is presented in Table 14.

Table 14 Hypotheses, predictions and tests for strategies to avoid or reduce the effects of brood parasitism, once a suitable nest has been discovered by cowbirds.

#	HYPOTHESIS	PREDICTIONS	TESTS
1	NEST GUARDING	-the male should coordinate his movements with the female to be near the nest most when she is absent and the total time that neither bird is near the nest should be very low during the early stages of nesting.	-measure the total time the male is within a certain area in the presence and absence of the female and the total time neither bird is near the nest at 3 nest stages.
2	AGGRESSION (RV-SV)	-Yellow Warblers should recognize the specific threat posed by female cowbirds and respond most strongly during the egg laying and early incubation stages.	-measure the aggression index of both sexes when 4 different stimuli are placed near the nest at 3 different nest stages.
3	REJECTION	-rejection is a response to the stimulus of the cowbird egg, not to any other disturbance. -rejection occurs when only a small portion of the clutch has been laid, and there is still enough time in the breeding season to initiate a new clutch.	-compare the level of rejection for unparasitized nests which have had human disturbance, altered clutch size or a female cowbird placed beside them to artificially and naturally parasitized nests. -record the time left in the season and the # of Yellow Warbler eggs already in the nest, for parasitized and unparasitized nests, and compare between accepted and rejected nests.

METHODS

Nest Guarding

Six Yellow Warbler nests were studied to determine whether these birds show any signs of nest guarding at the different nest stages of nest construction, egg laying and late incubation (Hypothesis 1, Table 14). All observations were recorded between 6 and 9 a.m. from a minimum distance of 15 m. With the exception of one nest which was parasitized and deserted, the same nests were observed for a period of 2 hours each during the stages of nest construction, egg laying and late incubation. Using the method described by Slack (1976), I marked a circumference of 5 m from the nest with small pieces of blue flagging tape. The time the male spent within this 5 m ring in the presence and absence of the female was recorded. If the male spent significantly more time in this area when the female was absent, then this would indicate that nest guarding may be occurring. The overall time when neither parent was within this area was also recorded.

Aggression

Aggression by Yellow Warblers (Hypothesis 2, Table 14) towards different stimuli was recorded for the egg laying, early incubation and nestling stages of 8 unparasitized Yellow Warbler nests. I could not always use the same 8 nests in all 3 stages of the experiment, because some of these nests were either preyed upon or parasitized.

Four different stimulus objects were used in the aggression trials. The female cowbird, while no threat to the mature warblers themselves, is the greatest threat to nest success during the early nest stages (chapter 1). The male cowbird is known to sometimes accompany the female on her nest visits (Mengel and Jenkinson, 1970; Rothstein et al., 1984), and therefore I wanted to test if the Yellow Warblers associated the male cowbird with the threat to nest success. The crow may be dangerous to the warblers themselves and presents a danger to all nest contents, but especially to nestlings. The House Sparrow was used as a control, as it is common in the area and presumably represents no threat to Yellow Warblers.

To determine the level of aggression towards the 4 different stimulus objects, each caged intruder was placed only 1 m from each nest and aggressive responses of the nest owners were then recorded for 5 minutes. All observations were made from a minimum of 10 m. To prevent biases due to habituation or carry-over aggression, only 2 consecutive trials were ever carried out during a period of testing. A 15 minute rest period was given between each trial and test periods at the same nest were never less than 2 hours apart. Responses to the stimuli were recorded by 1 observer with the aid of a UHER 4000 tape recorder. The index of aggression was based on the ranking system developed by Robertson and Norman (1976). However, two modifications to this system were implemented. I lowered the score for nest attentiveness when the birds are silent, because the female Yellow Warbler should ignore the control stimulus and attend the nest during the incubation stage. The original system did not differentiate between faster and slower rates of alarm calling. Different rates of alarm calling have been used as an indication of the level of aggressive response (Gottfried, 1979). Since I had Yellow Warblers which gave alarm calls at widely different rates, I rated the intensity of aggression as follows: 1) distant (5+ m) silent observation; 2) close (0-5 m) silent observation; 3) distant slow (1-20 calls/min) alarm calling, or nest attentiveness; 4) close slow alarm calling; 5) distant moderate (20-40 calls/min) alarm calling or fly-by investigation; 6) distant rapid (40+ calls/min) alarm calling; or close moderate alarm calling; 7) close rapid alarm calling or hovering above stimulus; 8) distraction (wing flapping, broken wing display); 9) attacking the model. The duration of the response was also ranked as: 1) brief (1-10 secs.) or only once; 2) several times or up to 1 minute; 3) 1-3 minutes; 4) 3-5 minutes. An individual's total score was calculated by summing up the products of the intensity of aggressiveness multiplied by its duration, for the 5 minute trial. By plotting the index of aggression for each nest stage, the pattern of the response towards each intruder was then compared with the prediction which was plotted from the RV-SV hypothesis.

Egg Stimulus

The rejection-acceptance study (Hypothesis 3, Table 14) used 2 sources to increase the sample size. Along with the 15 naturally parasitized nests in my main study area, I also artificially parasitized 6 nests during the late egg laying stage and 3 during the early egg laying stage in 2 old field habitats, 3 to 4 km south of Ottawa, Ontario. For these artificial cases I used some real cowbird eggs and some artificial cowbird eggs supplied to J. Picman by S.I. Rothstein. Rothstein (1975a, 1976) has shown with other rejecters that artificial cowbird eggs are treated no differently from real cowbird eggs. As I was unsure of the frequency with which cowbirds remove eggs from Yellow Warbler nests, I decided to remove 1 egg from 4 of the artificially parasitized nests; and I removed no eggs from the other 5 artificially parasitized nests. It is probable that no cowbird visited the 9 artificially parasitized nests (since they were not naturally parasitized) and the disturbance from nest checks was no greater than in the natural, unparasitized nests in the regular study area. In 4 other nests in this adjunct area, I removed 1 egg to alter the clutch size, during the early egg laying stage.

The stage of egg laying for those birds which accepted artificially and naturally laid cowbird eggs was compared to those which showed rejection. The number of days from the beginning of the Yellow Warbler breeding season in this area until the nest was parasitized was also recorded and compared between rejecters and accepters.

RESULTS

Nest Guarding

There were no significant differences (P>0.05) between the time the male spent within the 5 m ring in the presence and absence of the female during the nest construction and egg laying stage (Table 15). A significant difference (P=0.03) during the late incubation phase, does not support nest guarding, but suggests that the male may be protecting the female, as the male was significantly more often present in the area when the female was present (Table 15). The nest area was also void of either individual 57.7% and 75.4% of the time during nest construction and egg laying, respectively. During incubation, the time that both individuals were absent dropped drastically (15.8%) due to the demands on the female to incubate. However, when the female did leave the nest area during incubation, the male tended to follow her rather than moving into the 5 m ring (Table 15). Hence, I conclude that the nest guarding hypothesis (Table 14) is not supported by the results.

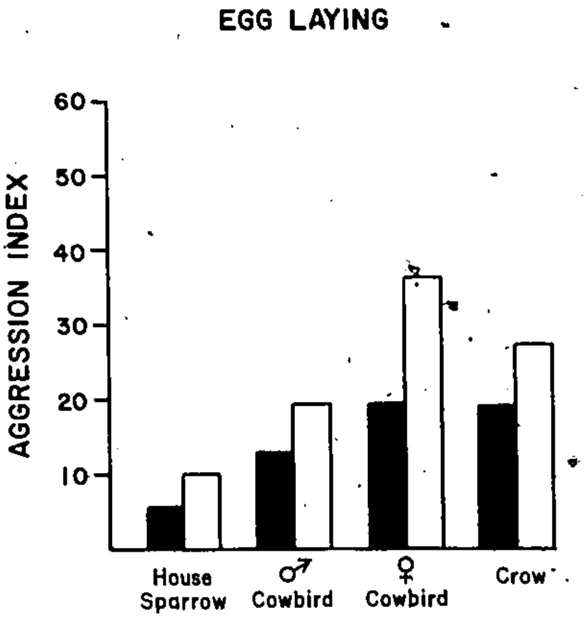
Aggression

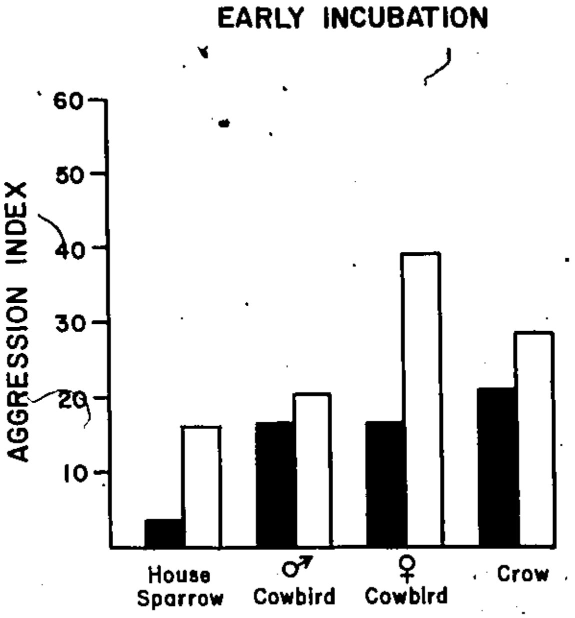
Female Yellow Warblers had significantly stronger aggressive reactions towards all the intruders than male warblers during the egg laying (U=277.5, P<0.01, Mann Whitney U test) and early incubation stages (U=137.5, P<0.001, Mann Whitney U test). Although not statistically significant, this trend continued in the nestling stage (Fig. 5). While the males response was generally lower, it was positively correlated with the female response during the egg laying (r=0.51,

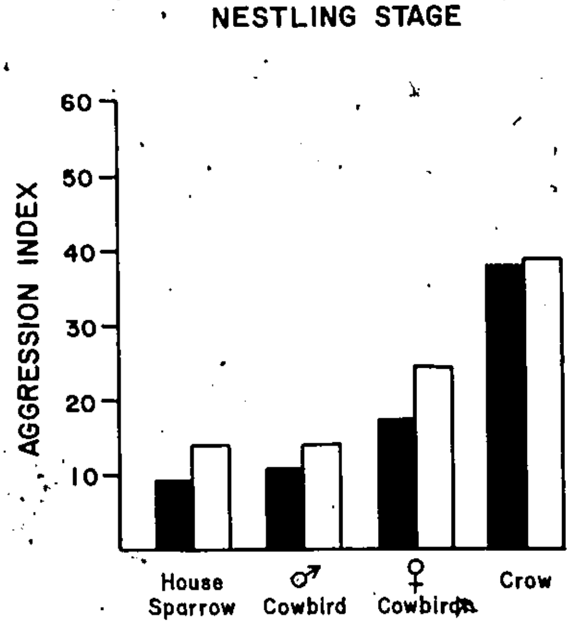
Table 15 Male Yellow Warbler presence for two hour periods with and without female for three nest stages.

	N	% both absent	% male presence without female	% male presence with female	Wilcoxon matched pairs test Z	P
NEST CONSTRUCTION	6	57.7±6.1	11.1±2.8	14.3±4.7	-1.153	0.25
EGG LAYING	6	75.4±8.3	5.6±3.6	7.9±3.8	-1.363	0.17
LATE INCUBATION	6	15.8±4.8	1.4±1.6	8.6±3.0	-2.201	0.03

Figure 5 Aggression index means for male (shaded bars) and female (open bars) responses at 3 different nest stages, towards different stimuli.


EGG LAYING
AGGRESSION INDEX
60
50
40
30
20
10
House Sparrow
♂ Cowbird
♀ Cowbird
Crow


EARLY INCUBATION
AGGRESSION INDEX
60
50
40
30
20
10
House Sparrow
♂ Cowbird
♀ Cowbird
Crow


NESTLING STAGE
AGGRESSION INDEX
60
50
40
30
20
10
House Sparrow
♂ Cowbird
♀ Cowbird
Crow

D.F.=30, $P<0.003$) and nestling stages ($r=0.75$, D.F.=30, $P<0.0005$), but not during the early incubation stage.

During all nest stages tested, females showed significantly different responses from males to the different stimuli (Table 16). To determine which stimuli were eliciting the different responses, I performed a series of non-parametric multiple comparisons (Zar, 1974).

During the egg laying stage, females reacted most aggressively to the female cowbird and had a significantly different response to each stimulus. Males gave a significantly stronger response to the female cowbird, crow and male cowbird than to the house sparrow (Fig. 5, Table 17). During incubation, the strongest response by the female Yellow Warbler was again towards the female cowbird. Females responded significantly differently to each stimulus during the incubation stage, with the exception of the male cowbird and House Sparrow, which elicited a similar low degree of aggression (Fig. 5, Table 18). The male again reacted similarly to the male and female cowbird and crow, but gave a significantly weaker response towards the House Sparrow during the incubation stage (Fig. 5, Table 18). During the nestling stage, male and female warblers gave a similar weak response to the male cowbird and House Sparrow, but reacted most strongly to the crow and then to the female cowbird (Fig. 5). The differences for both male and female warblers between the crow, female cowbird, and the sparrow and the male cowbird together, were statistically significant (Table 19).

Table 16 Kruskal-Wallis test for male and female Yellow Warblers to determine whether significant differences exist in the level of aggressive response towards different stimuli at each nest stage.

NEST STAGE	FEMALE		MALE	
	X^2	P	X^2	P
EGG LAYING	24.53	<0.001	4.83	<0.01
EARLY INCUBATION	21.81	<0.001	14.85	<0.01
NESTLING STAGE	24.48	<0.001	20.09	<0.001

Table 17 Non-parametric multiple comparisons for male and female Yellow Warblers during the egg laying stage to determine where the significant differences exist in the level of aggressive response towards different stimuli. (N=8 for all tests)

COMPARISON	q	p	P
MALE			
crow & house sparrow	4.30	4	<0.05
crow & male cowbird	2.00	3	>0.10
crow & female cowbird	0.45	2	>0.50
female cowbird & house sparrow	5.40	3	<0.001
female cowbird & male cowbird	2.53	2	>0.05
male cowbird & house sparrow	5.50	2	<0.001
FEMALE			
female cowbird & house sparrow	6.60	4	<0.001
female cowbird & male cowbird	5.75	3	<0.001
female cowbird & crow	4.01	2	<0.01
crow & house sparrow	6.05	3	<0.001
crow & male cowbird	4.53	2	<0.01
male cowbird & house sparrow	4.46	2	<0.01

Table 18 Non-parametric multiple comparisons for male and female Yellow Warblers during the incubation stage to determine where the significant differences exist in the level of aggressive response towards different stimuli. (N=8 for all tests)

COMPARISON	q	p	P
MALE			
crow & house sparrow	4.88	4	<0.01
crow & female cowbird	1.18	3	>0.50
crow & male cowbird	1.19	2	>0.10
male cowbird & house sparrow	5.63	3	<0.001
male cowbird & female cowbird	0.48	2	>0.50
female cowbird & house sparrow	7.87	2	<0.001
FEMALE			
female cowbird & male cowbird	6.35	4	<0.001
female cowbird & house sparrow	6.15	3	<0.001
female cowbird & crow	6.72	2	<0.001
crow & male cowbird	3.90	3	<0.05
crow & house sparrow	3.38	2	<0.05
house sparrow & male cowbird	2.41	2	>0.05

Female Yellow Warblers showed a similar low response to the male cowbird and House Sparrow throughout all 3 nest stages tested. However, there were significant differences in the response to the other two stimuli at different nest stages (Table 20). The male warblers, on the other hand, showed a significant difference in response only to the crow at different nest stages, while their response to the other stimuli were similar throughout the nesting cycle (Table 20).

Male and female Yellow Warblers responded similarly to the crow during the egg laying and early incubation stage, but both sexes gave significantly stronger responses to the crow during the nestling stage (Fig. 6, table 21). Female warblers responded to the female cowbird in a similar manner for both the egg laying and early incubation stages, but the response in both these stages was significantly different from less aggressive response during the nestling stage (Fig. 6, Table 22). The results on warbler aggression towards female cowbirds and crows support the aggression RV-SV hypothesis (Table 14).

At 5 out of 8 nests (repeated twice), on 10 different occasions, the trials with female cowbirds during the egg laying stage yielded interesting observations. The female warbler, after performing some initial short flights and alarm calls, went to the nest and placed herself on it, as if she was incubating, yet there were no eggs in the nest. This behaviour was not seen once any eggs had been layed, until incubation had begun, and was not seen during the nestling stage. This response during the early egg laying stage was a unique response

Table 19 Non-parametric multiple comparisons for male and female Yellow Warblers during the nestling stage to determine where the significant differences exist in the level of aggressive response towards different stimuli. (N=8 for all tests)

COMPARISON	q	p	P
MALE			
crow & house sparrow	5.86	4	<0.001
crow & male cowbird	6.55	3	<0.001
crow & female cowbird	6.20	2	<0.001
female cowbird & house sparrow	3.60	3	<0.05
female cowbird & male cowbird	3.53	2	<0.05
male cowbird & house sparrow	1.82	2	>0.10
FEMALE			
crow & house sparrow	6.03	4	<0.001
crow & male cowbird	7.68	3	<0.001
crow & female cowbird	5.27	2	<0.001
female cowbird & house sparrow	4.45	3	<0.01
female cowbird & male cowbird	6.13	2	<0.001
male cowbird & house sparrow	0.48	2	>0.50

Table 20 Kruskal-Wallis test for male and female Yellow Warblers to determine whether significant differences exist in the level of aggressive response within different nest stages for each stimulus.

STIMULUS	FEMALE		MALE	
	X^2	P	X^2	P
CROW	14.61	<0.001	9.83	<0.01
FEMALE COWBIRD	14.52	<0.001	0.50	>0.05
MALE COWBIRD	5.31	>0.05	4.00	>0.05
HOUSE SPARROW	5.79	>0.05	5.45	>0.05

Figure 6 Mean index of aggression in response to different stimuli, during different reproductive stages by female (dotted line) and male (dashed and dotted line) Yellow warblers. Theoretical levels of the reproductive and stimulus values (solid lines) were used to determine the predicted response (thick solid line).

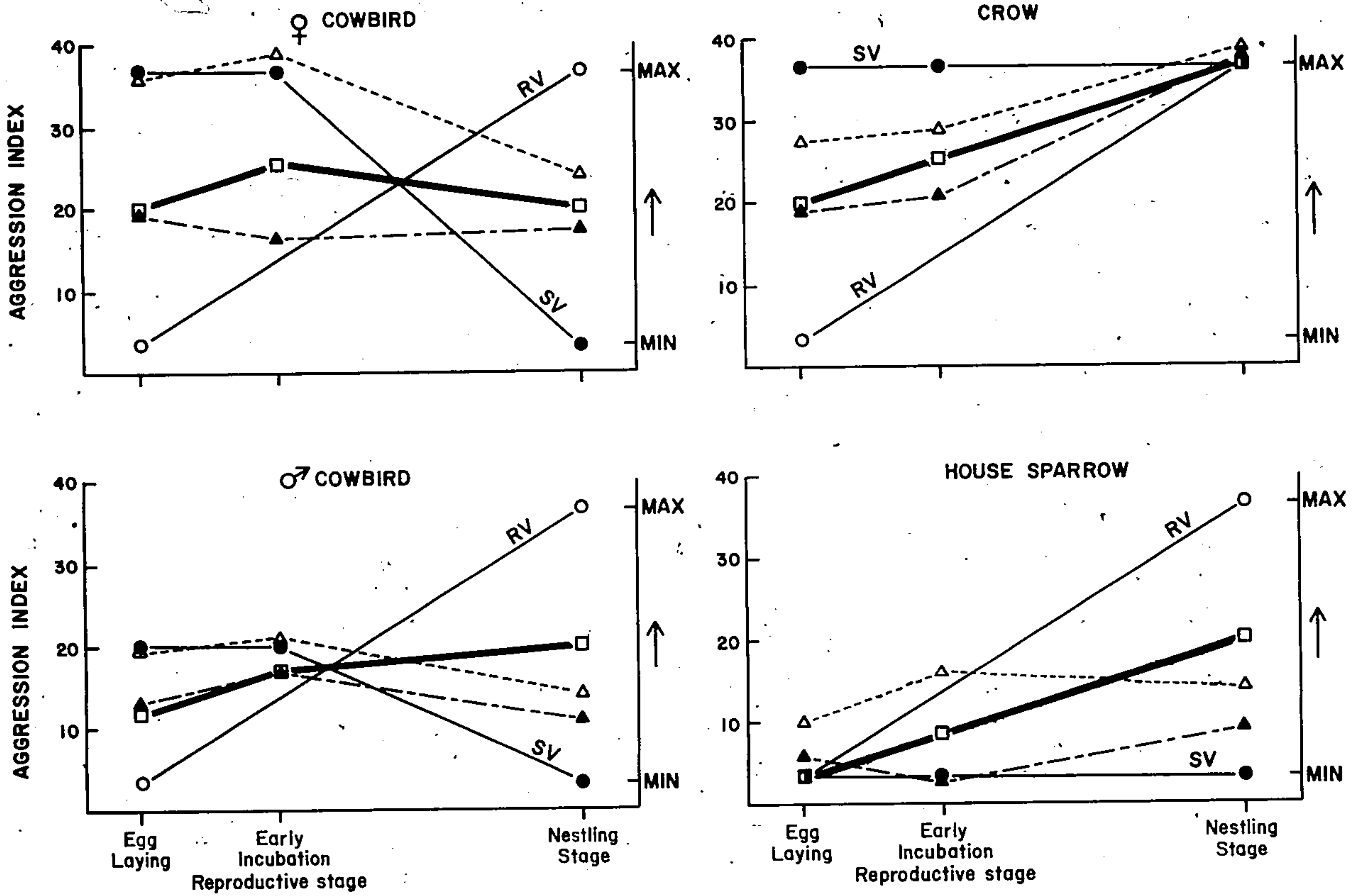

♀ COWBIRD
CROW
♂ COWBIRD
HOUSE SPARROW
AGGRESSION INDEX
AGGRESSION INDEX
40
30
20
10
MAX
MIN
RV
SV
Egg Laying
Early Incubation
Nestling Stage
Reproductive stage

Table 21 Non-parametric multiple comparisons for male and female Yellow Warblers with the crow stimulus to determine where the significant differences exist in the level of aggressive response during different nest stages. (N=8 for all tests)

COMPARISON	q	p	P
MALE			
nestling & egg laying	3.95	3	<0.05
nestling & incubation	5.50	2	<0.001
egg laying & incubation	0.37	2	>0.50
FEMALE			
nestling & incubation	4.68	3	<0.01
nestling & egg laying	6.87	2	<0.001
incubation & egg laying	0.07	2	>0.50

Table 22 Non-parametric multiple comparisons for female Yellow Warblers with the female cowbird stimulus to determine where the significant differences exist in the level of aggressive response during different nest stages. (N=8 for all tests)

COMPARISON	q	p	P
FEMALE			
incubation & nestling	4.80	3	<0.01
incubation & egg laying	0.45	2	>0.50
egg laying & nestling	6.68	2	<0.001

by Yellow Warblers to the female cowbird. The female warbler remained in this "premature incubation" position and gave alarm calls for up to 15 minutes, at which time I removed the female cowbird.

Egg Stimulus

There was a statistically significant difference ($P<0.01$) in the stage of clutch completion (the number of eggs layed by a Yellow Warbler) between those nests where acceptance and rejection of the cowbird egg was observed (Table 23). A cowbird egg tends to be rejected before and accepted after 3 Yellow Warbler eggs have been layed. The length of time left in the Yellow Warbler breeding season when a nest is parasitized, was also found to be a significantly ($P<0.01$) important determinant as to whether a cowbird egg was accepted or rejected (Table 23). Yellow Warblers tended to reject a cowbird egg early in the breeding season and accept a cowbird egg later in the season. Yellow Warblers twice accepted eggs when naturally parasitized, and on 3 occasions they rejected cowbird eggs when artificially parasitized.

In the experiment to determine whether egg rejection was a result of the cowbird egg in the nest, the groups of unparasitized nests with: 1) human disturbance; 2) altered clutch size; and 3) a female cowbird visit of the nest; were compared to the group of parasitized nests. In each case egg rejection was significantly greater in the group of nests that had cowbird eggs in them (Table 24). Thus, the egg stimulus hypothesis (Table 14) is supported by these results.

Table 23 Differences in the clutch size and date when parasitized, and their effect on rejection or acceptance of a cowbird egg.

		Clutch size when parasitized	Mann-Whitney		#of days from start of Yellow Warbler breeding when parasitized	Mann-Whitney	
	n	$\overline{X}\pm$S.D	U	P	$\overline{X}\pm$S.D.	U	P
REJECTION	15	1.4±0.9	16.5	<0.01	10.1±7.3	20.5	<0.01
ACCEPTANCE	9	3.1±1.1			20.2±6.0		

Table 24 Fisher Exact Probability test of clutch rejection. Comparisons were made separately, between the nests parasitized in the early egg laying stage with no alteration of clutch size, and each of the three other groups.

GROUP	# OF NESTS REJECTED	NOT REJECTED	m_1	m_2	P
parasitized nests in early egg laying stage with unaltered clutch size	3	0	---	---	---
unparasitized nests with human disturbance	0	21	3	3	<0.001
unparasitized nests with altered clutch size	1	3	3	3	<0.05
uparasitized nests visited by a female cowbird during trials	0	4	3	3	<0.001

DISCUSSION

Nest Guarding

Yellow Warblers showed no signs of nest guarding during the nest construction, egg laying or late incubation nesting stages (Table 15). The 5 m ring was unoccupied by either sex for 57.7% and 75.4% during the nest construction and egg laying stages, allowing ample opportunity for a female cowbird to visit the nest. Slack (1976) felt that the high incidence of vocalizations and visual signals by the female to the male, which preceded the female departures from the nest were essential to effective nest guarding. Communication prior to, or after, movements by the female was often absent in Yellow Warblers. One additional observation should be noted; during the temporary abandonment trials (chapter 2), frequently neither sex would appear during the early nesting stages, when the cowbird was placed 10 m from the nest.

Catbirds, which exhibit nest guarding, are larger than cowbirds and the absence of this behaviour in Yellow Warblers may be due to its possible lack of efficacy with small host species (Scott, 1977). However, as discussed below, aggression by Yellow Warblers in its proper context is probably a suitable deterrent, and the absence of nest guarding in Yellow Warblers is more likely a result of competing demands, such as mate guarding, and defence of the territory.

Aggression

My results support the findings of Robertson and Norman (1977), Folkers (1982) and Folkers and Lowther (in press), that Yellow Warblers do recognize the threat of female cowbirds. Contrary to Robertson and Norman (1976), and in accord with Folkers (1982), I found that the response to female cowbirds was significantly higher than the response to male cowbirds.

Folkers and Lowther (in press) found a trend that Yellow Warblers would respond most aggressively towards cowbirds during the egg laying stage, but this was not statistically significant. However, in my study, using live caged cowbirds, the response of female Yellow Warblers supported the prediction that the strongest response would be given to the intruder that was most likely the greatest threat at a particular nest stage. The males' response showed a trend (although not statistically significant) which was in agreement with this prediction (Fig. 5). This suggests the importance of the stimulus value in aggressive responses.

When the theoretical stimulus value is combined with the theoretical reproductive value (Fig. 6) the resulting responses towards the two most threatening intruders, the female cowbird and the crow, by the female Yellow Warbler can be explained. Male and female responses to the crow showed an increase as the RV increased and the SV remained constant. However, the rate of increase was much faster between the early incubation and nestling stages and this may reflect the fact that while crows are a danger to the nest contents and parents at all stages, they more commonly prey on nestlings than eggs. The aggressive response by female Yellow Warblers towards the female cowbird increases between the egg laying and early incubation phase, because while the SV remains constant the RV is increasing. During the nestling stage, while the RV is at a maximum, the SV has now dropped to a minimum as the female cowbird is no longer a threat to the young in the nest or to the mature Yellow Warblers. Thus the aggressiveness towards female cowbirds, does not appear to be a generalized anti-predator response, but a response tailored to the specific threat posed by a female cowbird.

Female responses towards the male cowbird and the House Sparrow appear to follow more closely the prediction from the stimulus value alone, rather than the SV-RV prediction. However, it seems clear that the female Yellow Warbler does recognize the male cowbird and associates it with a moderate threat. The House Sparrow, which is no threat to the warblers or their nest, elicited only a mild response.

Male Yellow Warbler responses to the female cowbird, House Sparrow and male cowbird all tend to be constant, with respective ranges for the aggression index of 3.3, 5.5 and 5.7 over the 3 nest stages tested (Fig. 6). This may show a certain reluctance by the male to participate in defence of the young, unless the danger directly threatens him (as with the crow). M. Studd (pers. comm.) found that male Yellow Warblers do not play an important role in defence of the nest. Competing demands of defence of the territory and defence of his mate against conspecific intruders may be his prime concern.

Although aggression in low nest density situations may be maladaptive for small birds, Yellow Warblers in this area were aggressive towards threatening intruders. While Yellow Warbler nest density was low in this area, inter-specific nest density may have been high. In several aggression trials I noticed other species such as Northern Orioles, Red-winged Blackbirds and Cedar Waxwings becoming alert and watchful. Although they did not directly participate in mobbing, they did give some alarm calls.

The behaviour exhibited by 5 out of 8 Yellow Warbler females in the presence of a female cowbird (sitting in an empty nest), until the stimulus is withdrawn appears to be a specific response to the unique threat posed by female cowbirds. This response is probably an effective deterrent despite the warbler's size, as the female cowbird has never been reported to physically force a bird off its nest. This supports the view that female Yellow Warblers recognize the nature of the threat posed by female cowbirds, as this response has no adaptive value if used towards a predator. This response was not exhibited when one or more eggs were in the nest, until incubation had begun. Therefore the nest is still accessible to female cowbirds during the egg laying phase after a host egg has been layed, and before incubation has begun.

It is interesting that 3 of the 8 Yellow Warbler females tested did not exibit this behaviour. This suggests that: 1) this behaviour is learned with experience and that inexperienced females, although showing strong aggression towards female cowbirds, do not exibit this response; 2) this behaviour is an innate response, but my presence influenced the 3 individuals not to behave normally; or 3) this behaviour is an innate response, but given the short time of exposure to cowbirds, the trait has not spread throughout the entire population.

Friedmann, (1963) suggested that recognition of the danger posed by cowbirds was caused by cultural transmission passed from parents to young, as the young observed the reactions of their parents. However, since the period of strongest aggressive response and stage of most important defence from cowbirds occurs while the progeny are still eggs in the nest, this is unlikely. Yet, learning by cultural transmission may occur between inexperienced nesting birds and birds with previous exposure to cowbirds. Folkers and Lowther (in press) had different patterns of responses for parasitized and non-parasitized Red-winged Blackbirds which was consistent with this idea.

Friedmann et al. (1977) suggested 2 possible mechanisms for a stronger response developing and spreading within a population: 1) natural selection has produced a stronger innate response for aggression towards cowbirds, or 2) the high degree of parasitism causes many individuals to gain experience with cowbirds and cowbird caused interference, and thus learn to respond more aggressively.

It would appear that the work by Nice (1937, in Friedmann, 1963), Robertson and Norman (1977) and Lowther (1983), all lend support to the role of learning in the aggressive response. However, this does not preclude selection for genes which may enable an individual to learn more quickly, to discriminate more accurately between types of threats or to respond more effectively.

Egg Rejection

Rothstein (1975a) felt that the bill size was probably very important in determining whether egg ejection, (a form of rejection) evolved in a species. The difficulty which a species such as the Yellow Warbler encounters in ejecting an egg probably largely explains the more complicated response that was demonstrated in Table 23.

Yellow Warblers reject cowbird eggs only early in the egg laying stage and if there is sufficient time to re-nest. Rothstein (1976, 1977) found that Cedar Waxwings and Northern Orioles, had difficulty ejecting eggs, and due to the higher potential costs of damaging their own eggs during an ejection attempt, they had higher tolerance to cowbird eggs and would not reject them during later incubation. For Yellow Warblers, as with these other 2 species, it appears that selection favours rejection when parasitized early in the egg laying stage, since acceptance at this time would cause greater reproductive loss as a cowbird egg would gain a competitive advantage in hatching first. Also, at this stage, the pair would lose less of their investment than they would later, and for Yellow Warblers there is probably still sufficient time in the breeding season to re-line or re-nest. However, towards the latter stage of clutch completion there is: 1) a greater chance that Yellow Warbler eggs will hatch before or near the cowbird egg hatching time (Clark and Robertson, 1981); 2) a greater parental investment in the existing clutch which they are less likely to sacrifice (Table 23); and 3) less time in the breeding season to attempt another clutch (Table 23). The higher the potential for a successful nest attempt, the more likely that Yellow Warblers, (and probably Northern Orioles and Cedar Waxwings) will accept a cowbird egg.

The manner of rejection by Yellow Warblers is not egg ejection but egg burial or nest desertion. Clark and Robertson (1981) demonstrated that it is unlikely that Yellow Warblers are physically capable of ejecting a cowbird egg without breaking it in the nest, which would probably cause the host eggs to stick to the nest as the spilled albumin dries. Rothstein (1976, 1977) found even larger birds with larger bills often damaged their own eggs when ejecting cowbird eggs.

Egg burial occurred much more frequently (75%), than nest desertion (25%) and this is probably because it is much more efficient in time and energy (Rothstein, 1975a). Clark and Robertson (1981) felt that while egg burial would be selected over desertion, desertion would still occur if the nest support is not strong enough to hold the extra weight that egg burial would entail. These results also support Clark and Robertson's (1981) finding that the timing in the breeding season and the number of host eggs already layed, determines the Yellow Warblers' response to the cowbird egg.

When the rate of rejection shown by nests parasitized in the early egg laying stage, with unaltered clutch size was compared with those unparasitized nests that had human disturbance, altered clutch size, or a female cowbird near the nest, the differences were significant (Table 24). The results from the natural and experimental nests support the hypothesis that the egg rejection seen in the form of nest desertion and egg burial is a response to the stimulus of the cowbird egg, and that this response is exhibited depending on the stage of clutch completion (Table 23).

To conclude, once a nest in an early stage has been found by a female cowbird, it is in danger of being parasitized. Although Yellow Warblers do not exhibit nest guarding, they do recognize the specific type of threat posed by female cowbirds and will respond in an appropriate manner. While the general aggressive response by Yellow Warblers towards cowbirds is probably effective only in a higher density situation, some female Yellow Warblers have shown during the early egg laying stage, a specific defence towards cowbirds that I termed the "premature incubation" behaviour. However, if a cowbird manages to parasitize a Yellow Warbler nest, egg rejection will occur as a response to the cowbird egg, if the advantages of re-initiating a new clutch outweigh the costs of accepting the cowbird egg.

GENERAL DISCUSSION

Originally, when cowbirds moved into any area where they were previously absent, the host populations lacked both experience with cowbirds and anti-parasite adaptations. Mayfield (1965) found that small passerines in eastern North America were more tolerant of cowbirds than species from the mid-west which have a long history of sympatry with cowbirds.

Over the last 50 to 100 generations (assuming an average life span of 2 - 3 years), natural selection has acted on the genetic variation that existed in the Yellow Warbler population. Individuals that could avoid parasitism or lessen its effects on their reproductive fitness, without compromising other important traits, have been at a selective advantage.

Eastern Yellow Warblers give a strong response to female cowbirds (chapter 3) and the eastern race now responds as aggressively towards cowbirds as those farther west (Norman and Robertson, 1975).

Friedmann (1963) thought that responses shown by some hosts towards cowbirds were not specifically anti-cowbird defences, but that these were generalized responses to intruders or to a foreign object in the nest. He even stated that, "it is difficult to imagine a clearly defined defence against an unspecialized parasite". It is true that some traits exhibited now, that are effective against parasitism, probably originated from an anti-predator behaviour. However, at least a certain percentage of the population has developed a cowbird-specific response during the early egg laying stage that probably has no other adaptive value, except as a deterrent to cowbirds (chapter 3). Rejection by Yellow Warblers is effective and also is now present in eastern Yellow Warbler populations (Clark and Robertson, 1981; Berger 1951). This rejection appears to be a direct response to the presence of a cowbird egg in the nest and not due to a coincidental disturbance (chapter 3).

Although the strategies of: 1) nesting in taller bushes; 2) nesting away from high perches; and 3) avoiding the peak cowbird laying period, have all been seen to be effective for Yellow Warblers in avoiding parasitism (chapter 2), not all nesting pairs in the population are exhibiting these traits. This may be due to: 1) the traits have not yet spread throughout the entire population; 2) these traits are cultural adaptations learned with experience; or 3) the competition for nesting sites and the pressure from predation may prevent some individuals from expressing these traits.

The rate of evolution of traits effective in avoiding or lowering the effects of parasitism depends on the genetic determinants. The more genes involved in the expression of the trait, the slower the rate of evolution (Rothstein, 1975b), and the slower its rate of spread throughout the population. The expression of some traits, such as aggression, may also depend on the age, social dominance, and reproductive state, and may vary with experience or local environmental conditions (Robertson and Norman, 1977). Competing pressures may also slow the evolutionary rate of a trait. A trait, while being beneficial to an individual in terms of helping to avoid the negative effects of parasitism, may also be costly to the individual, with respect to the energy expenditure, investment of time and exposure of the host or its nest to predators. If these costs associated with an anti-cowbird trait outweigh the benefits, then the trait will not be selected for. These reasons may explain why nest guarding, temporary abandonment of the nest area when a cowbird was near, and male avoidance of the nest area, were not seen in my sample of Yellow Warblers.

Finally, it is possible that the absence of a trait which could be beneficial for potential hosts is due to the lack of genetic variability in the population.

The most suitable method to gain a better understanding of the rate of evolution of anti-parasite traits, and thus behavioural traits in general, would be to conduct a comparative study on a wide ranging host species which is exposed to strong selective pressure from cowbirds in: 1) the original area of sympatry with cowbird (mid-western North America); 2) an area where the host has been exposed to cowbirds for a couple of hundred years; and 3) an area which is outside the present cowbird range.

CONCLUSIONS

1) Brood parasitism by the Brown-headed Cowbird is a strong selective pressure on Yellow Warblers in south-eastern Ontario, comparable to the pressure from nest predation. Thirty-one percent of the 49 Yellow Warbler nests were parasitized and parasitism was responsible for at least 41% of all the eggs lost.

2) Nest site characteristics are important in avoidance of parasitism. Breeding in tall bushes, or farther from tall perches lowers the chance of parasitism.

3) High nesting synchrony and/or nesting later in the season decreases the chance of parasitism.

4) Yellow Warbler females responded more aggressively to 4 types of intruders during the early nest stages than males. In contrast to Robertson and Norman (1977), female Yellow Warblers responded more strongly to female than to male cowbirds.

5) I demonstrated that female Yellow Warblers responded most aggressively to female cowbirds, during the egg laying and incubation stages when they are most vulnerable to parasitism.

6) I demonstrated experimentally for the first time that the rejection response by Yellow Warblers is a response to the stimulus of the cowbird egg and is not a result of observer disturbance, cowbird

presence or altered clutch size.

7) Traits effective against cowbird parasitism are exhibited in eastern Yellow Warblers after less than 200 years of exposure to parasitism.

LITERATURE CITED

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

Andersson, M., C. G. Wiklund, and H. Rundgren. 1980. Parental defence of offspring: a model and an example. Anim. Behav. 28:536-542.

Askenmo, C. 1979. Reproductive effort and return rate of Pied Flycatchers. Am. Nat. 114:748-753.

Batts, H. L. Jr. 1958. The distribution and population of nesting birds on a farm in southern Michigan. Jack-Pine Warbler 36:131-149.

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. Natl. Mus. Bull. 211.

Beidenweg, D. W. 1983. Time and energy budgets of the Mockingbird (Mimus polyglottos) during the breeding season. Auk 100:149-160.

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

Bryant, D. M. 1979. Reproductive costs in the House Martin (Delichon urbica). J. Anim. Ecology 49:655-675.

Buitron, D. 1983. Variability in the response of Black-billed Magpies to natural predators. Z. Tierpsychol. 45:209-235.

Burns, P., and C. M. Wang. 1981. Manova: Multivariate Analysis of Variance. pages 1-79 in C. H. Hull and N. H. Nie, Eds. SPSS Update 7-9. New York, McGraw-Hill.

Clark, K. L., and R. J. Robertson. 1979. Spatial and temporal multi-species nesting aggregations in birds as anti-parasite and anti-predator strategies. Behav. Ecol. Sociobiol. 5:359-371.

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

Darley, J. A. 1978. Pairing in captive Brown-headed Cowbirds (Molothrus ater). Can. J. Zool. 56:2249-2252.

Darley, J. A. 1982. Territoriality and mating behaviour of the male Brown-headed Cowbird. Condor 84:15-21.

Dawkins, R., and T. R. Carlisle. 1976. Parental investment, mate desertion and a fallacy. Nature 262:131-132.

Dufty, A. M. 1982. Movements and activities of radio-tracked Brown-headed Cowbirds. Auk 99:316-327.

Finch, D. M. 1982. Rejection of cowbird eggs by Crissal Thrashers. Auk 99:719-724.

Finch, D. M. 1983. Brood parasitism of the Abert's Towhee: timing, frequency and effects. Condor 85:355-359.

Finch, D. M. 1984. Parental expenditure of time and energy in the Abert's Towhee. Auk 101:473-486.

Folkers, K. L. 1982. Host behavioral defences to cowbird parasitism. Kansas Ornithol. Soc. Bull. 33:32-34.

Folkers, K. L., and P. E. Lowther. 1985. Responses of nesting Red-winged Blackbirds and Yellow Warblers to Brown-headed Cowbirds. J. Field Ornith.
(in press).

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

Friedmann, H. 1963. Cowbird parasite hosts. U. S. Natl. Mus. Bull. 233:1-276.

Friedmann, H. 1971. Further information on the host relations of the parasitic cowbirds. Auk 88:239-255.

Friedmann, H., L. F. Kiff, and S. I. Rothstein. 1977. A futher contribution to knowledge of the host relations of the parasitic cowbirds. Smithson. Contrib. Zool. 235:1-75.

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

Gottfried, B. M. 1979. Antipredator aggression in birds nesting in old field habitats: an experimental analysis. Condor 81:251-257.

Hamilton, W. J. III, and G. H. Orians. 1965. Evolution of brood parasitism in altrical birds. Condor 67:361-382.

Hanka, L. R. 1979. Choice of host nest by the Brown-headed Cowbird in Colorado and Wyoming. Condor 81:436-437.

Hann, H. W. 1937. Life history of the Ovenbird in southern Michigan. Wilson Bull. 49:145-237.

Hann, H. W. 1941. The cowbird at the nest. Wilson Bull 53:211-221.

Hatch, S. A. 1983. Nestling growth relationships of Brown-headed Cowbirds and Dickcissels. Wilson Bull. 95:669-671.

Hicks, L. E. 1934. A summary of cowbird host species in Ohio. Auk 51:385-386.

Hill, R. A. 1976. Host-parasite relationships of the Brown-headed Cowbird in a prairie habitat of west-central Kansas. Wilson Bull. 88:555-565.

Hofslund, P. B. 1957. Cowbird parasitism of the Northern Yellowthroat. Auk 74:42-48.

King, P. E. 1973. Some factors controlling egg laying in the parasitic cowbird (Molothrus ater). Am. Zool. 13:1259.

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

Long, J. L. 1981. Introduced birds of the world. Universe Books, New York.

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

Lowther, P. E. 1980. Gray Catbirds rear Brown-headed Cowbirds. Inland Bird Banding 52:29-30.

Lowther, P.E. 1983. Chickadee, Thrasher, and other cowbird hosts from Northwest Iowa. J. of Field Ornithol. 54:414-417.

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

Lowther, P. E., and R. F. Johnston. 1977. Influences of habitat on cowbird host selection. Bull. Kansas Ornithol. Soc. 28:36-40.

Mayfield, H. 1961. Vestiges of a proprietary interest in nests by the Brown-headed Cowbird parasitizing the Kirtland's Warbler. Auk 78:162-166.

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

Mayfield, H. 1977. Brown-headed Cowbird: agent of extermination? Am. Birds 31:107-113.

Mayr, E. 1976. Evolution and the diversity of life. Belknap Press. Cambridge, Mass.

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

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

Mengel, R. M., and M. A. Jenkinson. 1970. Parasitism by the Brown-headed Cowbird on a Brown Thrasher and a Catbird. Wilson Bull. 82:74-78.

Newman, G. A. 1970. Cowbird parasitism and nesting success of Lark Sparrows in southern Oklahoma. Wilson Bull. 82:304-309.

Nice, M.M. 1939. Observations on the behavior of a young cowbird. Wilson Bull. 51:233-239.

Nolan, V. Jr. 1963. Reproductive success of birds in a deciduous scrub habitat. Ecology 44:305-313.

Norman, R. F., and R. J. Robertson. 1975. Nest-searching behavior in the Brown-headed Cowbird. Auk 92:610-611.

Norris, R. L. 1947. The cowbirds of Preston Firth. Wilson Bull. 59:83-103.

Patterson, T. L., L. Petrinovich, and D. K. James. 1980. Reproductive value and appropriateness of response to predators by White-crowned sparrows. Behav. Ecol. Sociobiol. 7:227-231.

Payne, R. B. 1965. Clutch size and numbers of egg 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.

Putnam, L. S. 1949. The life history of the Cedar Waxwing. Wilson Bull. 61:141-182.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1-48.

Ricklefs, R. E. 1973. Ecology. Chiron Press. New York.

Robertson, R. J., and P. Blancher. 1982. Kingbird aggression: does it deter predation? Anim. Behav. 30:929-930.

Robertson, R. J., and R. F. Norman. 1976. Behavioral defences to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78:166-173.

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

Rothstein, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250-271.

Rothstein, S. I. 1975b. Evolutionary rates and host defences against avian brood parasitism. Am. Nat. 109:161-176.

Rothstein, S. I. 1976. Experiments on defences Cedar Waxwings use against cowbird parasitism. Auk 93:675-691.

Rothstein, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bull. 84:21-32.

Rothstein, S.I. 1978. Mechanisms of avian egg-recognition: additional evidence for learned components. Anim. Behav. 26:671-677.

Rothstein, S. I., J. Verner, and E. Stevens. 1984. Radio tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77-88.

Schrantz, F. C. 1943. Nest life of the eastern Yellow Warbler. Auk 60:367-387.

Scott, D. M. 1977. Cowbird parasitism on the Gray Catbird at London, Ontario. Auk 94:18-27.

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

Slack, R. D. 1976. Nest guarding behavior in male Gray Catbirds. Auk 93:292-300.

Smith, J. N. M. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. Condor 83:152-161.

Terrill, L. M. 1961. Cowbird hosts in southern Quebec. Can. F. Nat. 75:2-11.

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

Van Velzen, W. T. 1972. Distribution and abundance of the Brown-headed Cowbird. Jack Pine Warbler 50:110-113.

Verner, J., and L. V. Ritter. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk 100:355-368.

Walkinshaw, L. H. 1961. The effect of parasitism by the Brown-headed Cowbird on Epidonax flycatchers in Michigan. Auk 78:266-268.

Wittenberger, J. F. 1981. Animal Social Behavior. Duxbury Press. Boston.

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

Zar, J. H. 1974. Biostatistical analysis. Prentice Hall Inc. Englewood Cliffs, N.J.

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