Cowbird parasitism, predation, and host selection in fragmented grassland of southwestern Manitoba

by

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COWBIRD PARASITISM, PREDATION, AND HOST SELECTION

IN FRAGMENTED GRASSLAND OF SOUTHWESTERN MANITOBA

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A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

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ABSTRACT

The frequency of parasitism by Brown-headed Cowbirds (*Molothrus ater*) and predation on ground-nesting passerines was quantified in three fragments of grassland habitat in southwestern Manitoba. All bird species studied were parasitized by cowbirds but at different parasitism frequencies. Cowbird parasitism was higher (69% of nests examined) in the smaller (22-ha) plot compared with two 64-ha plots (17% and 20%, respectively). Of the nests parasitized in all plots, 69% were parasitized multiply with 2 to 8 eggs laid per nest. There was no difference among the plots with respect to the frequency of multiple parasitism. Western Meadowlarks were parasitized at a frequency of 44%, with an average of 3.1 cowbird eggs laid in each parasitized nest. Chestnut-collared Longspurs and Sprague's Pipits were parasitized at frequencies of 18% and 14%, respectively. Parasitized nests fledged significantly fewer young (0.95) than unparasitized (1.45) nests. Only parasitized Grasshopper Sparrow nests produced significantly fewer young than did unparasitized nests. Nesting success did not differ significantly between plots but nests in the smaller plot fledged significantly fewer young per nest than the other two plots. Exposed nests were more likely to be depredated than concealed nests.

Cowbirds parasitized more frequently hosts that nested at highest density on each plot but parasitism frequency did not decrease with declining density of hosts. The laying season of all hosts overlapped with the cowbirds' but late nesting longspurs and Savannah Sparrows were not parasitized. Concealed nests were more likely to be parasitized than exposed nests. Parasitism frequencies were significantly lower for nests located more than 150 m from a perch and/or 100 m from the habitat edge.

ACKNOWLEDGEMENTS

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General Introduction

Brown-headed Cowbirds (*Molothrus ater*) lay their eggs in the nests of other species of birds. The hosts in turn raise the cowbird offspring, often at considerable cost to their own productivity. Female cowbirds often remove or damage host egg(s) when they parasitize nests and cowbird nestlings sometimes outcompete host nestlings for food and space (Payne 1977). Historically, cowbirds were confined to the grasslands of central North America but during the last 150 years, after expanding their range and increasing their numbers due to deforestation and agriculture, cowbirds now range far beyond the grasslands (Mayfield 1965, Brittingham and Temple 1983). Much research has focused on how cowbird parasitism has affected the productivity of different hosts, but most of these studies have involved hosts nesting in forest-edge communities (e.g. Gates and Gysel 1978, Brittingham and Temple 1983). Few studies have occurred within the cowbird's original range (Wiens 1963, Hill 1976, Elliott 1978, Fleischer 1986), and no such study has been conducted on the Canadian prairies.

Cowbirds and their hosts in the grasslands presumably have coevolved so that potential hosts are less frequently parasitized than those encountered more recently in forested areas (Mayfield 1965). Recent studies, however, suggest that grassland birds are important hosts and that cowbirds lower their productivity. In Alberta, cowbirds parasitized Brewer's Sparrows (*Spizella breweri*) at a frequency of 52%, and the sparrows deserted 70% of the parasitized nests (Biermann et al. 1987). Maher (1973, p. 30) believed that cowbird parasitism is "potentially a serious source of mortality" in some areas of Saskatchewan. Elliott (1978) reported that 70% of the nests he found on a Kansas study site were parasitized, and most of these nests contained more than one

cowbird egg. Hill (1976) and Fleischer (1986) also reported high predation and parasitism frequencies on birds in prairie communities.

Nesting success of grassland birds is strongly influenced by the quality and quantity of the birds' habitat (Johnson and Temple 1986, 1990). Owens and Myres (1973) determined that different agricultural practices can change the existing avian community through incomplete disturbances such as haying and grazing, or eliminate the community (except for Horned Larks, *Eremophila alpestris*) by ploughing and cultivation. Agriculture and urbanization have reduced the prairies from a "sea" of grass to small, fragmented patches surrounded by woody vegetation, cultivation, roads and fences. Lowther and Johnston (1977) believed that this patchwork of vegetation probably is optimal habitat for cowbirds because it provides them with the perches they use to observe nest-building activities. This behaviour allows them to find nests and coordinate their egg laying with their hosts' (Norman and Robertson 1975, Gochfeld 1979, Lowther 1979, Thompson and Gottfried 1981). Results of Johnson and Temple's (1990) study are consistent with this hypothesis. They found that frequencies of parasitism (and predation) were greater in the smaller fragments of habitat, particularly at nests situated near the edges of such woodlands (see Gates and Gysel 1978)

To reproduce successfully, cowbirds must locate, select, and monitor many potential host nests (Briskie et. al. 1990). Some birds may be inappropriate hosts because they are uneconomical to parasitize due to high searching costs. Consequently, nest concealment and host abundance may be important determinants of which hosts are parasitized (Wiley 1988, Briskie et. al. 1990). Wiley (1988) hypothesized that well-

concealed nests should be parasitized less frequently than exposed nests because cowbirds probably have more difficulty locating them. Although several studies have examined the effects of nest concealment on predation rates (McLean et al. 1986, Bientema and Muskens 1987, Sugden 1987), few studies have examined the role of nest concealment with respect to parasitism (Briskie et al. 1990). Another important factor in determining which hosts are parasitized by cowbirds may be host abundance. Do cowbirds parasitize those hosts that nest at the greatest densities? The results have been equivocal. For example, Wiley (1988) found no relationship between parasitism frequency and host density, but Zimmerman (1983) and Freeman et. al. (1990) reported that frequency (i.e. percentage of nests parasitized) and intensity (i.e. percentage of nests parasitized more than once) of parasitism were inversely related to host nest density. Fleischer (1986), on the other hand, stated that parasitism was related to cowbird density, not host density.

Cowbirds may reduce searching costs by observing host activity from perches (Thompson and Gottfried 1981). Female cowbirds may use perches to find nests and coordinate their egg laying with their hosts', by observing nest-building activities (Norman and Robertson 1975, Gochfeld 1979, Lowther 1979, Thompson and Gottfried 1981). Few studies have attempted to quantify the relationship between cowbird parasitism and the availability of perches (but see Gochfeld 1979).

Host responses to parasitism may also influence host selection. Some birds eject foreign eggs deposited in their nests and others strongly defend their nests against parasitism making them poor-quality hosts (e.g. Rothstein 1975, 1977, 1982, Robertson and Norman 1976, Neudorf and Sealy 1992, Bazin and Sealy 1993). On the other hand,

some species that accept cowbird eggs may be unsuitable hosts because of diet constraints or inappropriate laying season (e.g. Middleton 1977; Carey 1982).

The objectives of the present study were to quantify the frequency and intensity of cowbird parasitism on hosts in three fragments of grassland habitat in southwestern Manitoba. Chapter 1 compares the frequency of parasitism and predation in habitat patches of different size to quantify the effects fragmentation has on breeding grassland birds. Because Manitoba offers no continuous unfragmented tract of grassland to use as a control, comparisons are drawn from the literature. The second chapter examines factors that may influence host selection such as host breeding density, laying chronology, nest concealment, and perch distance.

CHAPTER 1

COWBIRD PARASITISM AND PREDATION

INTRODUCTION

Historically, Brown-headed Cowbirds were restricted to the Great Plains of North America, but agriculture and deforestation have allowed them to expand their range and increase their numbers (Brittingham and Temple 1983). The resulting fragmentation of habitats has promoted changes that complement the cowbirds' requirements. Mayfield (1965) suggested that grassland hosts have coevolved with cowbirds and are thus parasitized less than host species of the eastern forests that have experienced little cowbird parasitism. Friedmann's (1963) examination of old nest records of many grassland birds supports this view as they contain few records of parasitism. However, recent studies of grassland birds reveal that cowbirds frequently use these species as hosts, and may have a detrimental effect on their nesting success (Hill 1976, Elliott 1978, Zimmerman 1983, Fleischer 1986). The first objective of this study was to determine the overall parasitism frequencies of birds in fragmented grassland of southwestern Manitoba. As the frequency of cowbird parasitism is greater near a habitat edge (Gates and Gysel 1978), I predicted that parasitism would be more frequent in smaller patches of grassland habitat due to the increased edge effect caused by the fragmentation (Temple 1986).

Ricklefs (1969) stated that predation was the major cause of nesting mortality in many habitats. Indeed, predation has been reported to cause the failure of approximately 30% to 75% of nests of several grassland bird species (e.g. Lanyon 1957, Newman 1970, Elliott 1978, Knapton 1978, Wray et al. 1982). One factor that may be involved in high

predation rates in grasslands is the drastic change the prairies have undergone in the past 150 years. Where there used to be continuous expanses of prairie, there now exists a mosaic of fragmented "islands" of grasslands in which the native flora and fauna must survive (Owens and Myres 1973). As predator activity is greater along the habitat edge, and since the relative amount of edge increases as habitat size decreases, it has been hypothesized that predation rate is inversely related to habitat size (Gates and Gysel 1978, Angelstam 1986). Gates and Gysel (1978) recorded a negative correlation between the production of young and distance to the habitat discontinuity, and Wilcove (1985) found that predation rates were higher in smaller woodlots (see also Temple and Carey 1988). Forest edge may also provide avian predators with perches from which they may locate prey (e.g. Preston 1957). Thus, I hypothesized that the frequency of predation on grassland birds increases as the size of the habitat decreases. A prediction from this hypothesis is that nests placed closer to the habitat edge, and hence to available perches, are more likely to be preyed upon than those located farther away.

Much research has focused on the effect of cover, or concealment, on nest predation (Colwell 1992; see review in Clarke and Nudds 1991). Clarke and Nudds (1991) found that 47% of the studies they reviewed showed that nest concealment did not influence nest success. However, once they grouped the studies according to whether the predators were birds or mammals, they found a correlation between nest concealment and nest success. Concealment influenced nest success where avian predators were involved, but it was less important when the predators were mammals, or when birds and mammals were involved. As the grasslands in southwestern Manitoba support a variety of

predators, I predicted that nest concealment should not influence predation. The role of nest concealment with respect to cowbird parasitism is discussed in Chapter 2.

METHODS

Study Sites

Research was conducted from 6 May to 17 August 1991 and 1 May to 25 August 1992, on three plots of grassland habitat in southwestern Manitoba (Fig. 1). Plot-1 (NE 22-5-27) was a 64-ha patch of idle hayland in the Broomhill Wildlife Management Area. This plot was periodically hayed in the fall, the last time in 1990. Plot-2 (SE29-6-26) was a 64-ha private pasture, gently rolling with numerous depressions. Elevated areas were extensively grazed by cattle. Plot-3 (NE25-1-29) was a 22-ha strip of native grassland surrounded by crop and rangeland.

Plots were staked out with labelled flagged pins to produce a 50-m grid system and fence lines were used to guide the initiation of the grid. Subsequent lines were kept straight by visual estimation, aided by two people at opposite ends of the plot. Markers were kept at approximately the same height as the vegetation throughout the field season to avoid possibly creating artificial perches.

Vegetation

Vegetation was analyzed in the third week of June, 1992, using the line-intercept method (Cox 1967). Plots-1 and -2 were divided into four equal sections and sampled with four 25-m lines in directions chosen at random. Sampling lines in plot-3 were chosen at random by selecting points along a transect line running through the middle of the plot. For all plots, line intervals were 25 cm long and sampled at every quarter-, and
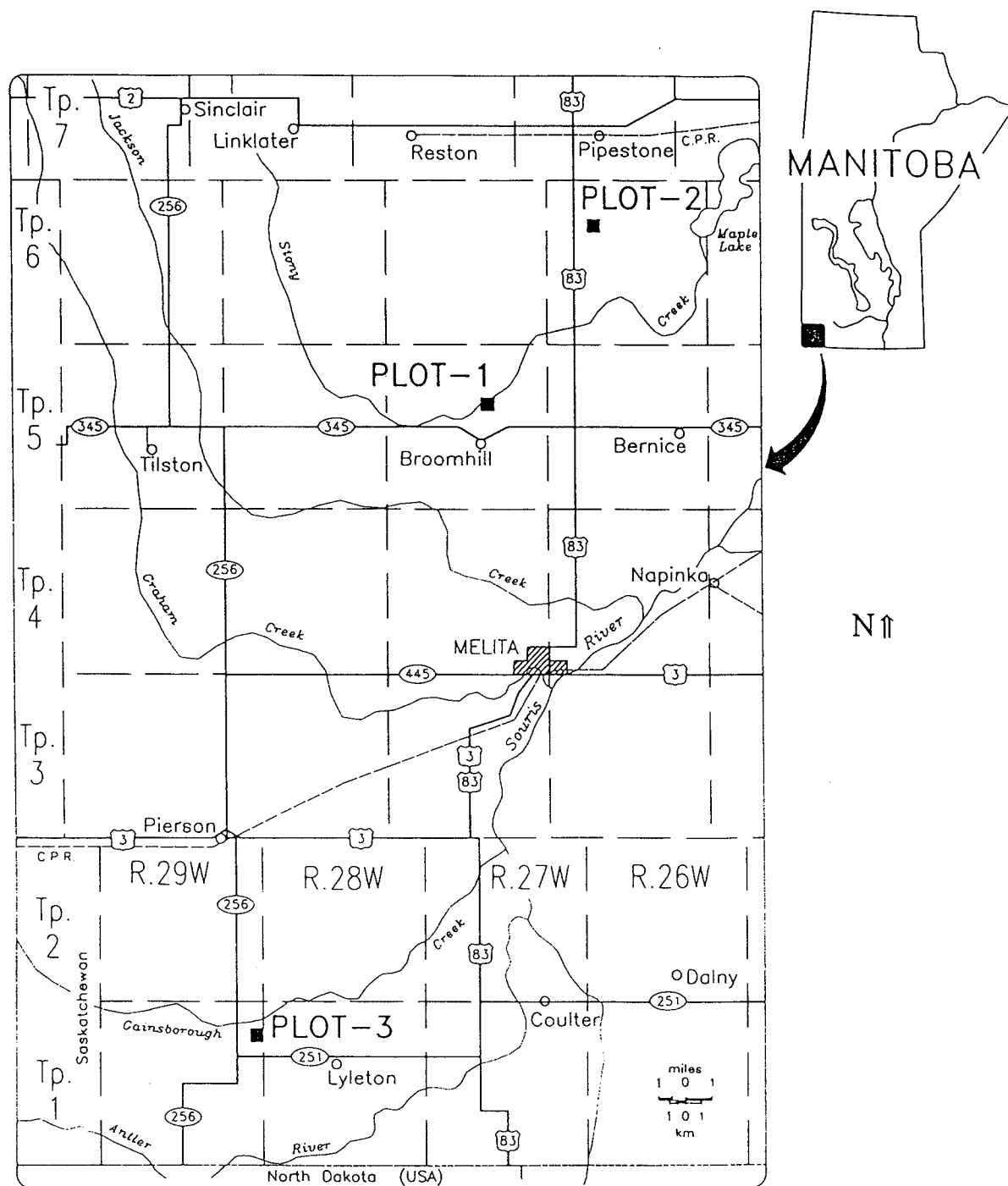
Figure 1. Location of three study plots in southwestern Manitoba. Outlined portion of provincial map represents the area encompassed in the exploded view.

three quarter-meter mark, resulting in 50 sampling points per transect line. Effective

vegetation height was measured at every 1-m interval. Cover and frequency values were

computed using equations in Cox (1967).

Nest Success

Females were flushed from their nests when my assistant and I dragged nesting

habitat with a 30-m nylon rope to which aluminum cans were attached every 0.5 m.

Each nest was marked with a small flag 5 m away in line with the nearest grid point, and

inspected nests every 2-4 days until fledging or until the nesting attempt was terminated.

Cues used to identify successful nests included nearly fledged nestlings, minimal nest

disturbance, and the presence of a nearby adult uttering alarm calls. Nests that fledged at

least one young (cowbird or host) were considered successful whereas failed nests were

unsuccessful but not depredated. Nest success was evaluated for each species by

examining the proportion of successful and unsuccessful nests and by using Mayfield's

(1975) method of nest success (computer program in Krebs 1992). The Mayfield method

calculates daily survival rates for each species based on the length of time the nests were

under observation (Mayfield 1975, Bart and Robson 1982). The nesting cycle was

divided into incubation and nestling stages. The incubation stage was analyzed using the

"egg-day" as the unit of exposure. Thus a nest containing five eggs over two days of

observation equals 10 egg-days. The nestling stage was analyzed similarly. The

probability of a nest fledging at least one young equals the product of the survival rates

of the incubation and nestling periods. Each plot was analyzed separately to identify

differences in nest success in different plots. Data was grouped together when no

significant differences were observed between plots and years.

Perch and Habitat Edge Distance

Nearest perch distances (m) from each nest were measured using a Rollo-tape, and recorded perch type (e.g. fence, shrub, etc.) after each nest was terminated. Only perches greater than 1 m in height were included (Gochfeld 1979). Habitat-edge distances were measured from the nest to the boundary of the study plot where the nearest change in land use occurred (e.g. road, cultivated field, etc.).

Nest Concealment

In 1992, nest concealment was quantified using a modified version of Holway's (1991) method. Two circular, egg-white pieces of plastic divided into 8 equal sections were placed alternatively into each nest. One disc representing a "general" size (8 cm) and another disc of "species-specific" diameter was also placed into each respective nest (sparrows and longspurs=6.5 cm; pipits, Lark Buntings and Bobolinks=8 cm; meadowlarks=11.5 cm). The number of sections visible to me were recorded while standing 1 m away at four points (north, south, east and west) and from overhead. Concealment values would thus range from 0 (concealed) to 40 (exposed). Nest concealment was measured on sunny days, 5-6 hours after sunrise because this is the time that cowbirds are believed to search for nests (Mayfield 1961, Rothstein et al. 1984).

Statistical Analyses

One-way ANOVA was used to determine whether the mean number of cowbird eggs laid differed between years and plots. If one-way ANOVA tests resulted in a significant difference, the data was analyzed further with Duncan's Multiple Comparison

Procedure to determine where the significant differences occurred. To ensure adequate sample sizes, nest-concealment values were divided into four groups of 10 and Chi-square contingency tables were used to determine if nest concealment influenced predation frequencies. Chi-square contingency tables were used to examine the influence of perch distance and distance to the habitat edge on the frequency of predation. Perch distances was divided into four categories (0-50, 50-100, 100-150, and 150+ m) and identified significant differences in the proportion of depredated and successful nests in each distance category. The analysis was similar for habitat edge distances. Wilcoxon Rank Sum Test was used to determine whether a significant difference was observed between concealment and predation frequency for each species. Means are given along with ($\pm$) standard error. Significance level was set at p=0.05.

RESULTS

Vegetation

Litter was the most prominent cover type on plot-1 whereas standing dead vegetation covered a greater area in plots-2 and -3. (Appendix I). Awnless brome grass (*Bromus inermis*) was the most common grass present on plot-1. Porcupine grass (*Stipa spartea*), bluegrass (*Poa* spp.) and june grass (*Koeleria cristata*) were present in all three sites. Quack grass (*Agropyron repens*) and northern reed grass, (*Calamagrostis inexpansa*) were relatively abundant only on plot-2 while mat muhly (*Muhlenbergia richardsonis*) and blue grama (*Bouteloa gracilis*) were two of the more common grasses on plot-3 (Appendix I). Although vegetation was not analyzed in 1991, sweet clover

(*Melilotus officianalis*) on plot-1 was noticeably more abundant in 1992. Sweet clover occurred in patches throughout the north part of that plot. Shrubs were scarce on plots-1 and -2 but plot-3 was bordered by large patches of wolf willow (*Eleagnus commutata*), western snowberry (*Symphoricarpos occidentalis*), and willow (*Salix* spp.).

Vegetation height in plot-1 was not significantly different among subplots ($F_{df=2}$=1.36, p=0.2473), but vegetation height differed significantly among subplots in plots-2 and-3 ($F_{df=2}$=20.46, p<0.0001 and $F_{df=2}$=20.39, p<0.0001, respectively). One transect bisected a dug-out in plot-2 causing this subplot to differ significantly from the other subplots (Duncan's Multiple Comparison Procedure, p<0.05). Vegetation was more heterogeneous in plot-3 as only two of four subplots were similar in height (Duncan's Multiple Comparison Procedure, p>0.05). Mean vegetation height was significantly different between plots ($F_{df=2}$=63.26, p<0.0001). Vegetation height was lower in plot-1 (28.6 cm) compared to plots-2 (38.8 cm) and -3 (39.1 cm) (Duncan's Multiple Comparison Procedure, p<0.05).

Avian Community

The composition of the avian communities in the three plots was similar. Baird's Sparrow (*Ammodramus bairdii*), Grasshopper Sparrow (*Ammodramus savannarum*), Savannah Sparrow (*Passerculus sandwichensis*), Spragues' Pipit (*Anthus spragueii*), Bobolink (*Dolichonyx oryzivorus*), Brown-headed Cowbird, and Western Meadowlark (*Sturnella neglecta*) laid eggs in all plots in 1991 and 1992. Chestnut-collared Longspurs (*Calcarius ornata*) nested in all plots in 1991, but were absent from plot-3 in 1992. Lark Buntings (*Calamospiza melanocorys*) nested in plot-3 in 1992.

Frequency of Parasitism

Parasitism frequencies did not differ significantly between years in plots-1 and -2 ($X^2_{df=1}=1.184$, p=0.277 and $X^2_{df=1}=0.096$, p=0.728, respectively) or between the plots ($X^2_{df=1}=0.240$, p>0.05) (Table 1). Parasitism frequency increased significantly from 53% (1991) to 80% (1992) for nests in plot-3 ($X^2_{df=1}=6.878$, p=0.009). The frequency of multiple parasitism was greater in plot-3 but the difference was not significant among the plots (Table 1). The number of cowbirds fledged per parasitized nest (Table 1) and the proportion of cowbirds fledged from eggs laid ($X^2_{df=2}=0.000$, p>0.05) did not differ between plots (Table 2).

More parasitized nests were present in plot-3 than plots-1 and -2 combined (Table 2). The average number of cowbird eggs laid per nest was slightly higher for plot-2 compared with plot-1, but lower than plot-3 (Table 2). One-way ANOVA showed that there was a significant difference between plots with respect to the average number of cowbird eggs laid per parasitized host nest ($F_{df=2}=4.37$, p=0.015). The number of cowbird eggs laid per parasitized nest was significantly higher in plot-3 than plot-1 (Duncan's multiple comparison procedure, p<0.05), but was not different from plot-2 (Duncan's multiple comparison procedure, p>0.05). Cowbirds consistently laid more eggs in Western Meadowlark nests than any other species, whereas Chestnut-collared Longspurs were parasitized with a lower intensity than the other species (Table 2). The three sparrow species fledged the greatest percentage of cowbirds, while Bobolinks and Lark Buntings raised only young of their own (Table 2).

Parasitized and unparasitized nests did not differ significantly among plots with

Table 1. Productivity and frequency of parasitism in a grassland community at three study sites in southwestern Manitoba, 1991 and 1992. Numbers separated by a comma indicates values for 1991 and 1992, respectively, as between-year differences were significant.

Parameter	Plot 1	Plot 2	Plot 3	P value	Plots Combined
Number of nests	115	100	83	-	298
% Successful	47	43	42	0.742^1	44
% Depredated	49	47	53	0.640^1	49
% Deserted	0	3	5	0.079^1	2
% Failed	4	7	0	0.037^2	4
Host young fledged (HYF)/nest	1.5	1.3	0.9	0.043^3	1.3
HYF/successful nest	3.3	3.0	2.7	0.112^3	3.1
% Parasitized	17	20	53,80	-	32
% Multiple parasitism	60	60	76	0.232^1	69
Cowbirds fledged/parasitized nest	0.3	0.3	0.5	0.787^3	0.4

[1] $= X^2_{df=2}$
[2] $=$ Fisher's exact test
[3] $=$ 1-way ANOVA

Table 2. Mean number (±SE) of cowbird eggs laid in parasitized nests and respective cowbird productivity, 1991 and 1992.

	# Parasitized nests	# Cowbird eggs laid/nest (±SE)	% Cowbirds fledged from eggs laid (n)[1]
Plot-1	20	1.6 (±0.15)	22 (32)
Plot-2	20	2.1 (±0.28)	16 (43)
Plot-3	54	2.6 (±0.21)	18 (145)
Sprague's Pipit	3	2.7 (±0.33)	12 (8)
Lark Bunting[2]	6	2.5 (±0.43)	0 (15)
Savannah Sparrow	10	2.1 (±0.31)	29 (21)
Baird's Sparrow	24	2.0 (±0.18)	23 (48)
Grasshopper Sparrow	13	2.0 (±0.20)	23 (26)
Chestnut-collared Longspur	8	1.4 (±0.16)	9 (11)
Bobolink[2]	3	1.7 (±0.67)	0 (5)
Western Meadowlark	28	3.1 (±0.38)	17 (86)

[1]Number of cowbird eggs laid.
[2]Values for 1992 nests only.

respect to the proportion that were successful ($X^2_{df=2}$=1.282 and 1.56, respectively,

p>0.05), depredated ($X^2_{df=2}$=0.071, and 0.534, respectively, p>0.05), deserted

($X^2_{df=2}$=0.873, and 3.685, p>0.05), and failed ($X^2_{df=2}$=5.974 and 0.389, respectively,

p>0.05). Parasitized and unparasitized nests did not differ significantly with respect to

their frequencies of success, depredation, desertion, or failure when the data were pooled

(Table 3). The number of host young fledged from parasitized and successful parasitized

(fledged at least one host young) nests was significantly lower than from unparasitized

nests (Table 3). Cowbirds cost Savannah and Grasshopper sparrows 1.1 and 1.3 young,

respectively, per successful nest, but the impact of parasitism was negligible for the other

host species (Table 4). Nesting success, frequency of parasitism and predation, and

productivity for each species are presented in Appendix IIa-h.

Nest Success

Nesting success was similar in the three study plots, with significant differences

between plots detected for only two of the nine parameters (Table 1). Fewer nests in

plot-3 failed compared with plots-1 and -2 (Table 1). Nests in plot-3 fledged fewer host

young per nest than plot-1, but no difference was found between plots-1 and -2, and

plots-2 and -3 (Duncan's Multiple Comparison Procedure, p>0.05) (Table 1).

Survival rates tended to be higher during the incubation stage for Sprague's Pipit,

Lark Bunting, Savannah Sparrow, Baird's Sparrow, and Chestnut-collared Longspur,

whereas Grasshopper Sparrow, Western Meadowlark and Bobolink had lower survival

rates during the incubation period than the nestling period (Appendix III).

Table 3. Nesting success in parasitized and unparasitized nests, 1991 and 1992.

	Parasitized Nests	Unparasitized Nests	Statistical Results
Number of Nests	84	198	-
% Successful	44	45	$X^2_{df=1}=0.51$, $p=0.82$
% Depredated	48	50	$X^2_{df=1}=0.14$, $p=0.70$
% Deserted	2	2	$p=0.81$[1]
%Failed	5	3	$p=0.89$[1]
Host Young Fledged (HYF)/Nest	0.95	1.45	$F_{df=1}=5.50$, $p=0.02$
HYF/Successful Nest	2.59	3.23	$F_{df=1}=6.61$, $p=0.01$

[1] = Fisher's exact test

Table 4. Comparison of host productivity in parasitized and unparasitized nests, 1991 and 1992.

Species	Hosts fledged/ unparasitized nest	Hosts fledged/ parasitized nest	1-way ANOVA (df=1)	Hosts fledged/ successful unparasitized nest	Hosts fledged/ successful parasitized nest	1-way ANOVA (df=1)
SPPI	1.15	0.00	F=1.77, p=0.21	2.50	-	-
LARB	0.00	1.17	F=0.35, p=0.58	-	3.50	-
SAVS	1.05	0.40	F=1.67, p=0.21	2.44	1.33	F=1.87, p=0.20
BAIS	1.51	1.26	F=0.31, p=0.58	2.50	2.42	F=3.21, p=0.08
GRSP	2.03	0.92	F=3.23, p=0.08	3.72	2.40	F=5.79, p=0.02*
CCLO	1.53	1.75	F=0.09, p=0.77	3.45	3.50	F=0.01, p=0.93
BOBO	1.33	1.33	F=0.00, p=1.00	4.00	4.00	F=0.00, p=1.00
WEME	1.14	0.67	F=1.45, p=0.23	3.00	2.57	F=0.49, p=0.48

* = Significant result
SPPI = Sprague's Pipit
LARB = Lark Bunting
SAVS = Savannah Sparrow
BAIS = Baird's Sparrow
GRSP = Grasshopper Sparrow
CCLO = Chestnut-collared Longspur
BOBO = Bobolink
WEME = Western Meadowlark

Perch and Habitat Edge Distance

Predation frequency was not significantly different for nests located under 50m

(51%) from the nearest perch compared with nests located between 50m and 100m (40%)

($X^2_{df=1}$=2.37, p=0.126). Nests located between 100m and 150m (74%) were depredated

more frequently than nests located under 100m (49%) from the nearest perch

($X^2_{df=1}$=4.45, p=0.035). The frequency of nest predation decreased significantly with

increased distance from the habitat edge ($X^2_{df=3}$=10.87, p=0.012).

Nest Concealment

The frequency of predation was significantly greater for exposed compared with

well-hidden nests ($X^2_{df=3}$=8.019, p=0.046) (Fig. 2.). No correlation was found between

nest concealment and predation for individual species in the community (Table 5).

DISCUSSION

Frequency of Parasitism

Cowbirds parasitized 32% of the nests inspected on the three grassland plots in

southwestern Manitoba (Table 1). Other workers have recorded similar parasitism

frequencies in grassland habitats, but they did not provide the area of the sites involved

(Hergenrader 1962, Wiens 1963, Hill 1976, Fleischer 1986). Elliott (1978) reported a

higher parasitism frequency (70%) on ground-nesting species in Kansas, a value similar

to that found on plot-3 (Table 1). The high frequency of multiple parasitism I recorded

(70%) was similar to that recorded for grassland hosts elsewhere (e.g., Hergenrader

1962, Elliott 1978). This contrasts with Mayfield's (1965) statement that grassland hosts

are infrequently parasitized by cowbirds compared to forest-dwelling hosts. Comparing
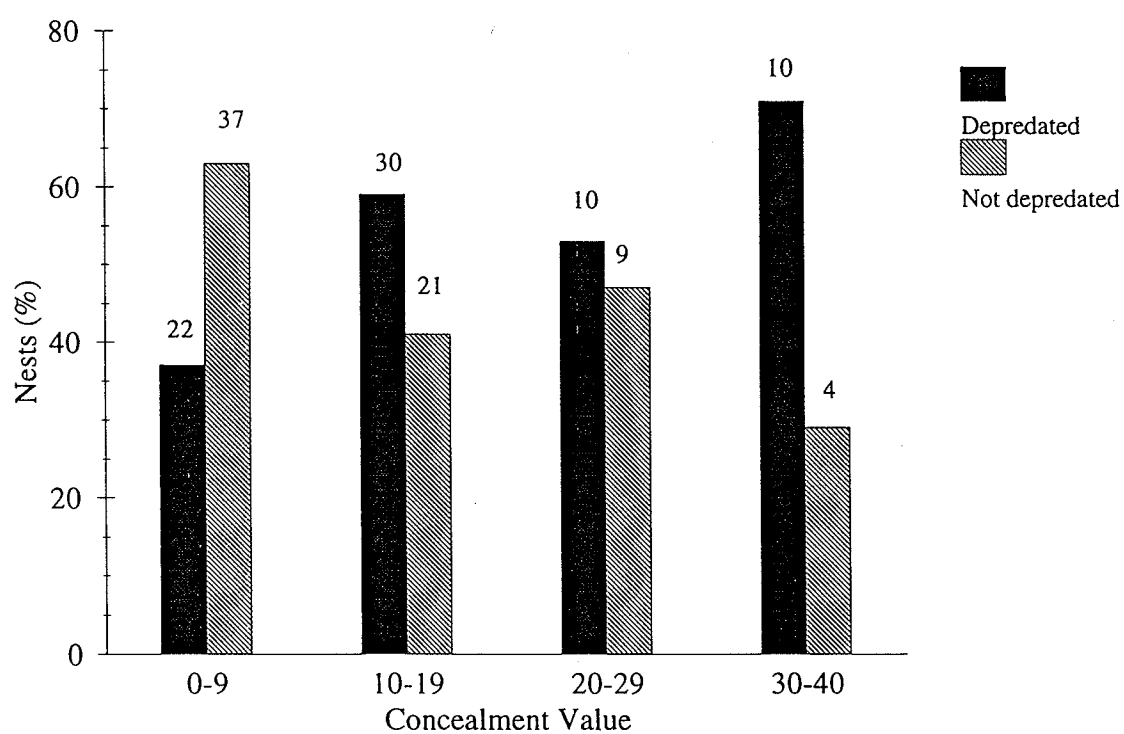
Figure 2. Frequency of predation on concealed and exposed nests, 1992. Sample size given as number above each bar.

Table 5. Results of statistical tests to determine whether a significant correlation
exists between nest concealment and predation frequency for 7 grassland hosts.

Species	Wilcoxon rank sum and P-value
Sprague's Pipit	$Z_{df=1}=0.000$, p=0.999 (7)[1]
Savannah Sparrow	$Z_{df=1}=-0.178$, p=0.859 (15)
Baird's Sparrow	$Z_{df=1}=1.767$, p=0.077 (33)
Grasshopper Sparrow	$Z_{df=1}=-0.262$, p=0.793 (15)
Chestnut-collared Longspur	$Z_{df=1}=0.839$, p=0.401 (26)
Bobolink	$Z_{df=1}=0.000$, p=0.999 (6)
Western Meadowlark	$Z_{df=1}=-0.647$, p=0.518 (38)

[1] Parentheses indicate number of nests at which concealment was quantified.

parasitism frequencies with these past studies is difficult as they provided little information concerning the size, shape, and extent of habitat fragmentation of their study areas. Do these studies reflect historic parasitism frequencies found in contiguous grassland habitat, or is the extent of habitat fragmentation in those areas comparable to southwestern Manitoba? This information is necessary to compare the effects of habitat fragmentation on parasitism frequencies. The high parasitism frequencies in this study suggest that the hosts are acceptors and most appear not to have developed anti-parasitic strategies. However, other studies have reported low parasitism frequencies for grassland hosts (see Friedmann 1963, Southern and Southern 1980). Thus parasitism frequency may vary geographically depending on habitat type, cowbird density and other host selection factors (Fleischer 1986, Briskie et. al. 1990, see Chapter 2 of present study). The low parasitism frequencies reported by Friedmann (1963) for the species in this study may reflect the relatively small number of nests of these species found in earlier studies (Mayfield 1965, Friedmann and Kiff 1985).

The high rates of multiple parasitism found in this study and others (Hergenrader 1962, Elliott 1978, Hoover and Brittingham 1993), may reflect a high female cowbird density relative to that of host nests (McGeen 1972), and the subsequent inability of cowbirds to locate enough different nests to parasitize. This may force cowbirds to lay eggs in nests already parasitized. McGeen (1972) developed an index to determine the pressure on a host species from cowbird parasitism (% parasitism + % multiple parasitism/2). This index depends on and reflects cowbird density with respect to available host nests (McGeen 1972). Plot-3 had a higher pressure index value (72.5) than

plots-1 and -2 (38.5 and 40.0, respectively) and a greater density of cowbirds (see Chapter 2). Apparently there were more cowbirds per available host nest in plot-3 than the other plots, which resulted in more nests being multiply parasitized (see Hoover and Brittingham 1990).

The inability of cowbirds to locate enough suitable host nests may also be reflected by the large number of inappropriately laid eggs. Of the 183 cowbird eggs laid in this study, 42 (23%) were laid after the hosts had completed their clutches. Most of these eggs were laid during the incubation stage (79%) but 11% were laid during the nestling stage and 9% after the nest was terminated. Freeman et al. (1990) reported that cowbirds laid more than 20% of their eggs in inactive Red-winged Blackbird (*Agelaius phoeniceus*) nests. These authors attributed the inappropriate layings to the lack of available perches which cowbirds could use to gain better information on the status of nests. Perch sites were relatively common on the study plots, particularly plot-3 (see Chapter 2). Another explanation for the relatively high number of inappropriately laid eggs may be due to the relatively long incubation period of hosts (12-14 days) in this study. Because cowbirds may require only 10 days for their eggs to be sufficiently incubated (Briskie and Sealy 1990), laying during the first few days of the hosts' incubation period (especially meadowlarks) would still allow cowbirds to hatch successfully.

Plot-3 differed from the other plots not only in size but also in the amount of shrub cover present (Appendix IIc). Plot-3 was especially attractive to cowbirds (see Chapter 2) as shrubs bordered nearly the entire plot providing perches for social displays

and nest searching. The results of the present study support Brittingham and Temple's (1983) suggestion that increased habitat fragmentation leads to higher cowbird densities and subsequent higher frequency and intensity of parasitism. These authors believed that fragmentation increased the amount of habitat that was available for cowbirds to use for locating host nests. Because cowbirds generally stay within 100 m of forest edges (Brittingham and Temple 1983, but see O'Connor and Faaborg 1992), forest fragmentation allows them to penetrate small patches that makes more hosts susceptible to parasitism. Fragmentation of grasslands apparently leads to the same results because cowbirds concentrate their activities near the habitat edge and are seldom seen within the interior of the grassland (Gates and Gysel 1978). In fact, Robinson et. al. (1992) stated that for reducing the impact of cowbirds on host populations, large continuous tracts of habitat are preferable to smaller tracts, and that habitat that is simple in shape is preferable to irregular shapes with more edge. The results of the present study support this claim. Plots-1 and -2 were larger, square tracts of habitat compared to the irregular, finger-like shape of the smaller plot-3. Cowbirds parasitized nests in plot-3 at a frequency of 69%, more than three times that found on the other two plots (Table 1).

Nest Concealment

Many studies have examined the effect of nest concealment on predation with results that appear to be equivocal (Clarke and Nudds 1991). Clarke and Nudds (1991) grouped nest-concealment studies according to principal predators (i.e. bird or mammal) and discovered that the importance of nest concealment depended on the predator involved. In the present study, exposed nests were more likely to be preyed upon than

well hidden-nests. This suggests that the predator community was probably dominated by animals using vision (i.e. birds) as the primary mode for locating prey. American Crows (*Corvus brachyrhyncos*) and Black-billed Magpies (*Pica pica*) were common in the area, and crows nested on one of the study sites. These birds are common nest predators which find exposed prey more readily than well concealed prey (Jones and Hungerford 1972, Sugden and Beyersbergen 1986, Sugden 1987), and effectively cue in on nest markers (Picozzi 1975). However, I did not observe these birds depredating nests during the study. Western Meadowlarks may also be an important cause of nest failure. Creighton and Porter (1974) reported nest destruction on Horned Lark and suggested this behaviour may be a form of predation or a means by which meadowlarks promote spatial and temporal segregation of ecologically similar species (see also Schaeff and Picman 1988).

Nesting Success

Nesting success of the grassland bird community in southwestern Manitoba was similar among the three plots (Table 1). I predicted that predation rates would be inversely related to the size of the habitat due to increased relative amount of habitat edge (Angelstam 1988). Indeed, several studies have shown that predation is greater in smaller habitat fragments (Nelson and Duebbert 1974, Gates and Gysel 1978, Wilcove 1985). As plot-3 was narrow, elongate, and irregular in shape the amount of edge was increased compared with plots-1 and -2, yet predation rates were not significantly different among the plots (Table 1). However, predation frequency was greater for nests situated closer to the habitat edge. Gates and Gysel (1978) attributed a decrease in nest

predation with increasing distance from a wooded edge to a functional response by predators to higher nest densities and the greater activity of predators near the edge. The plots in this study were bordered by shrub patches (plot-3), road, crop and/or hayland. Nest predators may prefer areas with extensive cover along the edge because many of them are potential prey to other animals and thus, may reduce their activity in open areas where escape cover is sparse (Johnson and Temple 1990). Fritzell (1978), for example, found that in prairie habitat, Raccoons (*Procyon lotor*) used shelterbelts as travel lanes. Thus each plot in the present study may have been equally attractive to nest predators as there was no forest edge along which predators could concentrate their activities. Another reason that predation frequency did not differ between plots may be that the 64 ha plots (plots-1 and -2) did not differ enough in size from plot-3 to permit relationships to be detected between habitat fragmentation and predation frequency. Johnson and Temple (1990), for example, found that predation rates were lower on nests located in tallgrass prairie fragments larger than 130 ha.

The combination of high predation and parasitism frequencies greatly affected the productivity of birds in the grassland community of southwestern Manitoba. Hosts suffered predation frequencies of 50% (Table 1) and parasitism frequencies upward to 100%, with many nests multiply parasitized (see Appendix II). However, the impact of parasitism and predation on the community was difficult to assess because information on the number of nesting attempts was lacking (see Smith 1981). Parasitism appeared to reduce the productivity of hosts in plot-3 as these hosts were parasitized more frequently and fledged significantly fewer young than on the other plots even though predation

frequency was similar among plots. Cowbird parasitism affected host productivity for the following reasons: (1) female cowbirds remove host eggs prior to laying their own (Sealy 1992), (2) cowbird egg shells are thick, and when laid, may break those of the host (Hofslund 1957, Weatherhead 1991), (3) cowbirds have a short incubation period giving young cowbirds a competitive advantage (Briskie and Sealy 1990); and (4) cowbirds usually parasitize hosts smaller than themselves (except for Western Meadowlarks in the present study) increasing the competitive advantage to young cowbirds. As a result of these factors, some nests fledged only cowbird young (four nests of Baird's Sparrow and one each of Savannah Sparrow, Sprague's Pipit and Western Meadowlark). Overall, cowbirds cost hosts in this study an average of 0.64 young per parasitized nest (Table 2), which is lower than in several other studies (Hill 1976, Elliott 1978, Trail and Baptista 1993). Cowbirds usually outcompete host young for space and food and impede the growth of the host nestlings (Smith 1981). However, grasslands are characterized by high primary production that is produced in a relatively short time. The resulting superabundance of food (Maher 1979, Weins 1974) may have allowed hosts in this study to feed more effectively their own young along with cowbirds, and thus reduce the cost of parasitism.

Trail and Baptista (1993) calculated that Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) cannot maintain their numbers at parasitism frequencies greater than 20%. Cowbirds have been implicated as a major factor in the population decline of several bird species including Kirtland's Warbler (*Dendroica kirtlandii*), and the extirpation of others (Robinson et.al. 1992). However, there has been little evidence

to justify implicating cowbirds as the reason for certain species' decline (Holmes 1993, see Bohning-Gaese et. al. 1993). Some species are more vulnerable to the negative effects of parasitism than others as their numbers have been reduced because of previous, and continuing factors, such as habitat loss on breeding and wintering grounds, for example (see Bohning-Gaese et al. 1993).

Robinson et. al. (1992) stated that hosts with a limited distribution and neotropical migrants are especially vulnerable to the effects of parasitism. Sprague's Pipit, Baird's Sparrow, Grasshopper Sparrow and Chestnut-collared Longspur are at the northern edge of their breeding range and their distribution in Manitoba has been reduced to a fraction of its former size (Godfrey 1986). Because these species are acceptors, they may be particularly vulnerable to increased parasitism frequencies. Although the host species in this study have been associated with cowbirds over a long time, anti-parasitic strategies do not seem to have evolved. In the past, grassland birds may have experienced low parasitism frequencies because of the large, unfragmented expanse of prairie habitat. Habitat fragmentation not only allowed cowbirds to expand their range and numbers (Brittingham and Temple 1983, Robinson et.al. 1992) but it allowed them to use grassland hosts that historically may have been inaccessible.

SUMMARY

1. Cowbirds parasitized 32% of the nests inspected in southwestern Manitoba.

2. All bird species were parasitized by cowbirds but at different frequencies.

3. Western Meadowlarks were parasitized at a frequency of 44%, with an average of 3.1 cowbird eggs laid in each parasitized nest. Chestnut-collared Longspurs and Sprague's

Pipits were parasitized at frequencies of 18% and 14%, respectively.

4. Cowbird parasitism was higher (69% of nests examined) in the smaller (22-ha) plot compared with two 64-ha plots (17% and 20%, respectively).

5. Of the nests parasitized in all plots, 69% were parasitized multiply with 2 to 8 eggs laid per nest. There was no difference among the plots with respect to the frequency of multiple parasitism.

6. Parasitized nests fledged significantly fewer young than unparasitized nests.

7. Cowbirds cost hosts an average of 0.64 young per parasitized nest. Parasitized Grasshopper Sparrow nests produced significantly fewer young than unparasitized nests.

8. Nesting success did not differ significantly between plots but nests in plot-3 fledged significantly fewer young per nest than the other two plots.

9. Predation frequency was significantly higher in exposed, compared with well-concealed nests.

10. Predation frequency declined significantly with increased distance to the habitat edge.

CHAPTER 2

HOST SELECTION BY BROWN-HEADED COWBIRDS

INTRODUCTION

Cowbirds must locate, select, and monitor a number of potential host nests to enhance their reproductive success (Briskie et. al. 1990). Gochfeld (1979) stated that host nests that are easy to find could be considered initially suitable for cowbirds and ultimately suitable if the host species is one that successfully raises cowbirds. Gochfeld (1979) subdivided initial suitability into primary suitability (e.g. egg laying of host coincides with parasite's, host nests can be found without a large energy cost) and secondary suitability (e.g. host does not reject parasitized nests). These are important distinctions as parasites may base their egg laying on primary suitability but will succeed if they can assess secondary or ultimate suitability. This chapter examines various cues that cowbirds may use to locate nests and determine the suitability of hosts.

Host Density

The relationship between nest density and cowbird parasitism has not been clearly assessed. Brittingham and Temple (1983) suggested that parasitism may be higher near forest edges because of the greater density of nesting songbirds. Fretwell (1977), however, hypothesized that the frequency of cowbird parasitism is inversely related to the density of host nests. Zimmerman (1983) confirmed this latter relationship in Dickcissels (*Spiza americana*) which nested less abundantly in prairie than old-field habitats, and were parasitized more frequently in the prairie. Freeman et al. (1990) also found a negative correlation between parasitism and nest density, and attributed the results to

increased mobbing in Red-winged Blackbirds nesting at higher densities (see also

Robertson and Norman 1977). Contrary to these findings, Fleischer (1983) found no

relationship between host nest density and cowbird parasitism and suggested that a

positive relationship exists between cowbird density and parasitism frequency. In this

chapter, my first objective is to examine if host nesting and/or cowbird density is

correlated with frequency of parasitism for Spragues' Pipit, Savannah Sparrow, Baird's

Sparrow, Grasshopper Sparrow, Chestnut-collared Longspur, Lark Bunting, Bobolink,

and Western Meadowlark.

Clutch Initiation

To maximize the probability of hosts successfully raising their young, cowbirds

must synchronize their egg laying with their hosts'. Eggs laid too late in the host's

nesting stage will not be sufficiently incubated, and will not hatch. Eggs laid too'early,

i.e. before the host lays its first or second egg, may be buried (Sealy 1992). Some

species may avoid cowbird parasitism by extending their breeding season beyond the

cowbird's laying season (Carey 1982). The second objective of the chapter is to

determine the egg-laying season of both the host community and Brown-headed Cowbird

to determine the degree to which their laying seasons overlap.

Nest Concealment

Nice (1937:165) believed that cowbirds did not find well-concealed nests as

readily as exposed nests. If this were true, cowbirds should parasitize exposed nests

more frequently than well-concealed nests. Although Smith (1981) found no statistically

significant differences between parasitized and unparasitized nests with respect to nest

concealment, he stated that parasitized nests tended to be more exposed than unparasitized nests. Buech (1982), however, reported that concealed nests were more frequently parasitized than exposed nests. These studies dealt with shrub and arboreal nesters and thus the results may have been confounded by nest height (Fleischer 1986, Briskie et.al. 1990, but see Smith 1981). Although studies have yet to report a significant difference between nest concealment and frequency of parasitism, Buech (1982) and Briskie et al. (1990) both stated that well concealed nests tended to be parasitized more frequently than exposed nests. Nest concealment may not be an important cue for finding nests if cowbirds observe the nest-building activities of hosts. Because well-concealed nests are less likely to be depredated (see Chapter 1 this study, Clarke and Nudds 1992 for a review), I hypothesized that cowbirds might be expected to parasitize well-concealed nests more frequently because such nests may allow cowbirds to lay their eggs unseen by the host and also reduce the probability that their eggs will be depredated. Thus my third objective of this study is to determine if nest concealment and frequency of parasitism are correlated for seven ground nesting passerines.

Perch and Habitat-Edge Distance

Cowbirds can reduce the cost of locating host nests by observing host nest-building activities from perches. Many observations of cowbirds perched, apparently watching potential hosts, have been reported, yet quantitative studies are few. Gates and Gysel (1978) demonstrated that nests situated closer to the forest edge where perches were numerous were parasitized more frequently than nests farther from the edge. This provides indirect evidence of the importance of the availability of perches to cowbirds

(see also Gochfeld 1979, Biermann et al. 1987, Freeman et al. 1990).

Thompson and Gottfried (1981) stated that watching potential hosts is important for cowbirds because it allows them to synchronize their egg laying with the hosts'. Experimental studies have attempted to show the importance of host activity, but they were poorly designed with small sample sizes (Laskey 1950, Thompson and Gottfried 1976, Lowther 1979). The trends, however, indicate a positive correlation between host activity and cowbird parasitism. My final objective of this chapter is to determine if a correlation exists between parasitism frequency on nests and their distances to the nearest perch and/or habitat edge.

METHODS

Cowbird and Host Densities

The number and activity of cowbirds was monitored while on the study plots during their laying period, from 10 May to 25 July, 1992. The activity period of cowbirds was divided into three time intervals (Central Standard Time, CST): morning (0400-1000 hr), afternoon (1000-1600 hr), and evening (1600+ hr). The number of cowbirds observed in each time-period were converted into an hourly rate, i.e. number of cowbirds/hour, to permit time periods and plots to be compared.

Breeding bird densities were determined using the line-transect method (Emlen 1971, 1977) and converting densities of singing males to nest densities according to the mating system of each species. Because in polygynous species one breeding male represents two mated females, or two nests, the nest densities for Western Meadowlarks (Lanyon 1957), Bobolinks (Bent 1968, Martin 1974), and Lark Buntings (Pleszczynska

1978) were doubled. The number of cowbird females encountered during the surveys were recorded and averaged for each plot. The means were converted to a density value (#/40 ha). In 1992, 10 surveys were conducted from 13 May to 22 July for plot-1, 11 May to 23 July for plot-2, and 12 May to 2 August for plot-3. The density of breeding birds was determined from the first five surveys only so as not to include birds incubating eggs or tending nestlings as males sing more vigorously earlier in the nesting cycle (Best 1981). Including later surveys may have under-estimated nesting densities. Three transects were established in plots-1 and -2 (two 300-m belts, one 200-m belt) to census adequately the entire study area and one central transect for plot 3. Song surveys were conducted at sunrise at each plot on days without rain and when winds were less than 20 km/hr.

Clutch Initiation

The date of clutch initiation was known for nests found during egg laying. For other nests, clutch initiation dates were estimated by back-counting the length of the incubation period from the day of hatching and then subtracting the size of the final clutch. Incubation periods established from previous work was used for Savannah Sparrow (Dixon 1978), Baird's Sparrow (Lane 1968), Grasshopper Sparrow (Smith 1968), Chestnut-collared Longspur (Fairfield 1968), Lark Bunting (Baumgarton 1968), Bobolink (Bent 1968), and Western Meadowlark (Lanyon 1957). Although the incubation period is not known for Sprague's Pipit, an incubation period of 12 days was used as two nests in this study were incubated for 11 to 13 days. Nests were eliminated nests if the clutch-initiation date could not be estimated.

Nest Concealment

Nest concealment was assessed as described in Chapter 1.

Perch and Habitat Edge Distance

Nearest perch and habitat edge distances were measured from each nest as described in Chapter 1.

Statistical Analyses

Chi-square contingency tables were used to determine if nest concealment, perch distance and distance to the habitat edge influenced parasitism frequency (technique as described in Chapter 1). For each species Wilcoxon Rank Sum Test was used to determine whether concealed and exposed nests differed with respect to parasitism frequency. Median clutch initiation dates were quantified using Chi-square and Fisher's exact test to determine if the laying season of each host differed significantly from that of the cowbirds'. Significance level was set at p=0.05. Means are given with (±) standard error.

RESULTS

Cowbird and Host Densities

Cowbirds parasitized hosts nesting at the highest density in each plot more frequently than hosts nesting at lower densities. Bobolinks and Savannah Sparrows had the highest density and were the most frequently parasitized species on plots-1 and -2, respectively (Fig. 3). Lark Buntings nested at the highest density on plot-3 followed by Baird's Sparrow (43 nests/40 ha), and all nests of these species were parasitized (Fig. 3). Parasitism frequency did not decline with decreasing host density in all plots but
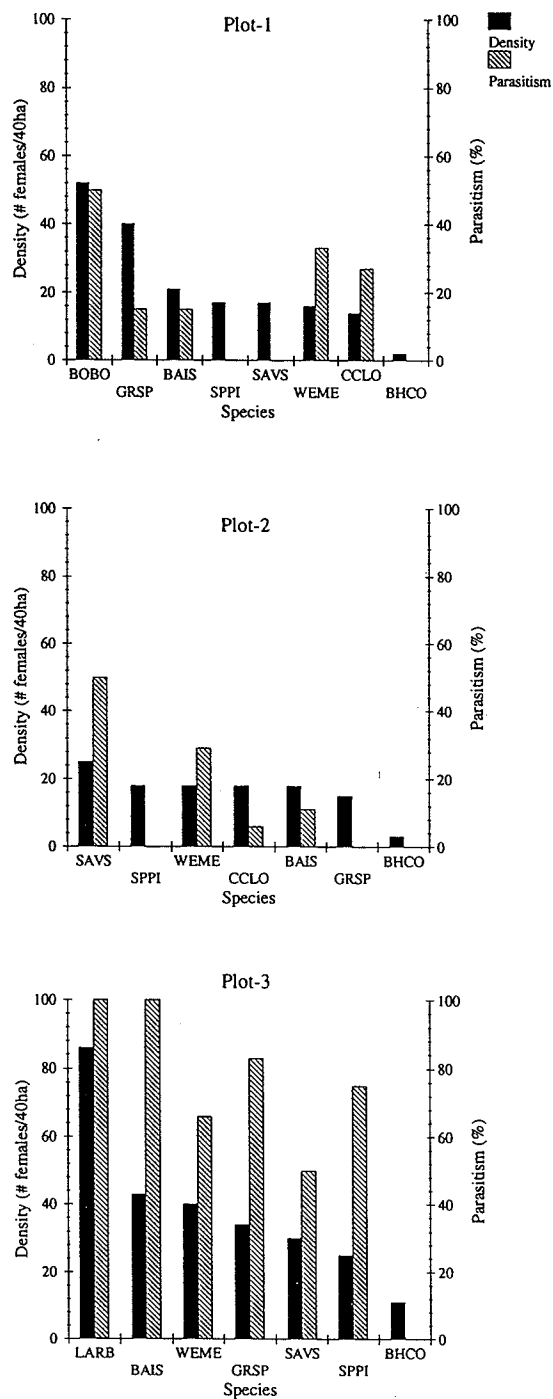
Figure 3. Frequency of cowbird parasitism with respect to cowbird and host density, 1992.
BAIS=Baird's Sparrow, BHCO=Brown-headed Cowbird, BOBO= Bobolink,
CCLO=Chestnut=collared Longspur, GRSP=Grasshopper Sparrow, LARB=Lark Bunting
SAVS=Savannah Sparrow, SPPI=Sprague's Pipit, WEME=Western Meadowlark.

parasitism frequency escalated with increasing density for the three sparrow species and buntings on plot-3 (Fig. 3).

Female cowbirds were more abundant in the mornings on all plots. Fewer cowbirds attended plot-1, regardless of the time of day whereas cowbirds were more abundant on plot-3 compared with the other plots (Fig. 4). Plot-3 also had the highest density of cowbirds, followed by plots-2 and -1 (Fig. 3).

Clutch Initiation

Clutch inititiation dates did not differ significantly between years for any species (Table 5). The cowbird laying season extended from the second week in May to the third week in July (Fig. 5) and completely encompassed that of Baird's ($X^2_{df=1}=2.774$, p=0.096), Grasshopper ($X^2_{df=1}=0.207$, p=0.649), and Savannah ($X^2_{df=1}=0.391$, p=0.532) sparrow. Clutch-initiation dates of Sprague's Pipit and Lark Bunting also indicated that their laying season did not differ significantly from the cowbird laying season (Fisher's exact test, p=0.170 and p=0.062, respectively) (Fig. 5). Median clutch-initiation dates of Chestnut-collared Longspurs ($X^2_{df=1}=16.452$, p<0.001), Western Meadowlarks ($X^2_{df=1}=14.919$, p<0.001) and Bobolinks (Fisher's exact test, p=0.018) differed significantly from the median egg-laying date of cowbirds. Longspurs and meadowlarks initiated 2.1% and 8.7% of their clutches, respectively, before cowbirds began laying (Fig. 6). Cowbirds parasitized Western Meadowlark nests throughout most of the meadowlark laying season but focused their egg laying in Baird's Sparrow nests during June, while they parasitized Grasshopper Sparrow and longspurs later in the season (Fig. 6). Early nesting longspurs were not parasitized.
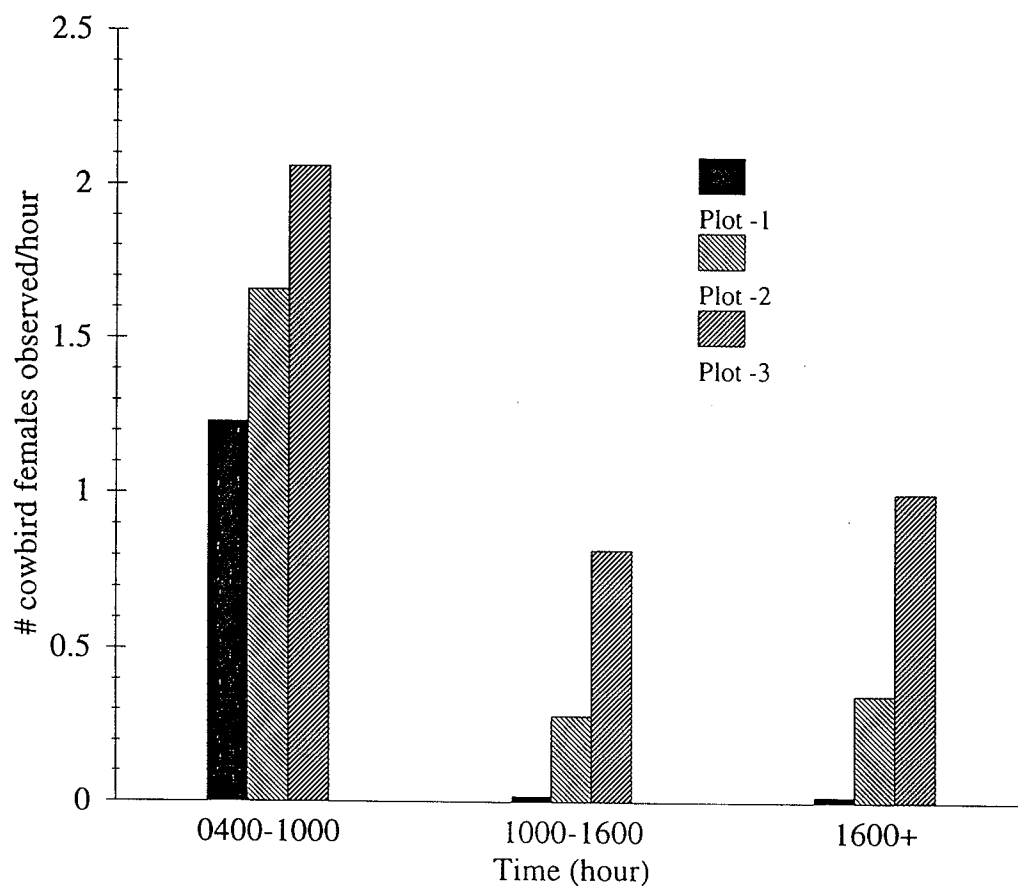
Figure 4. Cowbird abundance during different times (CST) of the day at plots
-1, -2 and -3 from 10 May to 25 July, 1992.

Table 6. Results of statistical tests to determine whether a significant difference between years exists for clutch initiation dates of 7 grassland species.

Species	Statistical Test and P-value
Brown-headed Cowbird	$X^2_{df=1}=0.591$, p=0.442 (92)*
Sprague's Pipit	Fisher's exact test p=0.175 (11)
Savannah Sparrow	$X^2_{df=1}=0.667$, p=0.414 (24)
Baird's Sparrow	$X^2_{df=1}=3.158$, p=0.077 (51)
Grasshopper Sparrow	$X^2_{df=1}=0.000$, p=1.000 (36)
Chestnut-collared Longspur	$X^2_{df=1}=0.085$, p=0.771 (48)
Western Meadowlark	$X^2_{df=1}=0.031$, p=0.861 (46)

Note: numbers in parentheses indicate nests for which clutch-initiation dates were known.
    * = number of eggs for which laying dates were known.
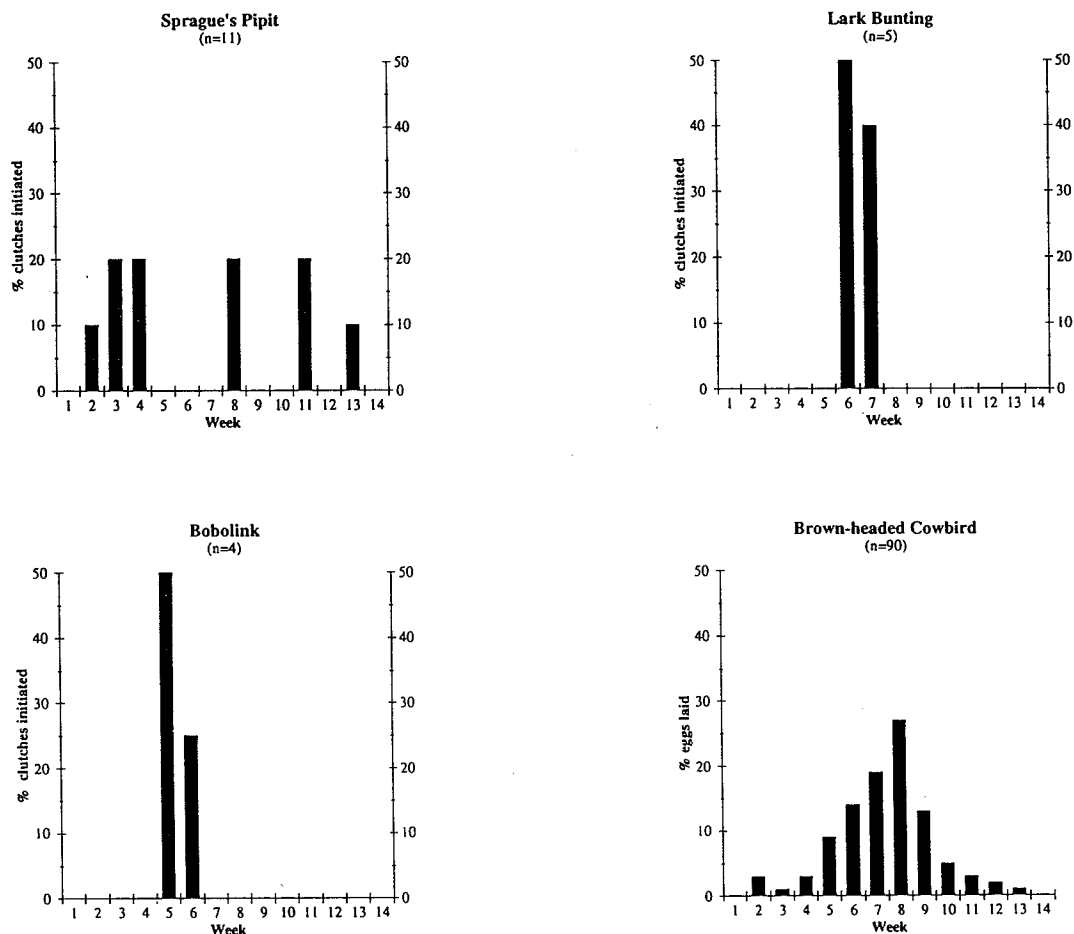
Figure 5. Distribution of cowbird egg-laying dates of three host species in which the dates nests were parasitized could not be determined, 1991 and 1992. Numbers in parentheses indicate total number of cowbird eggs and host nests. Week1= 1 to 7 May.
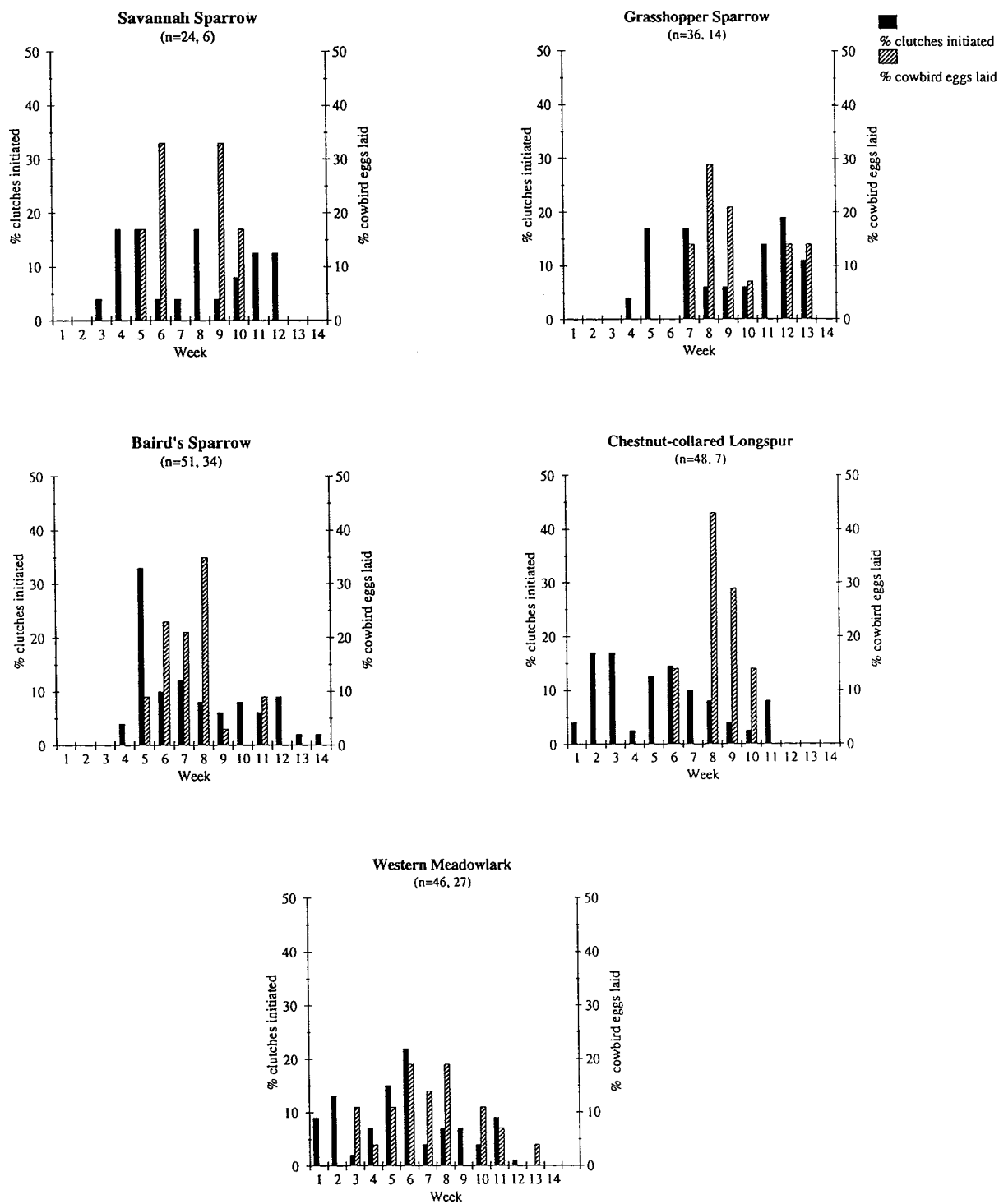
Figure 6. Synchrony of egg laying with host clutch initiation for 5 host species, 1991 and 1992. Numbers in parentheses indicate total number of clutches and cowbird eggs, respectively.

Nest Concealment

Concealed nests were parasitized more frequently than exposed nests (Fig. 7). This trend, however, was not statistically significant ($X^2_{df=3}$=4.798, p=0.187). No correlation was found for nest concealment and parasitism on individual species (Wilcoxon rank sum, p>0.05), except for Baird's Sparrow. Baird's Sparrow nests with concealment values greater than 20 were parasitized significantly less than well-concealed nests (Wilcoxon Rank Sum, p=0.031). Concealment means of all bird species were significantly different ($F_{df=7}$=45.60, p=0.001). Duncan's multiple comparison procedure revealed that Chestnut-collared Longspur nests were significantly more exposed than nests of other species (p<0.05) and Western Meadowlark nests were significantly more concealed (p<0.05) than all species except for pipit and bunting (p>0.05) nests (Fig. 8).

Perch and Habitat Edge Distance

Nests were parasitized more frequently when located close to perches (Fig. 9), although the trend was not significant ($X^2_{df=3}$ = 6.920, p=0.074). However, nests located more than 150 m from a perch were significantly less often parasitized than those closer to a perch ($X^2_{df=1}$ = 6.019, p=0.014). One-way ANOVA revealed a significant difference in the mean perch distance between the three plots ($F_{df=2}$ = 7.13, p=0.009). Nests in plot-1 were farthest from a perch with an average distance of 75.9 m while plot-2 and plot-3 nests were 59.5 m, and 40.1 m, respectively. Nests in plot-3 were significantly closer to perches than in the other two plots and mean perch-to-nest distances did not differ significantly between plots-1 and -2. The proportion of parasitized nests decreased with increasing distance from the habitat edge
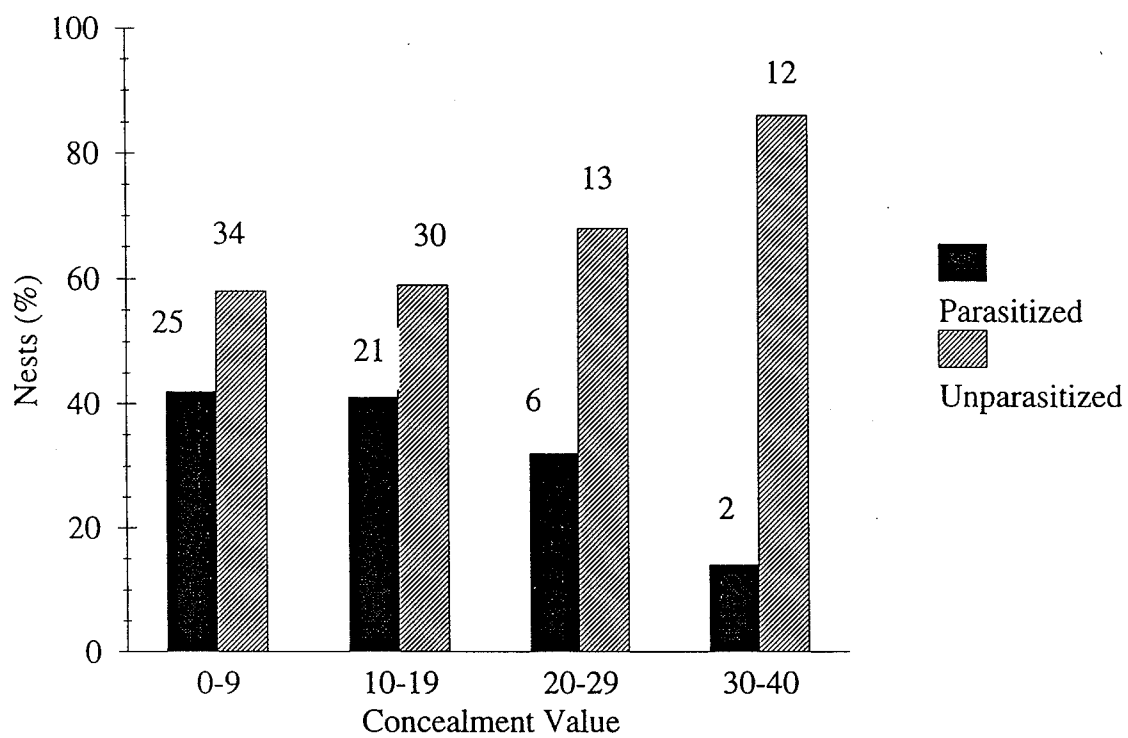
Figure 7. Parasitism frequency in concealed and exposed nests, 1992.
Sample sizes given as number above each bar.
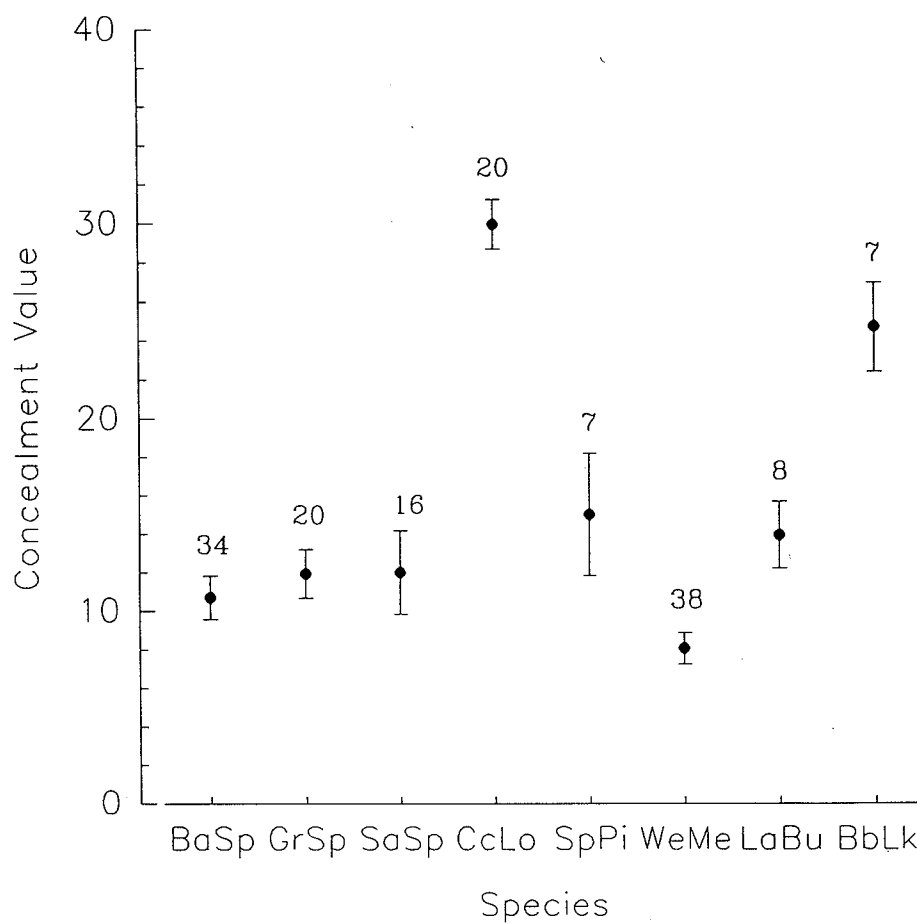
Figure 8. Mean concealment values for nests of 8 grassland hosts of southwestern Manitoba, 1992. Sample size given as number above each standard error bar.
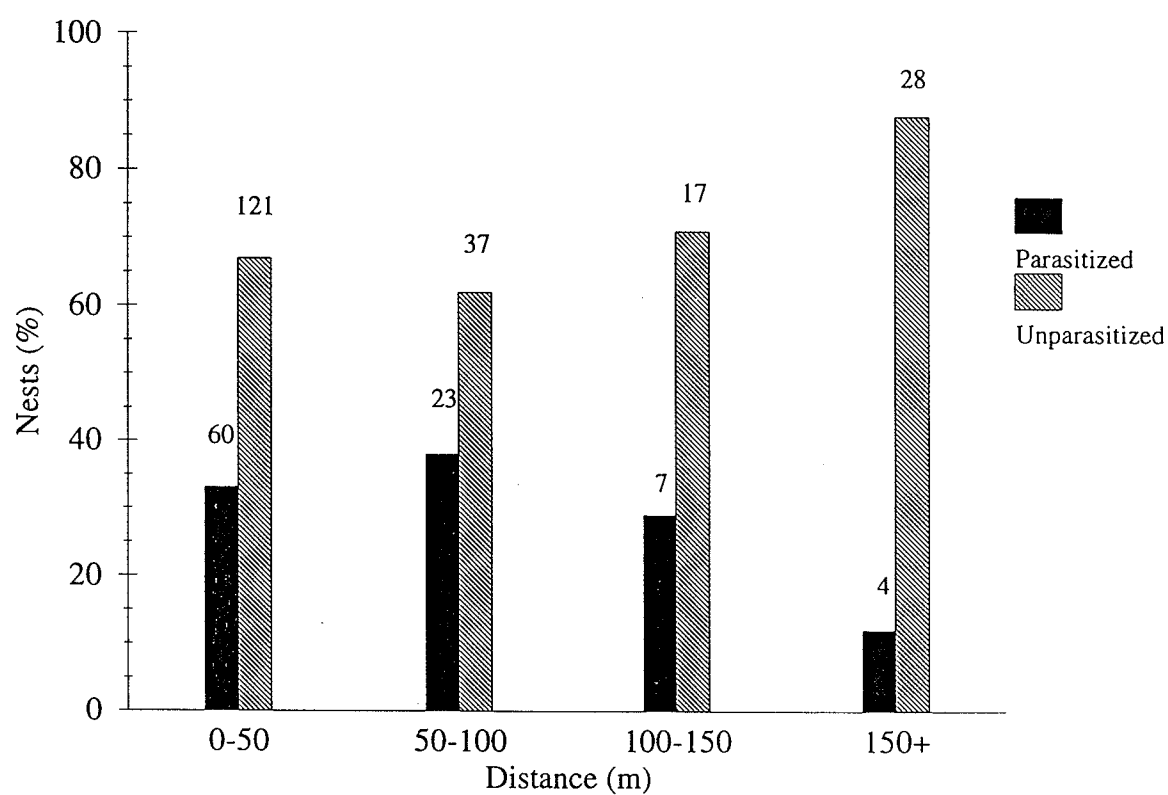
Figure 9. Proportion of parasitized nests with increasing distance from the nearest perch, 1991 and 1992. Sample sizes given as number above each bar.

$(X^2_{df=3} = 25.593, p < 0.001)$. Parasitism frequency was the same for nests between 0 and 100 m from the habitat edge $(X^2_{df=1} = 1.505, p=0.220)$ and declined significantly for nests situated more than 100 m from the habitat edge (Fig. 10, $X^2_{df=1} = 22.062$, $p < 0.001$).

DISCUSSION

Cowbird and Host Densities

On each plot, cowbirds parasitized most frequently hosts that nested at the highest densities. This supports Biermann et al.'s (1987) suggestion that high host densities attract cowbirds because more nests are available for parasitism. Further support was provided when each plot was examined individually. Parasitism was most frequent in the plot-3, which contained the highest host-nest and cowbird densities. These results do not support Fretwell (1977) and Zimmerman (1983) who reported an inverse relationship between host nesting density and parasitism frequency. If cowbirds parasitized hosts only on the basis of nest availability (density), the frequency of parasitism would be expected to decline as nesting densities decline. However, this did not occur. Parasitizing mainly the most abundant host would not be an effective strategy for cowbirds unless the particular species parasitized was a high quality host. Bobolinks and Lark Buntings did not raise any cowbird young yet they were parasitized most frequently in plots-1 and -3 (Fig. 4). Cowbirds may have parasitized them because they were more likely to encounter their nests. Because cowbirds lay consecutive clutches, with 1-2 days separating some of them (Scott and Ankney 1983), they may have chosen less appropriate nests when more suitable nests were not available. The large number of inappropriately
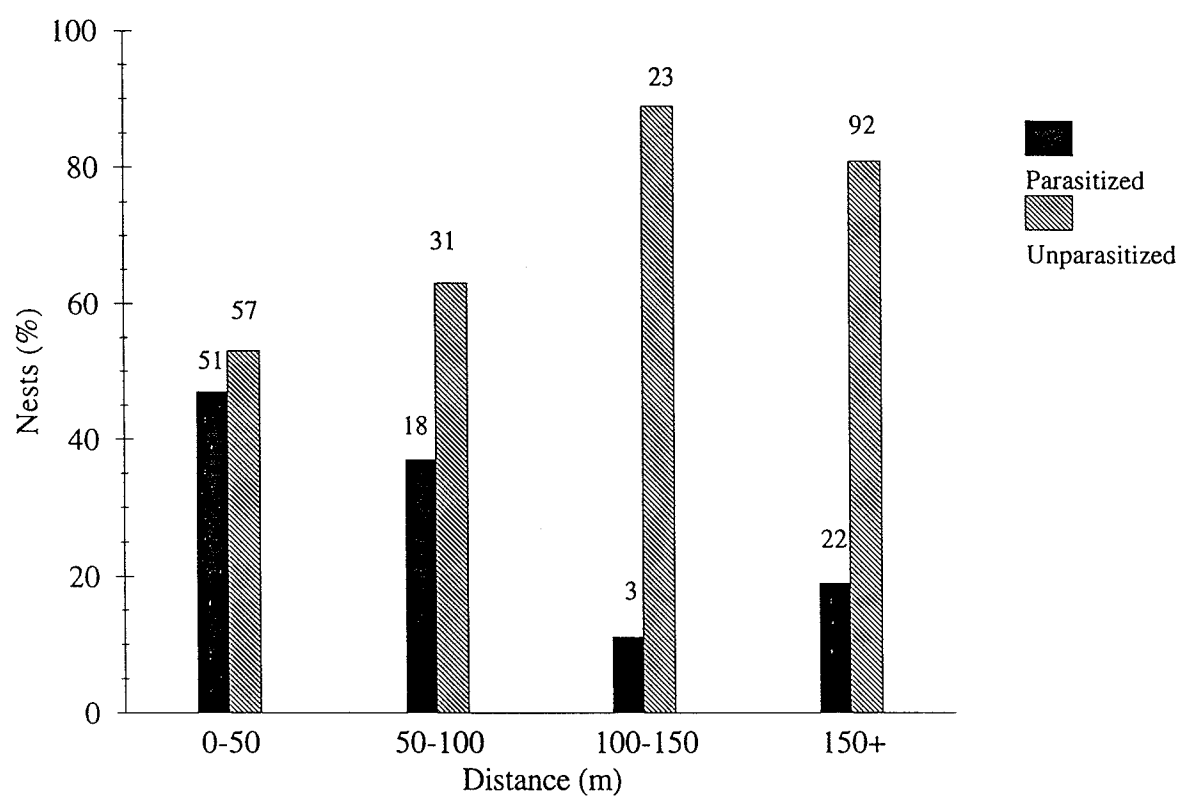
Figure 10. Proportion of parasitized nests with increasing distance from the habitat edge, 1991 and 1992. Sample sizes given as numbers above each bar.

laid eggs by cowbirds also indicates that they were selecting less appropriate nests when more suitable nests were unavailable (see Chapter 1). This might be an effective strategy in grasslands for a generalist brood parasite like the Brown-headed Cowbird because it lays over 40 eggs during the breeding season (Scott and Ankney 1980). As parasitism frequency did not decline with decreasing nest abundance, cowbird density may be more strongly correlated with parasitism frequency, as Fleischer (1986) reports, and/or cowbirds selected hosts based on factors other than nest abundance alone.

On all plots, most cowbirds were sighted in the morning (Fig. 3). Rothstein et al. (1984) recorded cowbirds present on the host nesting areas in the morning and in the afternoon they flew up to 7 km to foraging sites. That cowbirds were consistently present on plot-3 in larger numbers throughout the day may have been because this plot was located between two pastures so that cowbirds did not have to commute great distances between laying and feeding areas (Elliott 1980). This may have allowed cowbirds to spend more time searching for nests. However, cowbirds could also spend more time searching for nests in plot-2 because they also foraged on the pasture. The combination of more available nests in a relatively small area, and more female cowbirds searching for nests longer each day, may have contributed to the higher parasitism frequency in plot-3.

Clutch Initiation

The laying season of all hosts in this study largely overlapped with that of the cowbirds'. Cowbirds laid from the second week of May through late July (Fig. 5). This contrasts slightly with the laying season of cowbirds at Delta Marsh, Manitoba. Hill

(1992) demonstrated that cowbirds began laying in Clay-coloured Sparrow (*Spizella pallida*) nests during the last week of May and continued until the third week of June. Nests were rarely parasitized after this date (see also Briskie et. al. 1990). Grassland birds in Manitoba may be susceptible to cowbird parasitism for a longer time period than hosts elsewhere. Meadowlarks and longspurs were the only species to initiate clutches in the first week of May, before cowbirds began laying (Fig. 6). Nesting early in the season would allow these birds to reduce the risk of being parasitized by cowbirds. This may explain the infrequent parasitism on longspur nests but does not account for the high parasitism on meadowlark nests. Meadowlarks, however, initiated 91% of their nests throughout the cowbird's egg-laying period, which made nests almost continuously available to cowbirds. Longspurs, however, initiated a large proportion of nests prior to the peak cowbird laying period which reduced the chance of being parasitized (Fig. 6). Apparently cowbirds focused their egg laying on Grasshopper Sparrow nests later in the season (Fig. 6). Cowbirds have been known to switch host species as their laying season progresses. Fleischer (1986), for example, reported that cowbirds parasitized Red-winged Blackbird nests earlier in the season, and switched to Dickcissel nests when they became available. Briskie et. al. (1990) reported that cowbirds did not parasitize Least Flycatcher (*Empidonax minimus*) nests until Yellow Warbler (*Dendroica petechia*) clutch initiation declined. They suggested that cowbirds preferred the warblers, or were forced to parasitize flycatcher nests as Yellow Warbler nests became less available.

Nest Concealment

Longspur nests were more exposed than the other species' nests and they were parasitized at a low frequency. In contrast, Western Meadowlark nests were well hidden and were more frequently parasitized (Appendix IIh). Buech (1982) also found that parasitized nests were more concealed than unparasitized nests and suggested that host activity was important for locating nests. Briskie et al. (1990) found that Least Flycatchers were parasitized less frequently than Yellow Warblers even though the flycatcher nests were more exposed. These studies, including the present study, contradict Nice's (1947) suggestion that well-concealed nests should be parasitized less frequently because of the difficulty cowbirds would have in locating them (see also Smith 1981). Nest concealment, however, should not affect cowbirds' nest-locating ability if they watch nest-building activities of the host, as nests will be found regardless of how well they are concealed. Western Meadowlarks were the largest hosts in this study which may have allowed cowbirds to detect meadowlarks more readily than the smaller surreptitious birds. Although meadowlarks skulked through the vegetation when leaving the nest, they characteristically flew directly into their nests when arriving, even hovering above the nest briefly before entering (pers. obs.). I used this behaviour to locate several nests, and cowbirds may also cue into this behaviour. This is not to say that cowbirds do not use nest concealment as a cue in host selection. Cowbirds may choose well-hidden nests to reduce the risk of their eggs or young being depredated (see Clarke and Nudds 1992), or to avoid nest-defense behaviour of hosts. Robertson and Norman (1976, 1977) suggested that hosts may prevent cowbirds from laying in nests through vigilance and

aggression. The low parasitism frequency exhibited by longspurs may be due to nest

vigilance. Longspur females characteristically remained on, or close to their nest, when

nest checks were conducted. In fact, one female had to be held to keep from returning to

the nest when I inspected it. Nest sitting may be a strategy used to conceal the nest

against predators, or it could also be used as a nest-defense strategy against cowbirds.

Hobson and Sealy (1989) documented Yellow Warblers returning to their nest and sitting

when a female cowbird model was presented. They suggested that this behaviour was an

anti-parasite strategy that may prevent female cowbirds from gaining access to the nest.

Cowbirds may avoid exposed longspur nests because they would be visible in

approaching and laying eggs in the nest if longspurs were at the nest before dawn

(Neudorf and Sealy 1994). This would make cowbirds susceptible to aggressive nest

defence by the host. It has been shown that Yellow Warblers (Briskie et al. 1990, but

see Hobson and Sealy 1989) and American Robins (*Turdus migratorius*) (McLean et al.

1986) with exposed nests respond more aggressively to intruders than those at well-

concealed nests. This may aid in deterring cowbirds from parasitizing nests. However,

the effectiveness of this aggressive strategy is not clear. Cowbirds may avoid aggressive

host behaviour by parasitizing nests very early in the morning when hosts are not around

(Neudorf and Sealy 1994, Sealy et al., in press). Sealy et al. (in press) reported that

cowbirds spent less than one minute laying in host nests compared with up to 30 minutes

in six other icterids and 13 passerine species studied. These authors suggested that this

behaviour allows cowbirds to reduce the risk of being detected by hosts, and, if harassed,

still allows them to parasitize nests. Rothstein (1975) also reported that laying quickly in

hosts' nests would increase the chance of the cowbird egg being accepted by the host although studies by Hill and Sealy (in press) and Sealy (in press) do not lend support to this idea. Clearly, experimental (model) studies are needed to determine if any of the host species in this study have developed nest-defense strategies.

Perch and Habitat Edge Distance

Several studies have suggested the presence of perches for cowbirds potentially influences the frequency of brood parasitism (e.g. Gochfeld 1979, Biermann et al. 1987, Wiley 1988, Freeman et al. 1990). The results of this study support Gates and Gysel (1978) because nests 150 m or less from perches and/or 100 m from the habitat edge were more frequently parasitized than nests farther away. This may account for the highest parasitism frequency found in plot 3 because the widest point in this plot was 220 m compared with 800 m in the other two plots. Nests in plot-3 were also closer to perches.

Norman and Robertson (1975) described three nest-searching strategies that cowbirds apparently use to find nests: (1) cryptic, silent watching of hosts while they build nests; (2) secretive searching along the ground; and (3) active, noisy searching in dense shrubbery and forest edges. Not only does watching hosts facilitate nest-finding, but Thompson and Gottfried (1981) stated that observing hosts allows cowbirds to synchronize their egg laying with them. Arnold and Higgins (1986) provided indirect evidence of the importance of perches to cowbirds as they found that cowbirds were more abundant on shrubby, compared with shrubless transects. Perching allows cowbirds to gather information from cues provided by hosts (Lowther and Johnson 1977) without

expending much energy. Although there apparently was a correlation between parasitism frequency and perch/habitat edge distance, some nests were parasitized even though they were more than 150 m from the nearest perch and edge of the habitat.

How do cowbirds find nests that are situated well away from perches? Cowbirds may inadvertently locate nests while foraging, particularly in pastures. Cowbirds may also use cattle as mobile perches where shrubs are absent as I have observed, albeit infrequently, cowbirds perched on the back of grazing and resting cattle. Wiley (1988) observed Shiny Cowbirds making short flights and hops, often in the presence of a male and another female(s), and stated that this behaviour was a form of active nest-searching. Brown-headed Cowbirds in the present study were also regularly seen engaged in this activity. Although cowbirds were not observed making noisy flights into nesting areas as reported by Norman and Robertson (1975) and Wiley (1988), cowbirds may use another form of active searching in grasslands. Female cowbirds were frequently observed flying about 1 m from the ground in plots-1 and -2 possibly searching for nests or attempting to flush or induce aggressive nest defence from hosts to gain information on the location of host nests (see Wiley and Wiley 1980). Although host aggression to low-flying cowbirds was not evident, Robertson and Norman (1977) showed that host aggression may be used as a nest-finding cue by cowbirds where host nesting densities are low. Smith (1981) believed that adult female Song Sparrows (*Melospiza melodia*) responded more strongly to passing cowbirds thus facilitating the discovery of their nests. More observations and experiments are required to confirm or refute this nest-cue hypothesis.

Besides nest-building activities of the host, cowbirds may cue into host singing

from perches to find appropriate nests. Gochfeld (1979) showed that Shiny Cowbirds

(*M. bonariensis*) approached stuffed Red-breasted Meadowlarks (*S. loyca*) but not Pampas

Meadowlarks (*S. defilippii*) when their songs were played. Red-breasted Meadowlarks

were also parasitized more heavily than Pampas Meadowlarks in his study. Host singing

may be a reliable cue because it may give information about the nesting stage and fitness

of the host. Singing intensity is strongly correlated with the nesting stage of birds (see

Best 1981), and in some species, song increases just prior to the onset of incubation

(Lanyon 1957, Gochfeld 1979), a reasonable time for parasitizing nests. Grieg-Smith

(1982) showed that male Stonechat (*Saxicola torquata*) song rates were correlated with

later participation in parental care. Thus singing may serve as a cue for females in

assessing the fitness of prospective mates. Cowbirds could optimize their search costs by

cuing into the songs or calls of prospective hosts, gathering information on host fitness,

nesting stage, and possibly nest location (see Wiley 1988).

Cowbirds may also use perches to monitor previously parasitized nests to

determine ultimate suitability, i.e. host successfully raises cowbird young. Cowbirds

have been reported visiting nests during early egg laying to the brooding stage (Mayfield

1961, Wiley 1988). Monitoring nests would allow the cowbird to determine if a certain

host species is an appropriate host to parasitize by whether it successfully raises

cowbirds. Longspurs in this study may be infrequently parasitized because they rarely

raise cowbird young to fledging, i.e. they are a poor quality host (Appendix IIf). In fact,

one parasitized longspur nest contained a dead cowbird nestling. The death did not

appear to be related to an inappropriate diet, as in American Goldfinches (*Carduelis*

tristis) (Middleton 1977), since longspurs provide their nestlings with an invertebrate diet (Maher 1973, pers. obs. this study). It may be possible that longspurs selectively feed their own young or that they focus their feeding on the smaller nestlings (see Hatch 19). Experimental studies and more observations are required to support or refute this statement.

SUMMARY

1. Cowbirds parasitized more frequently hosts that nested at highest density on each plot but parasitism frequency did not decrease with declining density of hosts.

2. Cowbirds were more abundant, and present longer on the smaller plot-3 compared to the other plots.

3. The cowbird egg-laying season overlapped with that of all host species which made them susceptible to parasitism. Early nests of Chestnut-collared Longspurs were not parasitized by cowbirds.

4. Parasitism frequency was higher for well-concealed compared with exposed nests but the trend was not significant.

5. Parasitism frequencies were significantly lower for nests located more than 150 m from a perch and/or 100 m from the habitat edge.

6. Perch distances were significantly shorter in the smaller plot-3 compared with the other two plots.

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APPENDIX I. Vegetation analyses on plots-1, -2, and -3, 1992.

	Cover			Frequency		
Category/taxon	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3
Litter	33.12	4.56	0.20	94.00	18.75	0.88
Agropyron repens	-	11.92	-	-	39.63	-
Bromus inermis	18.55	2.05	0.22	57.50	10.63	1.75
Calamogrostis inexpansa	-	10.87	0.42	-	34.13	2.13
Standing Dead	9.64	19.84	28.49	56.63	69.25	89.50
Stipa spartea	8.98	4.32	14.23	38.00	14.63	51.13
Bare ground	8.00	7.95	1.11	35.38	24.88	3.50
Poa spp.	5.69	9.11	5.29	34.63	38.63	33.00
Artemisia frigida	5.22	0.05	-	20.00	0.13	-
Bouteloa gracilis	-	-	4.08	-	-	15.50
Potentilla anserina	-	3.69	1.18	-	14.13	5.38
Andropogan scoparius	-	1.92	0.32	-	3.88	1.13
Carex rostrata	-	1.81	-	-	5.38	-
Koeleria cristata	1.70	0.02	2.63	9.38	0.13	9.50
Hordeum jubatum	-	-	2.27	-	-	4.25
Carex stenophylla	-	-	2.22	-	-	5.25
Carex lanuginosa	-	1.66	-	-	5.00	-
Scirpus lacustris glaucus	-	1.03	-	-	3.88	-
Helianthus laetiflorus	1.61	0.18	1.60	5.13	1.25	9.63
Poa palustris	-	-	1.44	-	-	6.63
Artemisia ludoviciana	1.18	-	-	7.63	-	-
Sonchus arvensis	-	0.96	4.06	-	6.75	15.50
Anenome canadensis	-	-	3.73	-	-	14.00
Agropyron spp.	-	-	3.37	-	-	21.75
Sporobolus heterolepis	-	-	0.90	-	-	2.50
Melilotus officinalis	0.83	0.05	0.32	2.50	0.38	0.88
Galium boreale	0.73	-	-	5.38	-	-
Cirsium flodmanii	-	0.69	0.11	-	4.13	0.38
Solidago nemoralis	0.67	0.53	-	4.25	3.38	-
Selaginella densa	0.66	-	-	2.63	-	-
Psoralea argophilla	0.57	-	0.08	3.63	-	0.75

Appendix I cont'd.

Category/taxon	Cover			Frequency		
	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3
Andropogan gerardii	-	-	0.56	-	-	1.00
Juncus balticus	-	0.55	1.05	-	3.88	9.50
Panicum virgatum	-	0.54	-	-	2.13	-
Muhlenbergia richardsonis	-	0.48	11.73	-	1.63	38.38
Lactuca pulchella	-	-	0.45	-	-	2.50
Rosa arkansana	0.41	0.11	0.39	3.38	0.63	2.00
Chrysopsis villosa	0.32	-	-	1.38	-	-
Artemisia campestris	0.26	-	-	1.25	-	-
Commandra pallida	-	0.25	0.35	-	1.63	2.63
Panicum wilcoxianum	0.24	-	-	1.00	-	-
Aster laevis	-	0.22	0.34	-	1.00	1.25
Ratibida columnifera	-	0.22	-	-	1.00	-
Glycyrrhiza lepidota	0.21	0.21	-	1.25	0.50	-
Solidago rigida	-	-	0.19	-	-	0.63
Asclepias speciosa	-	0.19	0.05	-	0.75	0.13
Eleagnus commutata	-	0.19	0.63	-	1.00	1.63
Monarda fistulosa	-	0.18	-	-	1.63	-
Ambrosia psylostachya	0.17	3.64	0.11	0.88	19.50	0.75
Agoseris glauca	-	-	0.17	-	-	0.50
Lathyrus venosus	0.17	-	0.05	1.00	-	0.38
Bouteloa curtipendula	-	-	0.14	-	-	0.38
Astragalus crassicarpus	0.14	-	-	0.25	-	-
Cirsium arvense	-	-	0.13	-	-	0.75
Anenome cylindrica	0.13	0.04	-	0.25	0.25	-
Bouteloa gracilis	0.13	-	-	0.13	-	-
Stachys palustris	-	0.12	0.42	-	1.00	2.63
Equisetum hyemale	0.12	-	-	2.00	-	-
Campanula rotundifolia	0.11	-	-	0.38	-	-
Achillea millefolium	-	0.10	-	-	0.75	-
Eleocharis palustris	-	0.10	-	-	0.50	-
Eleocharis compressa	-	0.08	-	-	0.75	-
Gallium boreale	-	-	0.08	-	-	0.75

Appendix I cont'd.

Category/taxon	Cover			Frequency		
	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3
Oxytropis lambertii	0.08	-	-	0.25	-	-
Panicum virgatum	0.08	-	-	0.13	-	-
Fragaria virginiana	-	-	0.07	-	-	0.75
Zizia aptera	-	0.07	0.08	-	0.63	0.50
Symphoricarpos occidentalis	0.07	-	2.02	0.25	-	4.25
Equisetum laevigatum	-	0.06	0.04	-	0.75	0.38
Liatris ligulistylis	-	-	0.06	-	-	0.38
Senecio vulgaris	-	0.05	-	-	0.13	-
Deschampsia caespitosa	-	0.05	0.77	-	0.13	2.38
Salsola kali	-	-	0.05	-	-	0.38
Anenome patens	-	-	0.05	-	-	0.13
Sysyrinchium montanum	-	0.04	-	-	0.25	-
Aster ptarmicoides	-	0.04	-	-	0.13	-
Potentilla arguta	0.04	-	-	0.38	-	-
Polygala senega	-	0.02	0.10	-	0.13	0.63
Poa arida	-	0.02	-	-	0.13	-
Psoralea esculenta	0.04	-	-	0.25	-	-
Festuca saximontana	0.04	-	-	0.25	-	-
Lithospermum canescens	0.03	-	-	0.25	-	-
Erigeron canadensis	0.03	-	-	0.13	-	-
Aster pansus	0.02	0.25	0.09	0.13	1.88	0.50
Potentilla pensylvanica	0.02	-	-	0.13	-	-
Solidago missouriensis	0.02	3.79	-	0.25	17.50	-
Lithospermum incisom	0.02	-	-	0.25	-	-
Rudbeckia serotina	-	-	0.02	-	-	0.13
Lilium philadelphicum	-	-	0.02	-	-	0.25
Zizia aurea	-	-	0.02	-	-	0.13
Medicago sativa	0.02	-	0.09	0.13	-	0.25
Campanula rotundifolia	-	-	0.02	-	-	0.13
Astragalus canadensis	-	-	0.01	-	-	0.13
Androsace septentrionalis	0.01	-	-	0.25	-	-
Carex parryana	0.01	4.70	0.64	0.13	18.38	6.75

Appendix I cont'd.

Category/taxon	Cover			Frequency		
	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3
Solidago canadensis	0.01	-	0.69	0.13	-	4.38
Antennaria microphyllum	0.01	0.51	-	0.13	2.13	-
Linum lewisii	0.01	-	-	0.13	-	-
Spiraea alba	0.01	-	-	0.13	-	-

APPENDIX II. PRODUCTIVITY AND FREQUENCY OF PARASITISM AND PREDATION OF 8 GRASSLAND BIRD SPECIES IN THREE STUDY PLOTS, 1991 AND 1992.

Appendix IIa. Sprague's Pipit productivity and frequency of parasitism and predation in three study plots, 1991 and 1992.

Parameter	Plot 1	Plot 2	Plot 3*	P-value	Plots Combined
# of nests	10	2	5	-	17
% Successful	50	50	25	0.780^2	44
% Depredated	50	50	75	0.780^2	56
% Deserted	0	0	0	1.000^2	0
% Failed	0	0	0	1.000^2	0
% Pipit eggs laid fledging young	28	-	0	-	23
Pipits fledged/nest	1.3	1.0	0	0.304^3	0.90
Pipits fledged/successful nest	2.6	2.0	0	0.656^3	2.50
% Parasitized	0	0	60	0.037^2	18
% Multiple parasitism	0	0	100	-	100
Cowbirds fledged/parasitized nest	-	-	0.3	-	0.30
Survival rate	0.29	0.004	0.06	-	0.14

* = 1 nest with unknown outcome
2 = Fisher's exact test
3 = 1-way ANOVA

Appendix IIb. Lark Bunting productivity and frequency of parasitism, 1992.

Parameter	Plot-3
# of nests	7
% Success	29
% Depredated	71
% Eggs laid fledging young	29
Buntings fledged/nest	1.0
Buntings fledged/successful nest	3.5
% Parasitized	100
% Multiple parasitism	83
Cowbirds fledged/parasitized nest	0
Survival rate	0.20

Appendix IIc. Savannah Sparrow productivity and frequency of parasitism in three study plots. Numbers separated by a comma indicate values for 1991 and 1992, respectively, as between-year differences were significant.

Parameter	Plot 1	Plot 2	Plot 3	P-value	Plots Combined
# of nests	7	20	4	-	31
% Successful	100, 0	40	50	-	42
% Depredated	43	50	50	0.780^2	48
% Deserted	0	0	0	1.000^2	0
% Failed	14	10	0	1.000^2	10
% Eggs laid fledging young	0, 90	19	10	-	-
Sparrows fledged/nest	3.0, 0.0	0.7	0.2	-	-
Sparrows fledged/successful nest	3.7	1.7	1.0	0.031^3	2.2
% Parasitized	14	37	50	0.538^2	33
% Multiple parasitism	100	71	50	0.395^2	70
Cowbirds fledged/parasitized nest	0.5	0.4	1.0	0.728^3	0.5
Survival rate	0.22	0.05	0.04	-	0.07

[2] = Fisher's exact test
[3] = 1-way ANOVA

Appendix IId. Baird's Sparrow productivity and frequency of parasitism in three study plots. Numbers separated by a comma indicates values for 1991 and 1992, respectively, as between year differences were significant.

	Plot 1	Plot 2	Plot 3	P-value	Plots Combined
# of nests	29	16	22		67
% Successful	46	62	59	0.513[1]	54
% Depredated	46	26	36	0.364[1]	38
% Deserted	0	0	5	0.585[2]	2
% Eggs laid fledging young	32	34, 60	29	-	-
% Failed	8	12	0	0.281[2]	6
Sparrows fledged/nest	1.4	1.9	1.1	0.366[3]	1.4
Sparrows fledged/successful nest	2.9	3.4	2.5	0.306[3]	2.9
% Parasitized	10	25	58, 100	-	36
% Multiple parasitism	100	50	65	0.541[2]	67
Cowbirds fledged/parasitized nest	0.5	0.7	0.4	0.725[3]	0.4
Survival Rate	0.19	0.32	0.17	-	0.21

[1] = $X^2_{df=2}$
[2] = Fisher's exact test
[3] = 1-way ANOVA

Appendix IIe. Grasshopper Sparrow productivity and frequency of parasitism in three study plots, 1991 and 1992.

	Plot 1*	Plot 2	Plot 3*	P-value	Plots Combined
# of nests	25	7	16	-	48
% Successful	58	43	40	0.609^2	50
% Depredated	42	43	60	0.563^2	48
% Deserted	0	0	0	-	0
% Failed	0	14	0	0.152^2	2
% Eggs laid fledging young	47	52	11, 40	-	-
Sparrows fledged/nest	2.2	1.7	1.0	0.187^3	1.7
Sparrows fledged/successful nest	3.7	4.0	2.5	0.073^3	3.4
% Parasitized	12	14	56	0.003^2	27
% Multiple parasitism	67	100	78	1.000^2	77
Cowbirds fledged/parasitized nest	0.7	0.0	0.4	0.785^3	0.5
Survival rate	0.24	0.28	0.21	-	0.23

* = 1 nest with outcome unknown
^{2} = Fisher's exact test
^{3} = 1-way ANOVA

Appendix IIf. Chestnut-collared Longspur productivity and frequency of parasitism in three study plots, 1991 and 1992.

Parameter	Plot 1**	Plot 2*	Plot 3	P-value	Plots Combined
# of nests	31	24	2	-	57
% Successful	39	48	100	0.240^2	45
% Depredated	57	48	0	0.323^2	51
% Deserted	0	0	0	1.000^2	0
% Failed	4	4	0		4
% Eggs laid fledging young	45, 20	38	89	-	-
Longspurs fledged/nest	1.3	1.6	4.0	0.143^3	1.6
Longspurs fledged/successful nest	3.4	3.4	4.0	0.755^3	3.5
% Parasitized	22	4	0	0.159^2	14
% Multiple parasitism	29	100	0	0.375^2	37
Cowbirds fledged/parasitized nest	0.1	0.0	0.0		0.1
Survival rate	0.24	0.32	0.81	-	0.30

* = 1 nest with unknown outcome
** = 3 nests with unknown outcome
^{2} = Fisher's exact test
^{3} = 1-way ANOVA

Appendix IIg. Bobolink productivity and frequency of parasitism, 1992.

Parameter	Plot 1
# of nests	6
% Success	33
% Depredated	67
% Eggs laid fledging young	20
Bobolinks fledged/nest	1.3
Bobolinks fledged/successful nest	4
% Parasitized	50
% Multiple parasitism	33
Cowbirds fledged/parasitized nest	0
Survival rate	0.06

Appendix IIh. Western Meadowlark productivity and frequency of parasitism in three
study plots, 1991 and 1992.

	Plot 1	Plot 2	Plot 3	P-value	Plots Combined
# of nests	7	31	27	-	65
% Successful	57	32	30	0.394^2	34
% Depredated	43	55	59	0.773^2	55
% Deserted	0	10	11	0.809^2	9
% Failed	1.7	0.9	0.7	1.000^2	2
% Eggs laid fledging young	32	19	19	[1]	-
Meadowlarks fledged/nest	3.0	2.9	2.7	0.303^3	0.9
Meadowlarks fledged/successful nest	3.0	2.8	3.3	0.938^3	2.9
% Parasitized	43	23	72	0.000^2	44
% Multiple parasitism	33	43	83	0.065^2	68
Cowbirds fledged/parasitized nest	0.7	0.1	0.7	0.608^3	0.5
Survival rate	0.26	0.11	0.09		0.09

[1] $= X^2_{df=1} = 2.340$
[2] $=$ Fisher's exact test
[3] $=$ 1-way ANOVA

Appendix III. Incubation and nestling stage survival rates of eight species from plots-1, -2 and -3, 1991 and 1992.

Species	Incubation			Nestling		
	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3
Sprague's Pipit	1.00	0.06	0.29	0.29	0.06	0.23
Lark Bunting	-	-	0.70	-	-	0.28
Savannah Sparrow	0.55	0.23	0.18	0.40	0.22	0.21
Baird's Sparrow	0.49	0.57	0.48	0.39	0.57	0.35
Grasshopper Sparrow	0.45	0.55	0.25	0.54	0.52	0.82
Chestnut-collared Longspur	0.50	0.78	1.00	0.49	0.41	0.81
Bobolink	0.11	-	-	0.50	-	-
Western Meadowlark	0.43	0.34	0.15	0.62	0.32	0.61