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# Community-level patterns of parasitism: Use of three common hosts by a brood parasitic bird, the brown-headed cowbird<sup>1</sup>

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**Abstract:** Patterns of host use by avian obligate brood parasites are geographically and temporally variable and have been linked to parasite density, host quality and abundance, and the availability of alternative hosts. We tested three non-exclusive hypotheses addressing the relationships between these factors and patterns of parasitism on the three most important host species in a community. We collected 5 y of data (1994-1998) on the number of host nests, proportions of host nests that were parasitized (frequency) by brown-headed cowbirds (*Molothrus ater*), and the number of cowbird eggs per parasitized nest (intensity) at Delta Marsh, Manitoba. Parasitism on yellow warblers and red-winged blackbirds was positively related to overall host density, whereas parasitism on song sparrows was most frequent and intense but did not appear to be related to any of the factors tested. We suggest that host quality may explain the higher than expected use of song sparrows. Our findings demonstrate that host use was significantly different among host species and non-random. Observed patterns suggest that factors that alter the relative availability of hosts, such as host breeding synchrony, may modify the parasitism levels experienced by different host species.

**Keywords:** frequency-dependent parasitism, host nesting synchrony, host selection, *Molothrus ater*, parasite density.

**Résumé :** Les patrons d'utilisation des hôtes par les parasites aviaires des couvées sont variables dans l'espace et le temps. Ils sont également liés à la densité des parasites, à la qualité et à l'abondance des hôtes ainsi qu'à la disponibilité d'hôtes alternatifs. Nous avons vérifié trois hypothèses non exclusives sur les relations qui existent entre ces facteurs et les patrons de parasitisme chez les trois espèces d'hôtes les plus importantes d'une communauté. Pendant 5 a (de 1994 à 1998), nous avons récolté des données sur le nombre de nids des hôtes, la proportion (fréquence) de nids parasités par le vacher à tête brune (*Molothrus ater*) et le nombre d'œufs de vachers par nid parasité (intensité). L'étude a été menée dans le marais Delta, au Manitoba. Le parasitisme sur la paruline jaune et le carouge à épaulettes est relié de façon positive à la densité générale des hôtes. Le parasitisme sur le bruant chanteur s'est avéré le plus fréquent et le plus intense, mais il ne semble pas relié à un des facteurs testés. Cette plus grande utilisation des bruants chanteurs pourrait s'expliquer par la qualité de cet hôte. Nos travaux montrent que l'utilisation des hôtes diffère de façon significative entre les espèces d'hôtes et n'est pas aléatoire. De plus, les patrons observés suggèrent que des facteurs qui modifient la disponibilité relative des hôtes, tel le synchronisme de leur reproduction, peuvent altérer les niveaux de parasitisme chez différentes espèces d'hôtes.

**Mots-clés :** densité des parasites, *Molothrus ater*, parasitisme dépendant de la fréquence, sélection de l'hôte, synchronisme de la nidification des hôtes.

**Nomenclature:** American Ornithologists' Union, 1998.

## Introduction

Obligate brood parasites such as brown-headed cowbirds (*Molothrus ater*, hereafter cowbirds) lay their eggs in the nests of other bird species and depend on the host parents to rear their offspring. There is abundant evidence that brood parasitism negatively affects the reproductive success of individual host parents (reviewed by Lorenzana & Sealy, 1999). More controversial is the effect that brood parasitism can have on host populations, metapopulation dynamics of a host species (Pulliam, 1988), and

avian communities. While many studies have examined the effects of parasitism on host individuals and/or populations (reviews by Ortega, 1998; Rothstein & Robinson, 1998), comparatively less is known about factors that influence the underlying patterns of host use by cowbirds and other generalist brood parasites (but see Grzybowski & Pease, 1999). Independent tests of some of the factors have yielded ambiguous results. For example, host abundance has been shown to have no effect on parasitism in some communities (Strausberger & Ashley, 1997) and a negative effect in others (Scott, 1963; Fretwell, 1977; Clark & Robertson, 1979; Zimmerman, 1983; Freeman, Gori & Rower 1990; Hoover & Brittingham, 1993). Cowbird densities may also influence patterns of parasitism (Elliott, 1978; Hoover & Brittingham, 1993; Smith & Myers-Smith, 1998). In addition, observations of high-

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ly divergent parasitism frequencies on different host species within the same community (Fleischer, 1986; Briskie *et al.*, 1990) and of the general avoidance of inappropriate hosts (those yielding zero cowbird fledgling success) by cowbirds (Sealy & Bazin, 1995; Strausberger & Ashley, 1997) suggest that some degree of host selection may occur (Robinson *et al.*, 1995a,b). However, the preferential use of higher quality hosts (those most likely to fledge parasite young) by cowbirds has not been demonstrated unequivocally (Friedmann, 1963; Friedmann, Kiff & Rothstein, 1977; Payne, 1977).

In general, the available hosts within a community will vary in both their relative availability and quality. This variability is expected to influence the patterns of parasitism observed. Indeed, a survey of the literature reveals geographic differences in the frequency (proportion of available nests parasitized) and intensity (number of cowbird eggs in a single host nest) of parasitism on several common and widely distributed acceptable host species (Robertson & Norman, 1977; Weatherhead, 1989; Hoover & Brittingham, 1993; Smith, 1999; Grant & Sealy, 2002).

Despite the potential effects of alternate hosts in a host community, most studies of parasitism patterns have focused on single species even though several potential host species were present (Graber, 1961; Fretwell, 1977; Orians, Røskaft & Beletsky, 1989; Hoover & Brittingham, 1993; Kattan, 1997; Smith & Myers-Smith, 1998) or have been limited to reporting the proportion of nests parasitized in a community (Norris, 1947; Berger, 1951; Elliott, 1978; Brown, 1994). The few studies that have investigated patterns of parasitism on several co-existing hosts (Fleischer, 1986; Barber & Martin, 1997; Strausberger & Ashley, 1997; Strausberger, 1998) have yielded conflicting results regarding the effects of host availability, cowbird density, and host quality on parasitism patterns. A complete understanding of the factors that influence patterns of parasitism requires multiple-year studies documenting parasitism patterns on all potential hosts at a single location and the factors that affect the differential parasitism on the community of host species.

We analyzed 5 y of data on the availability of nests of the three most abundant and frequently parasitized species within the avian community at Delta Marsh, Manitoba (yellow warblers [*Dendroica petechia*, YEWA], red-winged blackbirds [*Agelaius phoeniceus*, RWBL], and song sparrows [*Melospiza melodia*, SOSPI]) to test several hypotheses (summarized by Smith & Myers-Smith, 1998) that may explain patterns of host use by cowbirds. We first tested the null hypothesis that host use was random, the “parasite density hypothesis” (Smith & Myers-Smith, 1998). This hypothesis assumes that cowbirds have no preferences for host species and suggests that parasitism can be predicted by parasite density alone. It predicts a strong positive relationship between both the frequency and intensity of parasitism and parasite density on all species of hosts (McGeen, 1972; Fretwell, 1977; Hoover & Brittingham, 1993; Smith & Myers-Smith, 1998).

As preliminary analyses indicated that patterns of host use were not random, we proceeded to test two alternative hypotheses, the “host selection hypothesis” (Smith

& Myers-Smith, 1998) and the “host synchrony hypothesis”. The “host selection hypothesis” predicts non-random host use and can take several forms (Smith & Myers-Smith, 1998), including “active host selection” and “frequency-dependant host selection”. “Active host selection” assumes that different host species vary in their value to brood parasites (*i.e.*, they rear more parasite young than other, less valuable species: Weatherhead, 1989; Grant & Sealy, 2002) and parasites actively choose to parasitize the more valuable host. This hypothesis predicts that valuable hosts will be parasitized more frequently and intensively than other host species and that the use of less valuable hosts will increase when valuable hosts are not available. “Frequency-dependant host selection” suggests that parasites will form a search image for the most common suitable host. This hypothesis assumes that parasites have no set preference for a particular species of host and predicts that rare species will be under-used.

The “host synchrony hypothesis” states that the degree of nesting synchrony will effectively alter host availability and predicts that parasitism will be negatively correlated with host nesting synchrony. Species that nest synchronously may “swamp” brood parasites with many more nests available simultaneously than can be parasitized (Clark & Robertson, 1979; Wiley & Wiley, 1980; Clotfelter, 1998; Clotfelter & Yasukawa, 1999a), thus reducing the proportion of host nests parasitized regardless of the absolute abundance of host nests.

These hypotheses are not mutually exclusive, nor do they consider all the possible factors that potentially influence host use by cowbirds. For example, cowbird density may act to modify the degree of host selectivity exhibited by cowbirds (Smith, 1999). At high parasite densities, cowbirds may lay at random or use sub-optimal hosts, while at lower densities cowbirds may exhibit a greater degree of host selectivity (Strausberger & Ashley, 1997; Hahn *et al.*, 1999).

## Methods

### FIELD METHODS

This study was conducted at the Delta Marsh Field Station in Manitoba, Canada (50° 11' N, 98° 23' W). We collected data during the cowbird breeding season (late May to early July) from 1994 through 1998. The 60-ha study area consisted of a 2-km strip of riparian habitat running parallel to the lakeshore, composed of a forested dune ridge (average width ~ 80 m) and the adjacent marsh (~ 200 m wide; for details see MacKenzie, Sealy & Sutherland, 1982; Alderson, Gibbs & Sealy, 1999). Three or four people searched for host nests daily between 0600h and 2000h (CST). The daily search effort averaged 24 person-hours. Red-winged blackbirds, yellow warblers, and song sparrows comprised more than 90% of the hosts on the site in each year and received most of the cowbird eggs (Table I and Figure 1). Other potential host species (Appendix I) were much less abundant and rarely parasitized (S. G. Sealy, unpubl. data; Neudorf & Sealy, 1994; Sealy & Bazin, 1995; Sealy & Neudorf, 1995; Sealy, 1996).

TABLE I. Number of host nests found and mean daily nesting synchrony index for each of the three main host species at Delta Marsh.

Species	Year	Number of nests	Synchrony index <sup>1</sup>
Yellow warbler	1994	36	0.454
	1995	121	0.337
	1996	91	0.630
	1997	49	0.424
	1998	150	0.259
	Mean ± SD	89.4 ± 47.8	0.421 ± 0.140
Red-winged blackbird	1994	127	0.217
	1995	55	0.186
	1996	42	0.419
	1997	85	0.251
	1998	85	0.297
	Mean ± SD	78.8 ± 32.9	0.274 ± 0.091
Song sparrow	1994	20	0.179
	1995	8	0.171
	1996	10	0.462
	1997	24	0.288
	1998	20	0.259
	Mean ± SD	16.4 ± 7.0	0.325 ± 0.174

<sup>1</sup>For details, see Data analysis in Methods.

In order to estimate our success at finding host nests, we quantified host nest availability based on censuses of singing males. Each week, we censused two 2,000-m transects, set 100-m apart, through the study site. Trained observers executed 10-min point counts every 100-m along each transect. All singing male yellow warblers, red-winged blackbirds, and song sparrows heard within a 50-m radius of each census point were counted. Numbers of nests were estimated by dividing the number of nests found by searchers by the number of males heard singing and comparing these values across weeks. As no attempts were made to determine the mated status of singing males or the levels of polygyny in red-winged blackbird harems, we may have overestimated the number of warbler and sparrow nests and underestimated the number of blackbird nests. Estimates based on these data suggest that we located more than 90% of the yellow warbler and red-winged blackbird nests and 50% of the song sparrow nests in each year. Female cowbird abundance (Figure 1) was quantified from mark-recapture data and opportunistic sightings of uniquely marked individuals (Woolfenden, Gibbs & Sealy, 2001).

Location and species were noted for all found nests, and nest contents were examined at least every other day until clutch completion, then at least weekly to determine the fate of the nest. All cowbird eggs were removed from host nests as they were discovered, and the eggs were used for genetic analyses of parentage (Alderson, Gibbs & Sealy, 1999; Woolfenden, Gibbs & Sealy, 2002; Woolfenden *et al.*, 2003). Cowbird eggs removed from song sparrow nests in all years were replaced with model cowbird eggs to maintain clutch volume (Rothstein, 1975). Cowbird eggs removed from red-winged blackbird nests were replaced with models in 1995 and 1996 as part of the protocol for another research project (Grant & Sealy, 2002). In 1998, all cowbird eggs were replaced with models in all host nests, including yellow warblers. The removal without replacement of cowbird eggs in

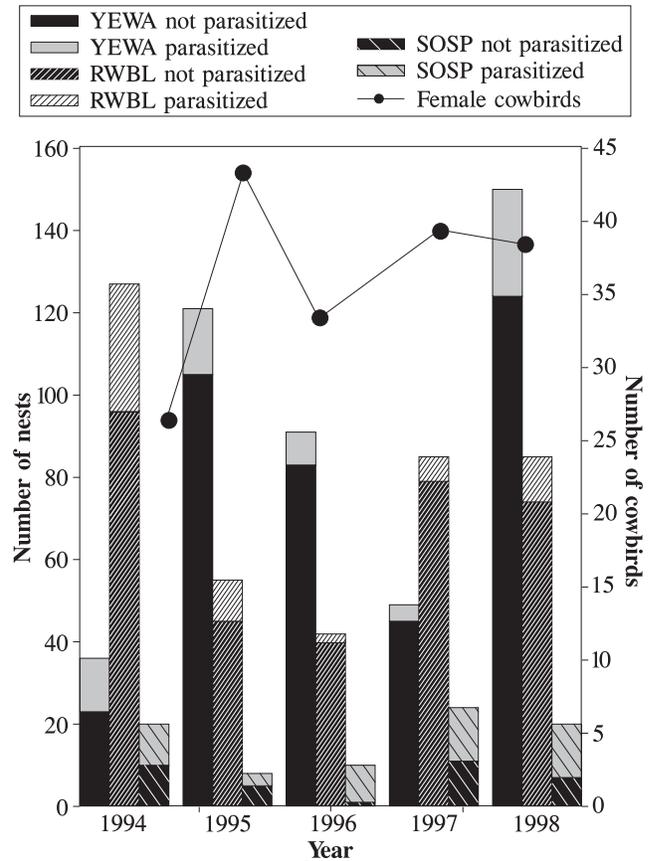


FIGURE 1. Annual number of host nests (YEWA = yellow warbler; RWBL = red-winged blackbird; SOSPA = song sparrow) monitored and number of female cowbirds in the cowbird host community at Delta Marsh, Manitoba from 1994 to 1998.

some years will not affect our conclusions because female cowbirds at Delta Marsh did not avoid laying in already-parasitized nests (S. G. Sealy and N. D. Grant, unpubl. data; but see Ortega, Ortega & Cruz, 1994). In this population, 20% of the parasitized nests were multiply parasitized (more than one cowbird egg laid in a single host nest) (McLaren, 2000; Woolfenden, 2000). Only cowbird eggs laid in nests that contained a real or model cowbird egg at the time of laying were considered to be cases of multiple parasitism. If a cowbird egg was found in a nest that had been parasitized but the first cowbird egg had been removed and not replaced, subsequent eggs were not considered to be cases of multiple parasitism in subsequent analyses. This is because the female cowbird that laid the second egg did not have information regarding the initial parasitism, unless she had the opportunity to see the first egg.

We determined the number of nests of each host species initiated during each week of the breeding season and the day of parasitism. Only nests that received an egg from either a host and/or a cowbird were included in subsequent analyses. Clutch initiation not directly observed was estimated by backdating from hatch date. For nests that failed before hatch, but found after clutch completion, we assumed the nest was found on the first day of incubation and back-dated accordingly to obtain the initiation date. When the date of laying of cowbird eggs was

not recorded, we assumed that it occurred on the first day of host laying. For nests that received a cowbird egg but no host eggs, clutch initiation was assigned as the date the cowbird egg was laid. Because nests were grouped by weeks and years for analysis, determination of the exact date of nest initiation and timing of parasitism at each nest was not critical. We restricted our analysis to data collected from yellow warbler, red-winged blackbird, and song sparrow nests because these species are parasitized more often than any other host species. Other potential host species, and the number of nests found on the study area are summarized in Appendix I.

DATA ANALYSIS

We determined the number of host nests available (see criterion below) and parasitism frequencies and intensities for each host species, weekly and annually. We used both parasitism frequency and intensity to quantify levels of parasitism because each measure describes a different aspect of parasitism. Cowbird responses to changing host availability may be to parasitize more nests or to lay more eggs in already-parasitized nests (Clotfelter & Yasukawa, 1999b; Mermoz & Reboreda, 1999). These two variables are not necessarily correlated (Strausberger, 1998), and both may reveal distinct information about cowbird responses to changes in host availability.

A synchrony index [Equation 1] (after Kempnaers, 1993) for host nests was calculated for each nest by determining the numbers of nests that were available for parasitism simultaneously. The period each nest was available for parasitism was defined as the 7-d period beginning 1 d prior to clutch initiation. The validity of this criterion is supported by data from this site (Sealy, 1995) that demonstrates most cowbird eggs are laid during this interval. The breeding synchrony index generates a number between 0 and 1, with values approaching one indicating more synchronous nesting. The index for each nest is equal to the total number of all nests (not including the focal nest) available on each day, divided by the product of the number of days a nest is available for parasitism (7 d) and the number of other nests in the study area.

$$SI = \frac{1}{F} \sum_{p=1}^{t_p} \left[ \frac{\sum_{i=1}^{t_p} (f_{ip})}{t_p(F-1)} \right] \times 100 \quad [1]$$

All results are presented as mean ± SD, unless otherwise indicated. Statistical significance was set at α = 0.05, and significance levels for multiple comparisons were adjusted using the sequential Bonferroni correction (Rice, 1989). Data were tested for normality and heteroscedasticity. Where violations of these assumptions were detected and where data consisted of discrete counts we used distribution free, non-parametric tests in the analyses. All statistical analyses were done using SPSS for Windows, release 11.0 software package (SPSS, Inc., Chicago, Illinois).

Results

Over the five breeding seasons, 923 nests of the primary host species (hereafter, host nests) were inspected: 447 (48.4% of total nests) yellow warbler nests, 394

(42.7%) red-winged blackbird nests, and 82 (8.9%) song sparrow nests (Table I and Figure 1). Timing of nest initiation (availability to cowbirds) varied among these species. Red-winged blackbirds and song sparrows generally initiated nesting first (Figure 2). In some years, their earliest nests were initiated before cowbirds started laying. Yellow warblers were consistently the last of the three hosts to begin nesting in each year, and cowbird laying overlapped with the warbler breeding season in all years.

PARASITISM FREQUENCY

We found 230 of 237 (97%) cowbird eggs and cowbird nestlings in nests of the primary host species and seven (3%) cowbird eggs in nests of other species (Appendix 1). On average, 18.8% (SD = 7.0%, minimum = 13%, maximum = 30%) of host nests were parasitized annually. Logistic regression analysis indicated that host species (Wald = 75.413; df = 2; P < 0.001) and synchrony index (Wald = 10.941; df = 1; P = 0.001) were significant predictors of parasitism, whereas year (Wald = 2.581; df = 1; P = 0.108) and week (Wald = 0.749; df = 1; P = 0.387) were not.

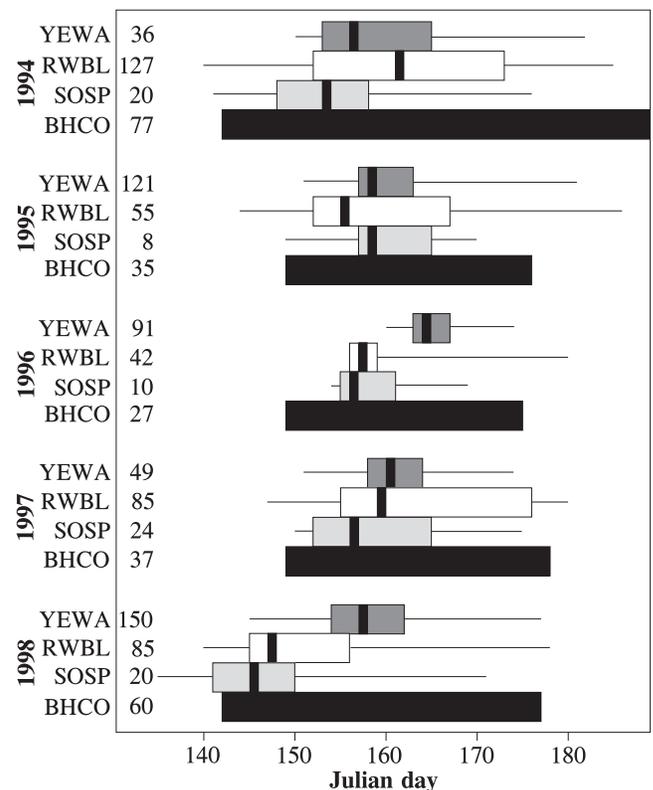


FIGURE 2. Timing of nest initiation for yellow warblers (YEWA), red-winged blackbirds (RWBL), and song sparrows (SOSP), and the start and end dates of the brown-headed cowbird (BHCO) laying period at Delta Marsh, Manitoba, during the 1994-1998 breeding seasons. The cowbird laying period was indicated by finding fresh cowbird eggs in host nests. The number to the left of the bar for each species indicates the number of nests for each host species and the number of eggs for cowbirds. Horizontal lines represent the range of nest initiation dates, thick, black, vertical lines represent the date on which 50% of the nests had been initiated and the shaded boxes represent the range of dates on which 25-75% of nests were initiated.

In general, song sparrows were parasitized most frequently in all years (range: 37% to 90%; mean = 59.3% ± 19.8; Figure 3). Comparing song sparrows to the other two host species, the odds of being parasitized were over 12 times higher (Wald = 73.145; df = 1;  $P < 0.001$ ; 95.0% confidence interval (C.I.) for EXP(B) = 6.803 - 21.273) than for red-winged blackbirds and almost 8 times higher than for yellow warblers (Wald = 49.564; df = 1;  $P < 0.001$ ; 95% C.I. for EXP(B) = 4.439 - 14.018). Parasitism frequencies on the other host species were lower than on song sparrows (YEWA: 16.7% ± 11.4; RWBL: 13.5% ± 8.0; Figure 3), and the odds of being parasitized were similar for red-winged blackbirds and yellow war-

blers (Wald = 3.442; df = 1;  $P < 0.064$ ; 95.0% C.I. for EXP (B) = 0.420 - 1.024).

PARASITISM INTENSITY

As parasitism intensity (number of cowbird eggs in each host nest, range 0-5) was not normally distributed, we tested for differences in parasitism intensities among species in each year using Kruskal-Wallis one-way rank ANOVAs. There were significant differences in parasitism intensity among the three host species in all years (Table II). Parasitism intensity was consistently highest for song sparrows, followed by red-winged blackbirds and yellow warblers ( $1.9 \pm 0.2$ ,  $1.3 \pm 0.2$ , and  $1.1 \pm 0.1$  cowbird

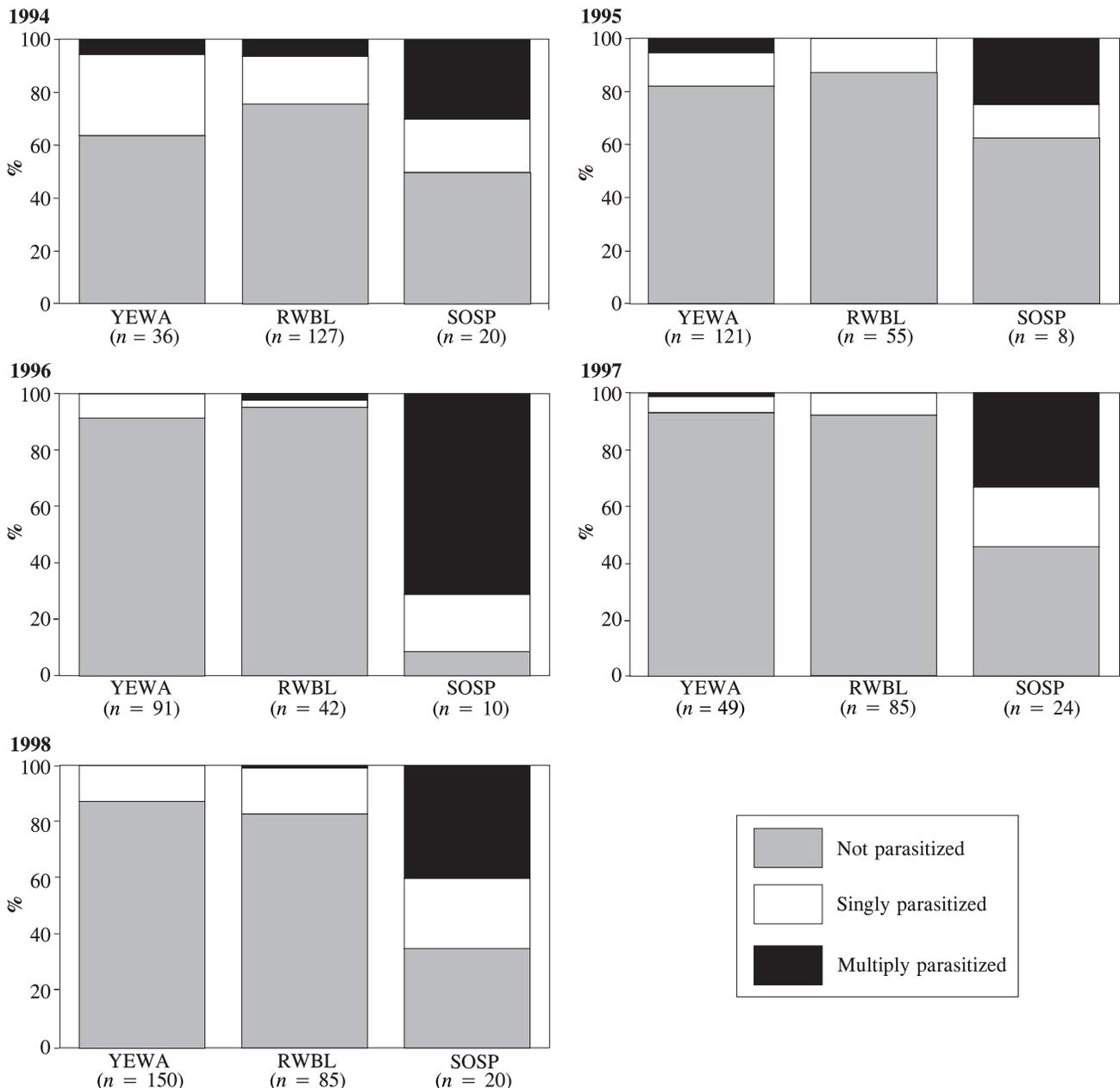


FIGURE 3. Variation in the frequency of host nests not parasitized (gray bar), singly parasitized (open bar), and multiply parasitized (black bar) for each host species in each year (1994-1998). The total number of nests monitored in each year is indicated in parentheses. YEWA: yellow warblers; RWBL: red-winged blackbirds; SOSP: song sparrows.

TABLE II. Mean annual parasitism intensity (number of cowbird eggs per nest) on yellow warblers, red-winged blackbirds, and song sparrows, and on all species combined. The numbers of multiply parasitized nests are indicated in parentheses. Kruskal-Wallis one-way rank ANOVAs were used to test for differences in parasitism intensities among species in each year.

Year	Yellow warbler	Red-winged blackbird	Song sparrow	Combined	H-value	P-value
1994	1.2 (2)	1.3 (8)	2.2 (6)	1.4 (16)	11.412	0.003
1995	1.0 (0)	1.4 (3)	1.7 (2)	1.2 (5)	8.580	0.014
1996	1.0 (0)	1.5 (1)	1.8 (7)	1.6 (8)	6.024	0.040
1997	1.0 (0)	1.2 (1)	2.0 (8)	1.6 (9)	6.374	0.041
1998	1.0 (1)	1.0 (0)	1.7 (8)	1.2 (9)	23.98	< 0.001
Mean ± SD	1.1 ± 0.1	1.3 ± 0.2	1.9 ± 0.2	1.4 ± 0.2		

eggs·nest<sup>-1</sup>, respectively; Table II). Spearman's rank correlation tests were used to test for correlations between the weekly frequency and weekly intensity of parasitism on each host species and all hosts combined. Following the Bonferroni correction (across the three species), parasitism intensity was significantly negatively correlated with parasitism frequency for song sparrows ( $r_s = -0.516$ ,  $n = 15$ ,  $P = 0.013$ ) but not for the other two hosts (YEWA:  $r_s = 0.383$ ,  $n = 13$ ,  $P = 0.111$ ; RWBL:  $r_s = 0.275$ ,  $n = 18$ ,  $P = 0.139$ ).

MULTIPLE PARASITISM

Logistic regression analysis indicated that host species (Wald = 66.359; df = 2;  $P < 0.001$ ) was a significant predictor of multiple parasitism (more than one cowbird egg in a single host nest) but year (Wald = 1.945, df = 1;  $P = 0.163$ ), week (Wald = 0.004; df = 1;  $P = 0.950$ ), and synchrony index (Wald = 0.240; df = 1;  $P = 0.624$ ) were not. A total of 5.3% of the available (includes parasitized and non-parasitized) host nests (three host species pooled) were multiply parasitized, and 29.2% of parasitized nests were multiply parasitized. Multiple parasitism was most frequent on song sparrows in all years (39.7% of available nests; Figure 3), and most parasitized song sparrow nests (65.5%) were multiply parasitized (Table II and Figure 3). By contrast, multiple parasitism occurred in only 3.1% of all available red-winged blackbird nests (Figure 3), and 24.5% of parasitized nests received more than one cowbird egg (Figure 3). Only 0.7% of yellow warbler nests were multiply parasitized (Figure 3), and in 3 of the 5 y no yellow warbler nests received multiple cowbird eggs (Table II). The odds of being multiply parasitized were over 20 times higher for song sparrows than for red-winged blackbirds (Wald = 49.439; df = 1;  $P < 0.001$ ; 95% C.I. for EXP(B) = 8.919 - 48.401) and over 217 times higher (Wald = 26.08; df = 1;  $P < 0.001$ ; C.I. for EXP(B) = 27.55 - 1,717.398) than for yellow warblers. The odds of being multiply parasitized were over 10 times higher for red-winged blackbirds than for yellow warblers (Wald = 4.741; df = 1;  $P < 0.029$ ; C.I. for EXP(B) = 1.264 - 86.702).

PARASITE DENSITY

Annual abundance of female cowbirds on the study site ranged from 25 to 42 resident individuals (mean = 33.6 ± 6.5; Figure 1). There were no significant correlations between annual female cowbird abundance and annual parasitism frequency on any of the host species (YEWA:  $r_s = 0.10$ ,  $n = 5$ ,  $P = 0.87$ ; RWBL:  $r_s = -0.30$ ,  $n = 5$ ,  $P = 0.62$ ; SOSp:  $r_s = -0.15$ ,  $n = 5$ ,  $P = 0.82$ ), nor

the three host species combined ( $r_s = -0.30$ ,  $n = 5$ ,  $P = 0.62$ ). Likewise, annual parasitism intensity was not correlated with female cowbird abundance for any species in any year (YEWA:  $r_s = -0.70$ ,  $n = 5$ ,  $P = 0.18$ ; RWBL:  $r_s = -0.10$ ,  $n = 5$ ,  $P = 0.88$ ; SOSp:  $r_s = -0.61$ ,  $n = 5$ ,  $P = 0.26$ ) nor for all host species combined ( $r_s = -0.31$ ,  $n = 5$ ,  $P = 0.60$ ). However, power analyses indicated that the power of these two correlation tests was low. The trend in both analyses is towards a negative correlation, suggesting that higher cowbird densities result in lower parasitism frequencies and intensities.

In order to account for changes in host densities (which would impact the abundance of cowbirds relative to the number of hosts) across years, we also tested for relationships between parasite-host ratios and the frequency and intensity of parasitism. There were no significant correlations between parasite-host ratios and parasitism frequency on any of the host species (YEWA:  $r_s = -0.62$ ,  $n = 5$ ,  $P = 0.27$ ; RWBL:  $r_s = -0.82$ ,  $n = 5$ ,  $P = 0.09$ ; SOSp:  $r_s = 0.00$ ,  $n = 5$ ,  $P = 1.00$ ), nor for the three host species combined ( $r_s = -0.820$ ,  $n = 5$ ,  $P = 0.09$ ), but there was a consistent trend towards a negative correlation in all species except the song sparrows.

Similarly, parasitism intensity was not correlated with parasite-host ratios for any species in any year (YEWA:  $r_s = -0.25$ ,  $n = 5$ ,  $P = 0.16$ ; RWBL:  $r_s = 0.15$ ,  $n = 5$ ,  $P = 0.80$ ; SOSp:  $r_s = -0.13$ ,  $n = 5$ ,  $P = 0.88$ ), nor for all host species combined ( $r_s = 0.49$ ,  $n = 5$ ,  $P = 0.41$ ), nor were there any clear trends in the data.

HOST SELECTION

We used ANOVAs to test for differences in the number of nests of each species available over all years and the number of nests available annually. There were significant differences in the number of nests of each species available ( $F = 5.56$ ; df = 2,8;  $P = 0.031$ ), but we did not detect differences in the number of nests available in each year ( $F = 0.44$ ; df = 4,8;  $P = 0.777$ ). The most abundant host alternated between red-winged blackbirds (1994 and 1997) and yellow warblers (1995, 1996, and 1998), but on average, yellow warbler nests were slightly more abundant (89.4 ± 47.8 nests) than red-winged blackbird nests (78.8 ± 32.9 nests) each year. Song sparrow nests (16.4 ± 7.0 nests) were least abundant in all 5 y (Table I and Figure 3). Estimates of relative host nest availability obtained from census data mirror the pattern of relative nest availability based on numbers of host nests located and monitored.

There were no significant correlations between weekly host nest abundance and weekly parasitism frequency for any

of the host species (YEWA:  $r_s = 0.301$ ,  $n = 20$ ,  $P = 0.198$ ; RWBL:  $r_s = 0.202$ ,  $n = 29$ ,  $P = 0.294$ ; SOSP:  $r_s = 0.287$ ,  $n = 21$ ,  $P = 0.206$ ) or all host species combined ( $r_s = 0.207$ ,  $n = 29$ ,  $P = 0.281$ ). Similarly, there were no significant correlations between weekly abundance of nests of each host species and parasitism intensities (YEWA:  $r_s = -0.269$ ,  $n = 13$ ,  $P = 0.375$ ; RWBL:  $r_s = -0.027$ ,  $n = 18$ ,  $P = 0.915$ ; SOSP:  $r_s = 0.302$ ,  $n = 15$ ,  $P = 0.274$ ) or all host species combined ( $r_s = -0.115$ ,  $n = 24$ ,  $P = 0.594$ ). However, there was a significant positive correlation between weekly abundance of all host nests combined and parasitism frequency on two of the three host species (YEWA:  $r_s = 0.881$ ,  $n = 25$ ,  $P < 0.001$ ; RWBL:  $r_s = 0.718$ ,  $n = 29$ ;  $P < 0.001$ ). In contrast, there was no significant relationship for song sparrows ( $r_s = 0.4690$ ;  $n = 26$ ;  $P = 0.016$ ). There was no correlation between weekly abundance of all host nests combined and parasitism intensity for any host (YEWA:  $r_s = 0.086$ ,  $n = 13$ ,  $P = 0.780$ ; RWBL:  $r_s = -0.153$ ,  $n = 18$ ,  $P = 0.546$ ; SOSP:  $r_s = 0.186$ ,  $n = 15$ ,  $P = 0.506$ ).

#### HOST SYNCHRONY

ANOVA indicated that host nesting synchrony varied significantly among host species ( $F = 9.691$ ;  $df = 8, 4$ ;  $P < 0.007$ ) and across years ( $F = 9.102$ ;  $df = 4, 8$ ;  $P < 0.005$ ). Yellow warblers were the most synchronous ( $0.42 \pm 0.32$ ), followed by song sparrows ( $0.33 \pm 0.17$ ) and red-winged blackbirds ( $0.27 \pm 0.09$ ; Table I). Overall weekly parasitism frequency was not significantly correlated with overall nesting synchrony ( $r_s = -0.121$ ,  $n = 28$ ,  $P = 0.538$ ), nor was weekly parasitism frequency correlated with nesting synchrony for any host (YEWA:  $r_s = -0.068$ ,  $n = 19$ ,  $P = 0.781$ ; RWBL:  $r_s = -0.119$ ,  $n = 29$ ,  $P = 0.537$ ; SOSP:  $r_s = 0.307$ ,  $n = 19$ ,  $P = 0.200$ ). Parasitism intensity was not correlated with the weekly nesting synchrony of any species, nor with all host species combined across weeks or among species within weeks (YEWA:  $r_s = 0.000$ ,  $n = 13$ ,  $P = 1.00$ ; RWBL:  $r_s = -0.053$ ,  $n = 18$ ,  $P = 0.834$ ; SOSP:  $r_s = 0.274$ ,  $n = 13$ ,  $P = 0.365$ ; ALL HOSTS:  $r_s = 0.054$ ,  $n = 23$ ,  $P = 0.807$ ).

## Discussion

#### PARASITE DENSITY

Female cowbird abundance was not related to parasitism frequency or intensity on any species in any year; however, there was a trend of decreasing parasitism with increasing cowbird density, suggesting that as cowbird density increases parasitism declines. This finding is difficult to interpret and contrary to the conclusions of several other studies (Elliott, 1978; Hoover & Brittingham, 1993; Smith & Myers-Smith, 1998). We suggest two possible explanations for the discrepancy. First, the scale of the analyses may be an important factor. Studies supporting the parasite-density hypothesis have typically used Breeding Bird Survey data to estimate cowbird abundance at a regional scale and have considered the relationship between cowbird abundance and parasitism frequency on a single species over a range of habitat types and communities (Hoover & Brittingham, 1993; Smith & Myers-Smith, 1998). Differences in habitat and the composition of host communities among geographic regions may be driven by variation in host and parasite densities among

habitat types. If this is the case, a relationship between parasite density and levels of parasitism is not expected within a single community, because host and habitat composition did not vary greatly within this community. Secondly, previous research on this population (Woolfenden, Gibbs & Sealy, 2002) has shown that not all resident female cowbirds breed on the study site and, therefore the numbers of female cowbirds estimated by census and/or mark-recapture data may not accurately reflect the actual risks of parasitism.

Another possible effect of parasite density may be to modify cowbird host selectivity. Specifically, selectivity may vary inversely with the female cowbird-to-host ratio within a landscape (Smith & Myers-Smith, 1998). This relationship was not detected in this study. The average female cowbird-to-host ratio (Robinson, Hoover & Herkert, 2000) for the Delta Marsh community was  $0.2 \pm 0.05$  (1994 = 0.14; 1995 = 0.23; 1996 = 0.22; 1997 = 0.24; 1998 = 0.15), which is much higher than those reported for other areas (Robinson, Hoover & Herkert, 2000). Despite the extremely high cowbird-to-host ratio, our data indicated that cowbirds did not parasitize hosts at random.

There was no relationship between parasitism frequency or intensity and host abundance for any species or among species in any year. In general, host species were not parasitized as expected based on the relative availability of nests of each species (*i.e.*, at random). However, there were significant, positive relationships between overall host abundance and parasitism frequency on both yellow warblers and red-winged blackbirds. The trend for song sparrows was also positive. This pattern may be due to the presence of conspicuous co-occurring host species that increase the risk of parasitism on alternative hosts in the community (Briskie, Sealy & Hobson, 1990; Martin, 1992; Barber & Martin, 1997). Cowbirds may initially be attracted to more conspicuous species such as red-winged blackbirds, but they parasitize yellow warblers because factors other than host abundance, such as less vigorous nest defence, interact to make yellow warblers more accessible (Robertson & Norman, 1977). A similar association was documented between black-capped vireos (*Vireo atricapillus*) and northern cardinals (*Cardinalis cardinalis*) in Texas (Barber & Martin, 1997).

#### HOST SYNCHRONY

When hosts nest synchronously, most nests are available for parasitism relatively simultaneously. This effectively "swamps" cowbirds because there are more host nests available than can possibly be parasitized (Clark & Robertson, 1979; Wiley & Wiley, 1980; Martinez, Soler & Soler, 1996; Mermoz & Reboreda, 1999). This effect may be enhanced in colonial species like the red-winged blackbird that also exhibit nest defence. However, our analysis did not detect any relationships between parasitism and host-nesting synchrony for any of the host species tested.

#### HOST SELECTION HYPOTHESIS

As all cowbird eggs were removed from host nests for use in a concurrent genetic parentage analysis (Woolfenden, Gibbs & Sealy, 2002; Woolfenden *et al.*,

2003), it was not possible to directly test for differences in the value of the hosts and the possible effects of differential host values on patterns of parasitism. However, several lines of evidence suggest that the non-random parasitism observed in this study is related to differences in host value to the parasites. First, data collected at Delta Marsh prior to this study (RWBL and YEWA) and from other host communities (SOSP) indicate differences in the value of these three hosts. The percent of cowbirds fledged per egg laid in a host nest was 3.9% ( $n = 51$ ) for yellow warblers (Goossen & Sealy, 1982; Weatherhead, 1989), 27.1% for red-winged blackbirds (Weatherhead, 1989), and ranged from 30.5 to 52.2% for song sparrows (Norris, 1947; Berger, 1951; Smith & Arcese, 1994). Additionally, the song sparrow is an acceptor species (Friedmann, 1963), whereas yellow warblers are rejecters in this population (Clark & Robertson, 1979; Goossen & Sealy, 1982; Weatherhead, 1989). Research indicates that female yellow warblers bury up to 36% of cowbird eggs laid in their nests (Sealy, 1995). Secondly, song sparrows were the most frequently parasitized of the three species studied despite being the least abundance host species. Parasitism on song sparrows was not simply opportunistic, because the observed frequencies were not simple responses to the relative number of song sparrow nests available. Finally, song sparrows were the most intensively parasitized host species. Multiple parasitism may be indicative of cowbird host preferences or simply a shortage of nests (Smith & Myers-Smith, 1998). However, our data support the interpretation that parasitism intensity is high on this species due to cowbird preferences. Parasitism intensity was high regardless of the abundance of song sparrow nests, parasitism of song sparrows was consistently high, whereas parasitism on the alternative hosts (YEWA and RWBL) was variable (Figure 3), and overall parasitism frequencies were below 100%. Taken together these observations suggest that song sparrow nests were not parasitized more often than expected simply because host nests were in short supply. It is also possible that the apparent over-use (relative to their abundance) of song sparrows as a host may also be due to cowbirds encountering them at a higher rate during nest searching or due to less overt nest defence by song sparrows when compared to aggressive species like the red-winged blackbird.

#### COMMUNITY PATTERNS OF PARASITISM

Parasitism patterns in this community were complex and resulted from interactions of several factors that differentially impacted the patterns of parasitism observed on each of the host species in the community. Data from other studies regarding the relative value of the three host species and our data on patterns of cowbird parasitism relative to host availability suggest that cowbirds non-randomly parasitize some host species (song sparrows), possibly on the basis of their abilities as surrogate parents. This warrants further investigation given the practical implications for the conservation of rare species that are highly valuable as cowbird hosts (*e.g.*, least Bell's vireo; Franzreb, 1985). If this relationship is real, then parasitism pressures on high-value host species will remain high regardless of the availability or the abundance of alternative hosts in the community. Ultimately, the effects

of preferential parasitism may contribute to the extirpation of locally rare species or, in extreme cases, to a decline in species abundance. This type of interaction may have been a factor in the extirpation of the veery (*Catharus fuscescens*) from the Delta Marsh study site. Veerys are valuable cowbird hosts that nested on the study site in relatively low numbers prior to the mid 1980s (S. G. Sealy, unpubl. data). Despite their low abundance, they were the most frequently parasitized host until their disappearance from the area.

By contrast, parasitism frequencies on alternative host species were affected by nest abundance and relative availability. This finding suggests that some of the variation in parasitism frequencies on a particular species in different communities is likely related to differences in the composition of the host communities and the availability of preferred and alternative host species (Freeman, Gori & Rower, 1990). Geographic variation in host use may result if a species is not the most valued host in all communities and if the numbers and/or diversities of alternative hosts vary.

Overall, this study provides the most complete analysis to date of the factors that determine host use by cowbirds within a single host community. Cowbirds in this community appear to be capable of fine-grain assessments of several host species, as evidenced by the non-random patterns of parasitism observed. These patterns are the result of the interactions of several factors, which each affect different hosts differently. Our findings confirm that parasitism patterns are complex and that complete information on all available host species is required to identify the factors and interactions that determine the levels of parasitism on different hosts within a community or on a single host species in different communities.

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APPENDIX I. Summary of the number of nests monitored annually, overall percentage of nests parasitized, and the mean number of cowbird eggs per parasitized nest for the alternate host species at Delta Marsh, Manitoba during the 1994-1998 cowbird breeding season.

Species	Number of nests					Mean number % nests parasitized	Cowbird eggs per parasitized nest
	1994	1995	1996	1997	1998		
Eastern kingbird ( <i>Tyrannus tyrannus</i> ) <sup>a</sup>					4	0	
Alder flycatcher ( <i>Empidonax alnorum</i> )	1	0	0	0	0	100	2
Marsh wren ( <i>Cistothorus palustris</i> ) <sup>a</sup>		6				0	
Gray catbird ( <i>Dumatella carolinensis</i> )		1	12	14	6	9	1
American robin ( <i>Turdus migratorius</i> )	1	10	15	10		0	
Veery ( <i>Catharus fuscescens</i> )	1	0	0	0	0	100	1
Warbling vireo ( <i>Vireo gilvus</i> ) <sup>a,b</sup>					6	0	
Common yellowthroat ( <i>Geothlypis trichas</i> ) <sup>c</sup>		1				100	1
Yellow-headed blackbird ( <i>Xanthocephalus xanthocephalus</i> ) <sup>a</sup>		29	17	1	1	0	
Common grackle ( <i>Quiscalus quiscula</i> ) <sup>a</sup>		15	10	2	11	0	
Baltimore oriole ( <i>Icterus galbula</i> ) <sup>a</sup>		6			5	0	
Savannah sparrow ( <i>Passerculus sandwichensis</i> )	0	2	0	2	0	0	
La Conte's sparrow ( <i>Ammodramus leconteii</i> )	0	0	0	0	1	0	
Swamp sparrow ( <i>Melospiza georgiana</i> )	0	0	0	0	1	0	

<sup>a</sup> Although this species nested on the study area, no parasitism was recorded and no data regarding the exact number of nests were recorded for that year.

<sup>b</sup> T. Underwood (unpubl. data).

<sup>c</sup> Common yellowthroat males were observed singing throughout the study area in all years, but a nest was only located in one year.