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Brown-headed Cowbird, *Molothrus ater*, Parasitism and Abundance in the Northern Great Plains

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The Brown-headed Cowbird (*Molothrus ater*) reaches its highest abundance in the northern Great Plains, but much of our understanding of cowbird ecology and host-parasite interactions comes from areas outside of this region. We examine cowbird brood parasitism and densities during two studies of breeding birds in the northern Great Plains during 1990–2006. We found 2649 active nests of 75 species, including 746 nonpasserine nests and 1902 passerine nests. Overall, <1% of nonpasserine nests and 25% of passerine nests were parasitized by Brown-headed Cowbirds. Although the overall frequency of cowbird parasitism in passerine nests in these two studies is considered moderate, the frequency of multiple parasitism among parasitized nests was heavy (nearly 50%). The mean number of cowbird eggs per parasitized passerine nest was 1.9 ± 1.2 (SD; range = 1–8 cowbird eggs). The parasitism rates were 9.5% for passerines that typically nest in habitats characterized by woody vegetation, 16.4% for grassland-nesting passerines, 4.7% for passerines known to consistently eject cowbird eggs, and 28.2% for passerines that usually accept cowbird eggs. The Red-winged Blackbird (*Agelaius phoeniceus*) was the most commonly parasitized species (43.1% parasitism, 49.6% multiple parasitism, 71.2% of all cases of parasitism). Passerine nests found within areas of higher female cowbird abundance experienced higher frequencies of cowbird parasitism than those found in areas of lower female cowbird abundance. Densities of female cowbirds were positively related to densities and richness of other birds in the breeding bird community.

Key Words: Brown-headed Cowbird, *Molothrus ater*, brood parasitism, grasslands, multiple parasitism, spatial variation, temporal variation, northern Great Plains.

The Brown-headed Cowbird (*Molothrus ater*; hereafter cowbird) is an obligate brood parasite that lays its eggs in nests of a variety of host species. Cowbird distribution, abundance, and brood parasitism have long been major topics in avian ecology in North America (Nice 1937; McGeen 1972; May and Robinson 1985; Ortega 1998; Herkert et al. 2003). Cowbird abundance and rates of brood parasitism vary geographically (Robinson et al. 1995; Ortega 1998; Rothstein and Robinson 1998). The cowbird reaches its highest abundance in the northern Great Plains (Sauer et al. 2005*), yet much of our understanding of cowbird parasitism and the dynamics of host and parasite populations comes from areas outside of this region. Nonetheless, some studies have reported high rates of cowbird parasitism and multiple parasitism in the northern Great Plains (e.g., Linz and Bolin 1982; Romig and Crawford 1995; Davis and Sealy 2000; Koford et al. 2000). Robinson and Smith (2000), however, suggested that some of these oft-cited studies may not be representative of the northern Great Plains. There are few published examples of community-wide studies of cowbird parasitism in the northern Great Plains (e.g., Granfors et al. 2001; Woolfenden et al. 2004). Rather, most reports of cowbird parasitism from this region focus on a single species (e.g., Linz and Bolin 1982), a subset of species (e.g., Winter et al. 2004), or species that have evolved defenses against cowbird parasitism (Sealy 1996).

At the continental level, cowbird abundance declines with distance from the center of the species' breeding range in the northern Great Plains (Thompson et al. 2000). The frequencies of cowbird parasitism appear to follow a similar biogeographical pattern (e.g., Smith and Myers-Smith 1998), especially for grassland birds (Jensen and Cully 2005a, 2005b), although this relationship may not be generalized across habitats (Robinson and Smith 2000) and may not be indicative of parasitism frequencies at the local level (Chace et al. 2005). Nonetheless, Chace et al. (2005) acknowledged that, at the continental scale, cowbird abundance appears to be a reasonable predictor of cowbird parasitism levels. Because of the difficulty in obtaining data on both cowbird abundance and brood parasitism across the continent (or even over a large region), there are few examples of studies that have evaluated this relationship using cowbird and nest data collected concurrently at the same study sites over a large region (e.g., Robinson et al. 2000; Jensen and Cully 2005a, 2005b). Only a few evaluations of this biogeographical relationship have included data from study sites in the northern Great Plains (e.g., Smith and Myers-Smith 1998; Herkert et al. 2003).

At local and regional scales, geographic differences in cowbird distribution and abundance also may result from differences in avian communities (e.g., Farmer 1999; Thompson et al. 2000). That is, given that cowbirds are host generalists, measures of avian abundance or richness might serve as proximate cues for cowbirds in determining where to settle (McGeen 1972; Farmer 1999). Chace et al. (2005) listed four nested levels of an avian community that cowbirds could use as cues for settlement: (1) all breeding birds in the avian community, (2) all passerine species, (3) all host species, and (4) a single host species. Very few studies have evaluated this relationship at all four levels (Farmer 1999). Using BBS (Breeding Bird Survey) data, Hahn and O'Connor (2002) concluded that cowbird distribution was not simply the result of shared habitat preferences with their hosts, but rather host abundance was an important predictor of cowbird occurrence in recently colonized regions of the United States (i.e., eastern and western states) and to a lesser extent in the cowbird's ancestral range (i.e., central Great Plains). Except for Hahn and O'Connor's (2002) evaluation using BBS data, the influences of avian abundance and richness on cowbird distribution and abundance have not been evaluated using regional data from the northern Great Plains (reviewed in Chace et al. 2005).

In this paper, we report cowbird densities and parasitism frequencies during two breeding-bird studies in the northern Great Plains: a statewide study in North Dakota (1992 and 1993: Igl and Johnson 1997; Igl et al. 1999) and a Conservation Reserve Program (CRP) grassland study in nine counties of four states (1990–2006: Johnson and Schwartz 1993a, 1993b; Igl and Johnson 1995, 1999; Johnson and Igl 1995, 2001). We use data from nests found incidentally during both studies to examine weekly and annual variation in parasitism rates in the northern Great Plains, and nest data from the CRP grassland study to examine regional variation in parasitism rates. We use data from the long-term CRP grassland study to evaluate the relationships between female cowbird densities and cowbird parasitism and between female cowbird densities and avian densities and richness in different regions of the northern Great Plains. CRP grasslands are a suitable habitat to evaluate these relationships because this habitat has been shown to be a dominant landscape predictor of cowbird distribution in the United States (Hahn and O'Connor 2002).

Study Areas

North Dakota statewide study

The study area for the North Dakota statewide study was described in detail by Stewart and Kantrud (1972) and Igl and Johnson (1997) and is only briefly described here. North Dakota was divided into eight major strata based on biogeographical, physiographical, and ecological characteristics. From these eight strata, 130 quarter-sections (about 64.75 ha each) were selected randomly (Figure 1). The number of sample units allocated to each stratum was proportional to the area of the stratum. Landowners denied access to one quarter-section in 1992 and a different quarter-section in 1993.

CRP grassland study

The CRP study is an ongoing investigation (1990 to present) that is examining breeding-bird communities annually in nearly 350 CRP grassland fields in nine counties of four states (Figure 2), including Fallon and Sheridan counties in Montana; Hettinger, Kidder, and Eddy counties in North Dakota; Butte, McPherson, and Day counties in South Dakota; and Grant County in Minnesota (Johnson and Schwartz 1993a, 1993b). Field size varied from <1.0 to 111.7 ha. In the northern Great Plains, most CRP land was planted to a mixture of native and/or non-native grasses and legumes (Johnson and Schwartz 1993a). Woody vegetation has encroached into some idle CRP fields, and some CRP fields contain wetlands or were partially inundated by water during a recent wet period (Igl 2001; Igl and Johnson, unpublished data).

Methods

Breeding bird and cowbird surveys

In both studies, we conducted total area counts of breeding birds using the strip-transect procedure employed by Stewart and Kantrud (1972; also see Igl and Johnson 1997). During the North Dakota statewide study, bird surveys were conducted by two observers on foot, and each observer surveyed cowbirds and other breeding birds on a rectangular half (805 * 402 m; 32.37 ha) of a quarter-section by following a standardized survey route. This route was 100 m inside of, and parallel to, the boundary of the rectangle. The rectangular halves were usually surveyed simultaneously, and an interval of 400 m was maintained between observers. Deviations of up to 100 m from the route were often necessary to adequately survey all habitats.

Bird species were identified by sight or sound. Counts during precipitation and strong winds (> 24 km/h) were avoided. Surveys of open country birds were conducted between 0.5 h after sunrise and 15:00 CST. Although some surveys occurred outside the time of

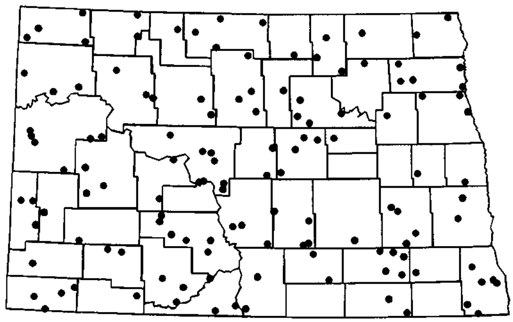

FIGURE 1. Distribution of 130 quarter-sections (64.75 ha each) in North Dakota in which bird surveys were conducted during the breeding seasons in 1992 and 1993.

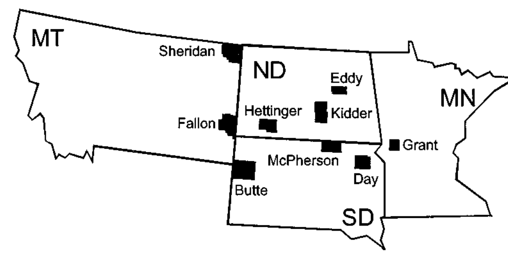

FIGURE 2. Counties in which Conservation Reserve Program grassland fields were surveyed for breeding birds in North Dakota, South Dakota, Minnesota, and Montana, 1990–2006.

most active bird vocalizations (i.e., early morning or late evening), Stewart and Kantrud (1972) concluded that singing and other activities of open-country birds were not appreciably affected by time of day (also see Vickery 1995*). Quarter-sections containing extensive woodland habitats were usually covered on relatively calm (<8 km/h), sunny days between 0.5 h after sunrise and 10:00 CST. These limitations were necessary because song frequencies and other activities of most woodland birds are reduced on cloudy days, in moderate or high winds, and at mid-day.

Counts of breeding birds were based primarily on the number of indicated breeding pairs on territories or home ranges during peak breeding periods. All sample units were surveyed for early-nesting species between 24 April and 7 June, for mid-nesting species between 14 May and 10 July, and for late-nesting species between 22 May and 21 July. When a survey was conducted during an overlapping portion of the peak breeding periods, counts of early-, mid-, and late-nesting species coincided. Thus, quarter-sections that were visited between 22 May and 7 June were only surveyed once, and those that were surveyed before 22 May were surveyed again after 7 June so as to include species from all three breeding periods. For most species, nearly all indicated pairs were observed as segregated pairs or as territorial males. For the sexually dimorphic Brown-headed Cowbird, we separately tallied the males and females seen per sample unit; herein, we report only female cowbird densities. We did not consider certain birds observed during the censuses to be breeding and excluded them from our results. These included late-migrating flocks and other birds passing overhead in high, direct flight. By counting birds only during their peak breeding periods, we maximized the potential for recording breeding birds and, at the same time, minimized the likelihood of confounding breeding birds with migrants.

In the CRP study, total area counts of breeding birds were conducted by using a minor modification of the strip-transect procedures used by Stewart and Kantrud (1972) and Igl and Johnson (1997). Small fields usually were surveyed by a single observer; large fields typically were surveyed by two observers on foot, each simultaneously covering about one-half of the field. The number and configuration of transects were consistent among years but varied depending upon the field size and shape to achieve total coverage of a field. We surveyed each CRP grassland field once each year between 21 May and 9 July in 1990–2006.

Nests and cowbird parasitism

Prior to entering the field in each year, the observers were trained in bird, nest, and egg identification. Nests were found serendipitously during breeding bird surveys and related research activities. Most nests were found by unintentionally flushing an adult host (or rarely a female cowbird) from the nest or nest vicinity. The remainder of the nests were found by observers as they were simply walking through a habitat. When a nest was located, we inspected it and recorded the species (based on the identification of the flushing adult, the nest, or the nest contents) and the number of eggs or nestlings of the host and of cowbirds. If the nest species could not be identified at the time of the initial observation, the nest location was temporarily marked and then revisited and identified at the end of the survey by an experienced observer. We classified a nest as parasitized if it contained at least one cowbird egg or nestling, regardless of the stage of the nesting cycle. Cowbird and host nestlings were identified based on size, gape and flange colors, and down or contour feather characteristics and development. We were unable to return to nests to monitor their outcome or to document additional brood parasitism. We rarely located or checked the contents of nests of upper-canopy nesting species. Most of the nests that we located were found in the egg-laying stage or the incubation stage (see below); cowbirds lay most of their eggs before or during the hosts' egg-laying stage (Johnsgard 1997). Although we found many nests in the nest-building stage (i.e., before the onset of egg laying), we summarize here only active nests, which we defined as nests attended by adults that contained at least one host or cowbird egg and/or nestling. We also found a few abandoned nests that contained cowbird eggs, but these are not reported because cowbirds are known to parasitize inactive nests (Freeman et al. 1990). The presence of cowbird fledglings that were fed by adult hosts also was noted during the surveys of breeding birds, although an observation of a potential host feeding a cowbird fledgling does not establish conclusively the true foster-parentage of the fledgling cowbird (sensu Klein and Rosenberg 1986).

We use the frequency (%) of nests parasitized as an index to the levels of parasitism. We define the frequency (%) of cowbird parasitism as the total number of parasitized nests (*100) divided by the total number of active nests found for a given species, group of species (e.g., grassland birds), county, or time period (week or year). We define the frequency (%) of multiple parasitism as the total number of nests containing more than one cowbird egg (*100) divided by the total number of parasitized nests found for a given species, group of species, county, or time period. The average (± SD) number of cowbird eggs per parasitized nest (i.e., parasitism intensity) was calculated by summing the number of cowbird eggs found in all parasitized nests in both studies and dividing by the total number of parasitized nests. Although cowbirds may avoid parasitizing nests of ejector species (Sealy and Bazin 1995), we include nests of all passerine species, because ejector species are sometimes parasitized (e.g., Scott 1977; Peer et al. 2000), because parasitism of ejector species may vary geographically (e.g., Haas and Haas 1998) or with time of sympatry with cowbirds (Briskie et al. 1992), and because it is difficult to estimate how often ejector species are parasitized (e.g., Scott 1977). To evaluate changes in cowbird parasitism within the breeding season, we divided each month into four, roughly weekly, periods (7, 8, 7[8] and 8 days, respectively) (sensu Orians et al. 1989). For discussion purposes, we grouped rates of parasitism and multiple parasitism into five categories: low (<10%), low-to-moderate (10–20%), moderate (20–40%), moderate-to-heavy (40–50%), and heavy (>50%) (sensu Ortega 1998: 184). Scientific names of potential host species are included in Table 2.

To determine whether cowbirds avoid laying eggs in previously parasitized nests (Mayfield 1965a; Orians et al. 1989), we evaluated the distribution pattern of cowbird eggs (i.e., random or non-random) using a zero-truncated Poisson distribution model for only parasitized nests (Lindsey 1997). A random distribution of cowbirds eggs suggests that female cowbirds did not discriminate among parasitized nests and that the proportion of nests with 1, 2, 3, 4, …, *i* cowbird eggs approximated a Poisson distribution (Orians et al. 1989). A non-random distribution of cowbird eggs indicated that the random distribution model was rejected ($P < 0.01$).

For both studies, we calculated overall parasitism frequencies, mean densities of female cowbirds, mean avian densities, and mean avian richness. For the CRP grassland study, we calculated mean avian density and richness among five groups (all of which excluded cowbirds): (1) all avian species, (2) all passerine species, (3) all passerines known to have raised cowbird young (Ortega 1998; Davis and Sealy 2000), (4) all passerines excluding ejectors (Peer and Sealy 2004), and (5) a single, preferred host (i.e., Red-winged Blackbird; see below). We were interested in the regional avian influences that affect cowbird distribution and abundance rather than short-term influences, and thus we averaged across the 17 years within a county and did not analyze the survey data separately for individual years. For the CRP grassland study, we used female cowbird densities both as an explanatory variable in relation to rates of cowbird parasitism and as a response variable in relation to avian community variables (i.e., density and richness). Linear regression analyses (PROC REG; SAS Institute, Inc. 2004) were performed (1) to determine the relationship between overall cowbird parasitism and female cowbird densities, and (2) to examine the relationship between female cowbird densities and the five levels of the avian community.

Results

In the North Dakota study, we observed 160 breeding bird species, including 78 nonpasserine species and 82 passerine species (Igl and Johnson 1997). Given that grasslands, croplands, and wetlands are the three most common habitats in North Dakota (Igl and Johnson 1997), most of the common breeding bird species in North Dakota are associated with such open habitats. The five most abundant species in the North Dakota study, in decreasing order of abundance, were the Horned Lark, Chestnut-collared Longspur, Red-winged Blackbird, Western Meadowlark, and Lark Bunting (scientific names given in Table 2). Average breeding bird densities in a quarter-section, excluding cowbirds, were 126 breeding pairs per 100 ha in 1992 and 143.9 breeding pairs per 100 ha in 1993 (Table 1). The average numbers of species observed in a quarter-section (64.75 ha) were 18.5 species in 1992 and 21.6 species in 1993. Average cowbird densities were 3.0 female cowbirds per 100 ha in 1992 and 4.3 female cowbirds per 100 ha in 1993. Female Brown-headed Cowbirds were found in 66.7 and 76.7% of the quarter-sections in 1992 and 1993, respectively.

In the CRP grassland study, we observed 143 breeding bird species, including 78 nonpasserine species and 65 passerine species. The five most abundant species, in decreasing order of abundance, were Savannah Sparrow, Grasshopper Sparrow, Red-winged Blackbird, Clay-colored Sparrow, and Western Meadowlark. Average breeding-bird densities within a county (averaged across years and excluding cowbirds) ranged from 104.1 to 208.1 breeding pairs per 100 ha, and the average number of species observed within a county ranged from 26.8 to 52.7 species (Table 1). Average cowbird densities within a county ranged from 0.6 to 8.0 female cowbirds per 100 ha, and the average annual

TABLE 1. Summary of Brown-headed Cowbird densities (females/100 ha), cowbird occurrence, breeding bird densities (all species excluding cowbirds; breeding pairs/100 ha), and number of breeding bird species per quarter-section in two studies in the northern Great Plains, 1990-2006.

Year or Study Location	Female cowbird density		Female cowbird occurrence		Breeding bird density		Number of breeding bird species	
	Mean	SE	Mean %	SE	Mean	SE	Mean	SE
North Dakota statewide study								
1992	3.0	0.3	0.67	–	126.0	7.8	18.5	0.8
1993	4.3	0.5	0.77	–	143.9	7.3	21.6	0.9
CRP grassland study (1990–2006)								
Butte County, South Dakota	0.6	0.1	0.14	0.02	105.8	5.9	28.5	1.4
Day County, South Dakota	8.0	0.7	0.54	0.03	208.1	14.5	48.8	2.7
Eddy County, North Dakota	6.3	0.4	0.49	0.03	188.7	15.1	45.5	2.5
Fallon County, Montana	0.9	0.2	0.12	0.02	104.1	9.1	26.8	1.2
Grant County, Minnesota	3.1	0.4	0.25	0.02	181.8	13.7	39.6	2.2
Hettinger County, North Dakota	5.7	0.5	0.52	0.03	160.0	9.3	33.2	1.3
Kidder County, North Dakota	5.9	0.3	0.50	0.01	160.2	14.1	52.7	2.8
McPherson County, South Dakota	7.1	0.5	0.54	0.02	164.5	9.8	43.8	2.4
Sheridan County, Montana	2.8	0.9	0.29	0.05	122.3	7.4	30.4	1.1

frequency of female cowbird occurrence ranged from 12.4 to 54.1%. Average cowbird densities and frequencies were lowest in the counties on the eastern and western edges of our study area (Table 1, Figure 2). This pattern mirrors cowbird distribution maps from the North American BBS (Price et al. 1995; Sauer et al. 2005*), which show cowbird abundance declining both east and west of central North Dakota and South Dakota.

We found 351 active nests of 51 species (18 nonpasserine and 33 passerine species) during the North Dakota statewide study and 2298 active nests of 62 species (23 nonpasserine and 39 passerine species) during the CRP grassland study, for a total of 2649 nests of 75 species (Table 2). Most of the nests of nonpasserine species were found during the egg-laying or incubation stages; 89.9% of the 746 nests of nonpasserine species contained only eggs, and 10.1% contained only nestlings or both eggs and nestlings. Only one nonpasserine nest was parasitized by a cowbird (Table 2). An Upland Sandpiper nest with four sandpiper eggs and one cowbird egg was found in a CRP grassland field in Sheridan County, Montana, on 28 June 1993. Hereafter, we summarize data only for passerine nests.

Most of the active nests of passerines were found during the egg-laying or incubation stages; 85.8% of the 1902 passerine nests contained only eggs, and 14.2% of the nests contained only nestlings or both eggs and nestlings. Overall, the parasitism rate of passerine nests was moderate; 476 of the 1902 (25%) passerine nests that we found during the two studies were parasitized by cowbirds (Table 2).

Twenty-four of the 45 passerine species were found parasitized (Table 2). Among species with 25 or more nests, parasitism levels were low for Western Kingbird (0%), Eastern Kingbird (1.7%), Brown Thrasher (3.8%), Savannah Sparrow (9.8%), Chestnut-collared Longspur (7.7%), and Common Grackle (1.1%); low-to-moderate for Horned Lark (15.6%), Clay-colored Sparrow (11.7%), Lark Bunting (19.4%), Grasshopper Sparrow (19.7%), Bobolink (19.2%), and Western Meadowlark (16.1%); moderate for Brewer's Blackbird (33.3%); and moderate-to-heavy for Red-winged Blackbird (43.1%). The Red-winged Blackbird was the most commonly parasitized species in the two studies (71.2% of all cases of parasitism), and we classified it as a preferred host in subsequent analyses.

Parasitized passerine nests contained from zero to six host eggs and/or nestlings and from one to eight cowbird eggs and/or nestlings (Table 3). Of the 476 parasitized passerine nests, 50.6% contained one cowbird egg, 28.6% contained two, 12.0% contained three, and 8.8% contained four or more cowbird eggs. The maximum number of eggs or nestlings in a parasitized nest (host and cowbird combined) was nine. The average number of cowbird eggs per parasitized nest was 1.9 ± 1.2 (Tables 2 and 3). Multiple parasitism occurred at 12.4% of all passerine nests and at 49.4% of all parasitized passerine nests. Parasitized nests of 18 passerine species contained multiple cowbird eggs and/or nestlings (Table 2). Among parasitized species with 25 or more nests, multiple parasitism rates were low for Eastern Kingbird (0%), Brown Thrasher (0%), and Common Grackle (0%); moderate-to-heavy for Clay-colored Sparrow (43.5%), Lark Bunting (38.9%), Grasshopper Sparrow (44.4%), Chestnut-collared Longspur (50.0%), and Red-winged Blackbird (49.6%); and heavy for Horned Lark (80.0%), Savannah Sparrow (62.5%), Bobolink (53.3%), Western Meadowlark (100%), and Brewer's Blackbird (58.3%). Among these species, the average number of cowbird eggs per parasitized nest was highest for the Western Meadowlark (3.4 ± 1.6); all nine parasitized nests of the Western Meadowlark contained two or more cowbird eggs.

TABLE 2. Brown-headed Cowbird parasitism in nests of birds found incidentally during two breeding-bird studies in the northern Great Plains, 1990–2006.

Species [a]	Breeding habitat association[b]	Incidence of cowbird parasitism: North Dakota statewide study[c]	Incidence of cowbird parasitism: Conservation Reserve Program grassland study[c]	Frequency (%) of cowbird parasitism (maximum number of cowbird eggs)[d]	Frequency (%) of multiple parasitism (parasitism intensity)[e]
Willow Flycatcher (*Empidonax traillii*)	SHRU	0/1	0/2	0	0
Least Flycatcher (*Empidonax minimus*)	OPWO		0/1	0	0
Say's Phoebe (*Sayornis saya*)	RESI	0/1		0	0
Western Kingbird (*Tyrannus verticalis*) ‡	OPTR	0/11	0/22	0	0
Eastern Kingbird (*Tyrannus tyrannus*) ‡	OPTR	0/36	2/83	1.7 (1)	0 (1.0 ± 0.0)
Loggerhead Shrike (*Lanius ludovicianus*) ‡	SHRU	0/5	0/1	0	0
Horned Lark (*Eremophila alpestris*)	GRAS	5/25	0/7	15.6 (3)	80.0 (2.0 ± 0.7)
Barn Swallow (*Hirundo rustica*)	RESI		0/1	0	0
House Wren (*Troglodytes aedon*)	OPWO	0/1		0	0
Marsh Wren (*Cistothorus palustris*)	WETL	0/2	0/5	0	0
Sedge Wren (*Cistothorus platensis*)	GRAS		0/3	0	0
American Robin (*Turdus migratorius*) ‡	OPWO	0/6	0/6	0	0
Gray Catbird (*Dumetella carolinensis*) ‡	SHRU	0/1		0	0
Northern Mockingbird (*Mimus polyglottos*) ‡	SHRU		0/1	0	0
Brown Thrasher (*Toxostoma rufum*) ‡	SHRU	0/10	1/16	3.8 (1)	0 (1.0 ± 0.0)
Sprague's Pipit (*Anthus spragueii*)	GRAS	0/1	0/1	0	0
Cedar Waxwing (*Bombycilla cedrorum*) ‡	OPWO		0/3	0	0
Yellow Warbler (*Dendroica petechia*)	OPWO	0/3	8/21	33.3 (1)	0 (1.0 ± 0.0)
Ovenbird (*Seiurus aurocapillus*)	WOOD	0/1		0	0
Common Yellowthroat (*Geothlypis trichas*)	WETL		2/17	11.8 (2)	25.0 (1.3 ± 0.5)
Spotted Towhee (*Pipilo maculatus*)	OPWO	0/3		0	0
Chipping Sparrow (*Spizella passerina*)	OPWO		0/1	0	0
Clay-colored Sparrow (*Spizella pallida*)	SHRU	3/13	20/183	11.7 (4)	43.5 (1.5 ± 0.7)
Brewer's Sparrow (*Spizella breweri*)	SHRU		0/5	0	0
Field Sparrow (*Spizella pusilla*)	SHRU	0/3		0	0
Vesper Sparrow (*Pooecetes gramineus*)	GRAS	2/10	1/10	15.0 (4)	66.7 (2.3 ± 1.5)
Lark Sparrow (*Chondestes grammacus*)	GRAS	1/4	1/3	28.6 (3)	50.0 (2.0 ± 1.4)
Lark Bunting (*Calamospiza melanocorys*)	GRAS	4/9	14/84	19.4 (6)	38.9 (1.9 ± 1.4)
Savannah Sparrow (*Passerculus sandwichensis*)	GRAS	0/1	8/81	9.8 (3)	62.5 (1.8 ± 0.7)
Grasshopper Sparrow (*Ammodramus savannarum*)	GRAS	3/4	9/57	19.7 (2)	44.4 (1.4 ± 0.5)
Baird's Sparrow (*Ammodramus bairdii*)	GRAS	0/1	0/4	0	0
Henslow's Sparrow (*Ammodramus henslowii*)	GRAS		0/2	0	0
Le Conte's Sparrow (*Ammodramus leconteii*)	GRAS		3/12	25.0 (2)	33.3 (1.3 ± 0.6)
Song Sparrow (*Melospiza melodia*)	SHRU	0/2	4/15	23.5 (5)	75.0 (3.0 ± 1.8)
Swamp Sparrow (*Melospiza georgiana*)	WETL		1/2	50.0 (3)	100.0 (3.0 ± 0.0)
Chestnut-collared Longspur (*Calcarius ornatus*)	GRAS	2/20	0/6	7.7 (3)	50.0 (2.0 ± 1.4)

TABLE 2. (*Continued*)

Species [a]	Breeding habitat association[b]	Incidence of cowbird parasitism: North Dakota statewide study[c]	Incidence of cowbird parasitism: Conservation Reserve Program grassland study[c]	Frequency (%) of cowbird parasitism (maximum number of cowbird eggs)[d]	Frequency (%) of multiple parasitism (parasitism intensity)[e]
Dickcissel (*Spiza americana*)	GRAS		2/3	66.7 (2)	50.0 (1.5 ± 0.7)
Bobolink (*Dolichonyx oryzivorus*)	GRAS	0/1	15/77	19.2 (6)	53.3 (2.2 ± 1.6)
Red-winged Blackbird (*Agelaius phoeniceus*)	WETL	9/28	330/758	43.1 (8)	49.6 (1.9 ± 1.2)
Western Meadowlark (*Sturnella neglecta*) ‡	GRAS	4/6	5/50	16.1 (6)	100.0 (3.4 ± 1.6)
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	WETL	1/7	0/1	12.5 (1)	0 (1.0 ± 0.0)
Brewer's Blackbird (*Euphagus cyanocephalus*)	SHRU	0/7	12/29	33.3 (3)	58.3 (1.8 ± 0.8)
Common Grackle (*Quiscalus quiscula*)	OPTR	0/7	1/87	1.1 (1)	0 (1.0 ± 0.0)
Orchard Oriole (*Icterus spurius*)	OPWO	0/1	5/7	62.5 (2)	40.0 (1.4 ± 0.5)
American Goldfinch (*Carduelis tristis*)	SHRU	1/3	0/5	12.5 (1)	0 (1.0 ± 0.0)
Passerines	–	35/234	441/1668	25.0 (8)	49.4 (1.9 ± 1.2)
Nonpasserines [f]	–	0/117	1/630	<0.1 (1)	0 (1.0 ± 0.0)

[a] Species known to eject cowbird eggs are identified with "‡". Ejection status is based on information provided in Peer and Sealy (2004).

[b] Breeding habitat associations of passerine species defined as: GRAS: Grassland; WETL: Wetland; WOOD: Woodland; SHRU: Shrubland; OPTR: Open habitat with scattered trees or shrubs; OPWO: Open or semi-open deciduous woodland and edge; RESI: Residential (rural development, urban, human-made structures). Categories follow Igl and Johnson (1997).

[c] Number of nests parasitized / number of nests found.

[d] The overall frequency (%) of cowbird parasitism is the total number of parasitized nests (*100) divided by the total number of nests found (North Dakota statewide study and the CRP grassland study combined). The maximum number of cowbird eggs represents the greatest number of cowbird eggs found in a single nest of that species during both studies combined.

[e] The overall frequency (%) of multiple parasitism is the total number of nests containing more than one cowbird egg (*100) divided by the total number of parasitized nests found (North Dakota statewide study and the CRP grassland study combined). The average number of cowbird eggs per parasitized nest (± SD) is the sum of all individual cowbird eggs found in all parasitized nests in both studies divided by the total number of parasitized nests.

[f] Nonpasserine species (n = no. nests) include: Pied-billed Grebe (*Podilymbus podiceps*, $n = 1$), Red-necked Grebe (*Podiceps grisegena*; $n = 1$), American Bittern (*Botaurus lentiginosus*; $n = 6$), Canada Goose (*Branta canadensis*; $n = 1$), Gadwall (*Anas strepera*; $n = 113$), American Wigeon (*Anas americana*; $n = 12$), Mallard (*Anas platyrhynchos*; $n = 123$), Blue-winged Teal (*Anas discors*; $n = 65$), Northern Shoveler (*Anas clypeata*; $n = 12$), Northern Pintail (*Anas acuta*; $n = 29$), Canvasback (*Aythya valisineria*; $n = 1$), Redhead (*Aythya americana*; $n = 3$), Ring-necked Duck (*Aythya collaris*; $n = 1$), Lesser Scaup (*Aythya affinis*; $n = 5$), Northern Harrier (*Circus cyaneus*; $n = 48$), Swainson's Hawk (*Buteo swainsoni*; $n = 3$), Ferruginous Hawk (*Buteo regalis*; $n = 2$), Ring-necked Pheasant (*Phasianus colchicus*; $n = 35$), Sharp-tailed Grouse (*Tympanuchus phasianellus*; $n = 14$), Wild Turkey (*Meleagris gallopavo*; $n = 1$), Sora (*Porzana carolina*; $n = 2$), American Coot (*Fulica americana*; $n = 10$), American Avocet (*Recurvirostra americana*; $n = 1$), Upland Sandpiper (*Bartramia longicauda*; $n = 7$), Wilson's Snipe (*Gallinago delicata*; $n = 2$), Wilson's Phalarope (*Phalaropus tricolor*; $n = 5$), Mourning Dove (*Zenaida macroura*; $n = 233$), Black-billed Cuckoo (*Coccyzus erythropthalmus*; $n = 2$), Short-eared Owl (*Asio flammeus*; $n = 5$), and Common Nighthawk (*Chordeiles minor*; $n = 4$).

TABLE 3. Contents of parasitized passerine nests found incidentally during breeding bird surveys in two studies in the northern Great Plains, 1990–2006.

Number of host eggs or nestlings per nest	Number of Brown-headed Cowbird eggs or nestlings per nest								Total number of nests
	1	2	3	4	5	6	7	8	
0	37	21	8	3	5	1	1	1	77
1	40	23	9	6	2	3			83
2	50	41	14	5	2	2			114
3	58	37	18	4	1	2			120
4	45	13	3	3					64
5	10	1	5	1					17
6	1								1
Total number of nests	241	136	57	22	10	8	1	1	476

TABLE 4. Yearly variation of Brown-headed Cowbird parasitism in passerine nests (all species combined) found incidentally during breeding bird surveys in two studies in the northern Great Plains, 1990–2006.

Year	Total number of nests	Frequency of cowbird parasitism (%)	Frequency of multiple parasitism (%)	Parasitism intensity (mean ± SD)[a]	Distribution of cowbird eggs in parasitized nests[b]
1990	57	29.8	35.3	1.6 ± 0.9	random
1991	52	15.4	50.0	1.8 ± 0.9	random
1992[c]	181	12.7	52.2	2.2 ± 1.5	random
1993[c]	90	20.0	55.6	2.2 ± 1.6	random
1994	41	19.5	62.5	1.9 ± 0.8	random
1995	32	18.8	33.3	1.3 ± 0.5	random
1996	20	0	0	–	–
1997	42	16.7	42.9	1.6 ± 0.8	random
1998	96	24.0	60.9	2.0 ± 1.4	random
1999	96	25.0	62.5	2.4 ± 1.6	random
2000	75	25.3	57.9	1.9 ± 1.2	random
2001	129	35.7	34.8	1.5 ± 1.0	random
2002	184	34.8	50.0	1.9 ± 1.1	random
2003	189	24.9	46.8	1.8 ± 1.2	random
2004	234	29.9	57.1	1.8 ± 0.8	random
2005	231	23.8	36.4	1.7 ± 1.4	non-random
2006	153	26.8	56.1	1.9 ± 1.2	random
Mean ± SE	111.8 ± 17.2	22.6 ± 2.1	46.9 ± 3.8	–	–

[a]Mean number of cowbird eggs or nestlings per parasitized nest.
[b]Random distribution of cowbird eggs in parasitized nests was evaluated using a zero-truncated Poisson distribution model (Lindsey 1997). Random distribution of cowbirds eggs indicated that female cowbirds did not discriminate among parasitized nests and that the proportion of nests with 1, 2, 3, 4, …*i* cowbird eggs approximated a Poisson distribution. Non-random distribution indicated that the random distribution model was rejected ($P < 0.01$).
[c]Data for the North Dakota statewide study and the CRP study were combined for 1992 and 1993.

Not including nests of the Red-winged Blackbird, our sample of passerine nests from the two studies included mostly nests of grassland-nesting (e.g., Western Meadowlark) and edge-nesting (e.g., Yellow Warbler) species and very few nests of cavity-nesting (e.g., House Wren) or woodland-interior (e.g., Ovenbird) species (Table 2). We found 482 nests of 15 passerine species that typically nest in grasslands. Overall, the parasitism rate of grassland bird nests was low-to-moderate (16.4%). We found 602 nests of 23 passerine species that typically nest in habitats characterized by woody vegetation (i.e., woodland, shrubland, open habitat with scattered trees or shrubs, open or semi-open deciduous woodland, and edge). The parasitism rate of bird species associated with woody vegetation was low (9.5%).

Of the 45 passerine species for which nests were found, nine species are known to eject cowbird eggs (Table 2; Peer and Sealy 2004). Of the 257 nests of these nine ejector species that we found, 12 (4.7%) contained cowbird eggs. The overall parasitism rate for nests of all non-ejector (i.e., acceptor) passerine species combined was 28.2% ($n = 1645$). In addition, Yellow Warblers often bury the contents of parasitized nests under a new nest floor (Clark and Robertson 1981; Burgham and Picman 1989). Eight of 24 (33.3%) Yel-

TABLE 5. Weekly variation of Brown-headed Cowbird parasitism in passerine nests (all species combined) found incidentally during breeding bird surveys in two studies in the northern Great Plains, 1990–2006.

Weekly period[a]	Total number of nests	Frequency of cowbird parasitism (%)	Frequency of multiple parasitism (%)	Parasitism intensity (mean ± SD)[b]	Distribution of cowbird eggs in parasitized nests[b]
April IV	5	0	0	–	–
May I	0	0	0	–	–
May II	6	0	0	–	–
May III	11	9.1	100.0	4.0 ± 0.0	–
May IV	91	11.0	60.0	2.6 ± 2.0	random
June I	274	19.7	50.0	2.1 ± 1.5	random
June II	4020	37.3	51.3	1.8 ± 1.1	non-random
June III	421	27.8	53.0	1.9 ± 1.1	random
June IV	454	20.9	41.1	1.6 ± 0.9	non-random
July I	162	21.0	50.0	2.0 ± 1.4	random
July II	39	23.1	33.3	1.4 ± 0.7	random
July III	37	16.2	50.0	2.2 ± 1.6	random
Mean ± SE	158.5 ± 51.9	20.7 ± 2.8[c]	54.3 ± 6.2[c]	–	–

[a]To evaluate changes in cowbird parasitism within the breeding season, each month was divided into four, roughly weekly, periods (week I = 7 days, week II = 8 days, week III = 7[8] days, and week IV = 8 days) (sensu Orians et al. 1989).
[b]See Table 4 for explanation.
[c]Mean includes third week in May to third week in July (i.e., weeks with cowbird parasitism).

low Warbler nests each contained a single cowbird egg. During the CRP study, buried (but visible) cowbird eggs were observed in two Yellow Warbler nests (one in Kidder County, North Dakota, on 27 June 2003 and one in Eddy County, North Dakota, on 25 June 2005) and one Clay-colored Sparrow nest (McPherson County, South Dakota, on 13 June 2006).

Parasitized nests of passerines were found in 16 of the 17 years (Table 4). No parasitized nests were found in 1996, which also is the year that we found the fewest number of active passerine nests. Excluding 1996, annual parasitism rates ranged from 12.7 to 35.7% and averaged 22.6% (Table 4). The average annual rate of multiple parasitism was 46.9%. The zero-truncated Poisson distribution model for parasitized nests was rejected in one (i.e., 2005) of the 16 years in which parasitized nests were found.

In both studies combined, passerine nests were found in 11 of 12 weekly periods from the last week of April through the third week of July (Table 5). Eleven passerine nests were found in two of the three weeks before the first cowbird egg was found (i.e., before the third week in May), although cowbirds were recorded in each of those three weeks (Igl and Johnson, unpublished data). In the North Dakota statewide study, we found active nests between 27 April and 20 July, parasitized nests between 20 May and 18 July, and multiply parasitized nests between 20 May and 18 July. In the CRP grassland study, we found active nests between 22 May and 9 July, parasitized nests between 29 May and 9 July, and multiply parasitized nests between 29 May and 9 July. During both studies, non-parasitized and parasitized nests were found largely between late May and early July, which corresponds with the peak breeding periods of most passerine species in the northern Great Plains, including the Brown-headed Cowbird (Stewart 1975; Igl and Johnson 1997; Tallman et al. 2002). After the third week in May, weekly parasitism rates ranged from 9.1 to 37.3% and averaged 20.7%; the highest parasitism rates were found in the second and third weeks of June (Table 5). The average weekly rate of multiple parasitism was 54.3%. The zero-truncated Poisson distribution model for parasitized nests was rejected in two (i.e., second and fourth week of June) of eight weekly periods.

In the CRP grassland study, parasitized and multiply parasitized nests of passerines were found in all nine counties (Table 6). Cowbird parasitism of passerine nests was low in Fallon County in southeastern Montana (5.8%) and Grant County in western Minnesota (9.3%). Parasitism rates were low-to-moderate in Butte County in western South Dakota (12.8%) and Sheridan County in northeastern Montana (11.6%), and moderate in Hettinger (29.9%), Kidder (25.3%), and Eddy (23.8%) counties in North Dakota and Day County in northeastern South Dakota (28.9%). Heavy parasitism was found in McPherson County in north-central South Dakota (51.5%). The frequency of multiple parasitism was moderate in Butte (21.4%) and Day counties in South Dakota (39.8%) and Fallon County, Montana (25%), and moderate-to-heavy to heavy in the other six counties (range: 42.9–58.7%). The zero-truncated Poisson distribution model for parasitized nests was rejected in one (i.e., Day County, South Dakota) of the nine counties (Table 6). Nests within the counties of highest female cowbird abundance experienced higher frequencies of cowbird parasitism (R^2 = 0.64, F = 12.65, P = 0.0093) than those found in counties with the lowest female cowbird abundance (Figure 3). The quadratic term for cowbird densities was nonsignificant (P = 0.62) and was not included in the final model.

TABLE 6. Regional variation in Brown-headed Cowbird parasitism in passerine nests (all species combined) found incidentally during breeding bird surveys in Conservation Reserve Program grassland fields in nine counties in the northern Great Plains, 1990–2006.

County	Total number of nests	Frequency of cowbird parasitism (%)	Frequency of multiple parasitism (%)	Parasitism intensity (mean ± SD)[a]	Distribution of cowbird eggs in parasitized nests[a]
Butte, South Dakota	109	12.8	21.4	1.2 ± 0.4	random
Day, South Dakota	322	28.9	39.8	1.6 ± 1.1	non-random
Eddy, North Dakota	172	23.8	46.3	1.8 ± 1.1	random
Fallon, Montana	69	5.8	25.0	1.3 ± 0.5	random
Grant, Minnesota	151	9.3	42.9	1.5 ± 0.7	random
Hettinger, North Dakota	211	29.9	58.7	2.2 ± 1.5	random
Kidder, North Dakota	332	25.3	45.2	1.7 ± 0.9	random
McPherson, South Dakota	233	51.5	59.2	2.0 ± 1.1	random
Sheridan, Montana	69	11.6	50.0	2.1 ± 1.3	random

[a]See Table 4 for explanation.

In the CRP grassland study, cowbird densities, total breeding bird densities, and total breeding bird richness were lowest in the southwestern counties (Butte County, South Dakota, and Fallon County, Montana) and highest in counties near the center of the cowbird's breeding bird range. There was a positive relationship between female cowbird densities and all measures of avian abundance and richness. That is, female cowbird densities increased with increasing density and richness at all levels of the avian community (Table 7). Breeding bird density for all bird species ($R^2 = 0.72$) was a better predictor of cowbird abundance than the other four levels of avian densities (Table 7, Figure 4a). Breeding bird richness for all bird species ($R^2 = 0.69$) was a better predictor of cowbird abundance than the other three levels of avian richness (Table 7, Figure 4b). There was only a weak suggestion that cowbirds use, as a settlement cue, the number of passerines species known to have raised cowbird young ($P = 0.115$).

During breeding bird surveys in both studies, observers noted 586 instances of adult passerines provisioning food to individual fledglings, of which only 26 (4.4%) instances involved hosts feeding cowbird fledglings. These 26 observations occurred between 4 June and 7 July and involved eight host species: Clay-colored Sparrow (5 cases), Grasshopper Sparrow (1 case), Le Conte's Sparrow (1 case), Savannah Sparrow (6 cases), Song Sparrow (4 cases), Brewer's Blackbird (2 cases), Red-winged Blackbird (5 cases), and Orchard Oriole (2 cases). These eight species accounted for 83.6% of the total cowbird parasitism in these two studies (Table 2). Although we cannot establish conclusively the true foster-parentage of these fledgling cowbirds, we did not observe any non-parasitized species (i.e., species whose nests were not parasitized during the two studies) feeding cowbird fledglings during the two studies.

Discussion

Brown-headed Cowbirds parasitize nests of a wide variety of host species (Friedmann 1963; Lowther 1993), including some inappropriate hosts. As in other studies (Ortega 1998), we found almost no cowbird parasitism of nonpasserine nests. Most nonpasserines are considered unsuitable hosts, and their nests usually are avoided by Brown-headed Cowbirds (Rothstein and Robinson 1998). Although the only parasitized nonpasserine, an Upland Sandpiper, was clearly an unsuitable host (i.e., a large-bodied host with precocial, nidifugous young), several other studies have documented cowbird eggs in Upland Sandpiper nests (Higgins and Kirsch 1975; Faanes and Lingle 1995*; Davis and Duncan 1999).

Our overall frequency of cowbird parasitism (25%) for passerine species was within the range that Ortega (1998) considered moderate (20–40%). This overall rate seems low given that cowbird densities are highest in the northern Great Plains (Sauer et al. 2005*) and that cowbirds are more abundant than many of their common hosts in this region (Igl and Johnson 1997; Igl et al. 1999). However, our combined parasitism rate is based on nests from two studies, an extensive region, 17 years, and numerous passerine species, including several species that ostensibly have developed behavioral defenses against cowbird parasitism (see below). After we excluded nests of ejector species, our overall parasitism rate remained moderate (28.2%). Some studies in this region have found higher combined rates of cowbird parasitism than those reported herein. For example, Koford et al. (2000) found an overall parasitism rate of 40.3% for passerines nesting in seeded and native grasslands and cropland in North Dakota and Minnesota, and Davis and Sealy (2000) found an overall rate of 32.6% for species nesting in grasslands in southwestern Manitoba. In both of these studies, some individual species experienced moderate-to-heavy levels of cowbird parasitism (e.g., >40% parasitism for Western Meadowlarks in both studies). Robinson and Smith (2000) suggested that some of these commonly cited reports of high parasitism rates from the northern Great Plains might not be representative of this region. Indeed, some recent reviews of geographic patterns of cowbird parasitism (e.g., Peer et al. 2000; Chace et al. 2005) focused on the extreme

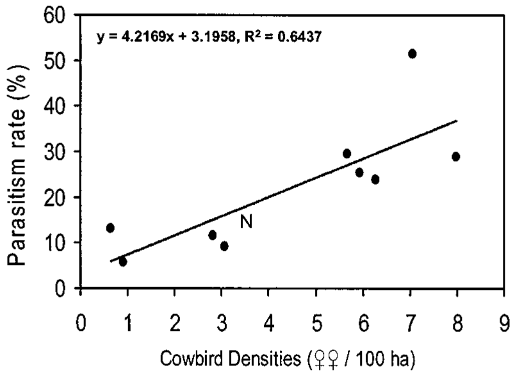

FIGURE 3. Relationship between female cowbird densities and the percentage of the total number of passerine nests that were parasitized in Conservation Reserve Program grasslands in North Dakota, South Dakota, Minnesota, and Montana, 1990–2006. The data from the North Dakota (N) statewide study were included for comparison (1992 and 1993 were averaged).

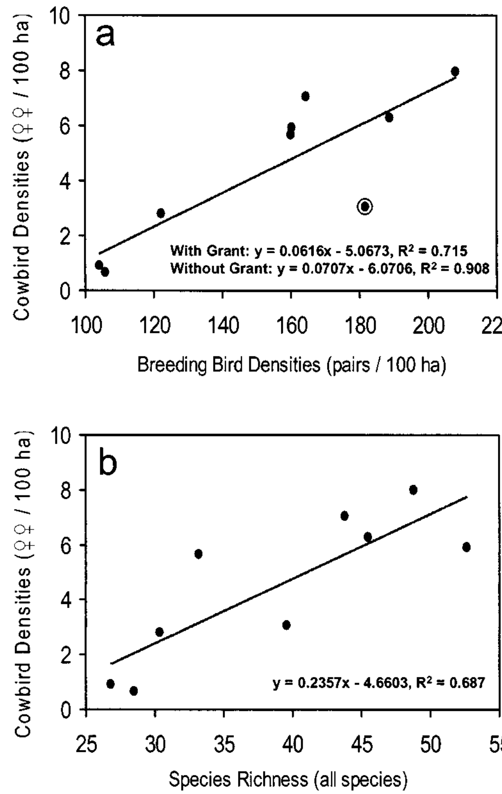

FIGURE 4. Relationship between (a) mean female cowbird densities and average densities of all other breeding bird species, and (b) mean female cowbird densities and mean species richness within the breeding bird community (excluding cowbirds) in Conservation Reserve Program (CRP) grasslands in North Dakota, South Dakota, Minnesota, and Montana, 1990–2006. The circle in Figure 4a indicates a potential outlier, Grant County in Minnesota, which is discussed in the text.

cases of parasitism in the northern Great Plains (e.g., Linz and Bolin 1982; Davis and Sealy 2000; Koford et al. 2000). There are many less-cited studies of cowbird parasitism (see Shaffer et al. 2003) with low-to-moderate rates of cowbird parasitism in this region (e.g., Hill and Sealy 1994; Granfors et al. 2001; Davis 2003; Woolfenden et al. 2004). For example, in Manitoba, Davis (2003) found an overall parasitism rate of 19.9% for six grassland species in southern Saskatchewan over a 5-year period.

Although our overall rate of cowbird parasitism was 25%, we did find higher rates of parasitism in some years (e.g., 35.7% in 2001), weeks (e.g., 37.3% in the second week of June), counties (e.g., 51.5% in McPherson County, South Dakota), and individual species (e.g., 43.1% for the Red-winged Blackbird). The results from our studies can serve as a reminder that cowbird parasitism rates are not constant across space or time (i.e., among years or within a breeding season) and that cowbirds differentially parasitize hosts within the same habitats. Differences in parasitism levels among studies in the northern Great Plains may simply reflect variation among species, regions, habitats, or years. For example, Davis and Sealy's (2000) overall parasitism rate of 32.6% was based on data collected at three study sites over two years; parasitism rates were low-to-moderate at two of the study sites (18 and 20%) and heavy at the third study site (67%). We echo Hahn and Hatfield's (1995) caveat that patterns of cowbird parasitism are complex and variable, and that field studies of cowbird parasitism would be more effective if they were long-term, community-wide studies set in strategically chosen communities in different regions.

Our nest data were slightly unorthodox compared to nest data from many other studies. We located all of our nests fortuitously and observed each nest only once. Any cowbird eggs ejected before our surveys, any nests abandoned before our surveys, any cowbird eggs buried completely in the nest lining, and any cowbird eggs added or removed after our brief observations were not recorded in our studies, and thus our frequencies of cowbird parasitism should be considered minimal estimates. These limitations, however, are not unique to our data but rather are common features of all studies of cowbird parasitism that do not involve cameras, because most nests are not monitored continuously throughout the nesting cycle but rather are visited at relatively fixed intervals (e.g., every 2–4 days) for relatively brief periods of time (e.g., less than a few minutes). Even systematic nest searches are neither incessant nor comprehensive, but rather occur at fixed intervals (e.g., Koford et al. 2000; Davis 2003; Winter

TABLE 7. Five levels of avian abundance (density) and richness (number of species) that female Brown-headed Cowbirds could use as proximate cues for settlement in Conservation Reserve Program grassland fields in nine counties in the northern Great Plains, 1990–2006. Linear regression analyses were performed to examine the relationship between female cowbird densities and each different subset of avian abundance and richness at the five levels of the avian community (also see Figure 4).

Level of avian community[a]	Breeding bird density			Number of breeding species		
	R^2	F	*P*	R^2	F	*P*
All breeding birds	0.72	17.53	0.004	0.69	15.56	0.006
All passerines	0.63	12.02	0.011	0.40	4.65	0.068
All passerines that have raised cowbirds	0.66	13.64	0.008	0.32	3.25	0.115
All passerines that are non-ejectors	0.62	11.39	0.012	0.38	4.32	0.076
Preferred host (Red-winged Blackbird)	0.54	8.35	0.023	–	–	–

[a] Excluding cowbirds.

et al. 2004). In addition, many studies that use systematic nest searches also include a fortuitous component to their nest searching methodology (e.g., Koford et al. 2000; Davis 2003). Thus, nearly all estimates of cowbird parasitism in the literature could be considered minimal estimates.

In our two studies, female cowbirds did not avoid laying eggs in previously parasitized nests. Nearly one-half of the parasitized nests in our two studies contained more than one cowbird egg, with the average parasitized nest containing about two cowbird eggs. The assumption that female cowbirds laid eggs randomly in parasitized nests could only be rejected in two of eight weekly periods, one of 16 years, and one of nine counties in the CRP grassland study. Deviations from a random Poisson distribution were likely related to a greater number of nests with multiple cowbird eggs or nestlings than would be expected by chance. Multiple parasitism has been widely documented in nests parasitized by the Brown-headed Cowbird (McLaren et al. 2003). Although multiple parasitism can vary by region or host species, it typically occurs in about one-third of all reported cases of cowbird parasitism (Friedmann 1963; Lowther 1993; Johnsgard 1997; Ortega 1998) and seems to be more common in nests of larger hosts (Lorenzana and Sealy 1999; Trine 2000). Little is known about the factors that might influence multiple parasitism, but some mechanisms have been proposed or investigated. For example, multiple parasitism might occur if (1) a female cowbird exhibits host preference (Smith and Myers-Smith 1998), (2) there is a high ratio of female cowbirds to host nests (McGeen 1972), (3) there is a shortage of alternative host nests (Smith and Myers-Smith 1998), or (4) an inexperienced and nonselective female makes a poor host choice (McLaren et al. 2003). Cowbird hosts in the Great Plains seem to be particularly vulnerable to multiple parasitism (e.g., Elliott 1978; Davis and Sealy 2000; this study), which may reflect higher densities of cowbirds (Elliott 1977; Ortega 1998) or lower densities of available or suitable hosts (Robinson and Smith 2000).

We likely underestimated the frequency of cowbird parasitism of those species that eject or bury cowbird eggs or that abandon parasitized nests (Ortega 1998). Less than 5% of the nests of ejector species in the two studies contained cowbird eggs, which was much lower than the overall parasitism rate (28.2%) for acceptor species. Ejection of cowbird eggs by a host is an effective anti-parasite strategy among some North America passerines (Ortega 1998; Peer and Sealy 2004), especially among edge-nesting passerines that are common in the northern Great Plains (Igl and Johnson 1997; Table 1). Even within acceptor species, however, some individuals are prone to abandon parasitized nests and then re-nest (Lorenzana and Sealy 1999). Hosoi and Rothstein (2000) showed that the frequency of desertion of parasitized nests was higher in non-forest than forest species and suggested that increased nest desertion was an evolved response to cowbird parasitism. Among small-sized hosts, nest desertion seems to be a common response to parasitism or defense against parasitism (Ortega 1998). Many species that breed in the northern Great Plains are known to abandon their nests occasionally as a result of parasitism or cowbird removal of host eggs (e.g., Ortega 1991; Hosoi and Rothstein 2000), including some grassland and shrub-grassland species, although the frequency of abandonment may be quite low (Sealy 1999; Davis and Sealy 2000).

The Red-winged Blackbird was the third most abundant species observed in both of our studies. Despite its aggressive nest-defense behaviors against cowbirds and its colonial-nesting tendencies (Freeman et al. 1990), the Red-winged Blackbird was the most commonly parasitized species in the two studies (43.1% parasitism, 49.6% multiple parasitism, 71.2% of all cases of parasitism) and appears to be a preferred cowbird host in the northern Great Plains. Our data support Hanka's (1979) contention that cowbirds may show a phylogenetic preference for Red-winged Blackbirds and other Icterine species (e.g., Brewer's Blackbird, Orchard Oriole; Table 2) in the cowbird's range. Linz and Bolin (1982) and Koford et al. (2000) reported similar parasitism rates (42 and 43%, respectively) for Red-winged Blackbirds in this region. In the eastern portion of the cowbird's range, Red-winged Blackbirds are rarely parasitized (e.g., Hahn and Hatfield 1995). Although we categorized the Red-winged Blackbird as a wetland species (Table 2; Igl and Johnson 1997), many of the red-wing nests that we found during the CRP grassland study were scattered in upland habitats (grassland, shrub-grassland), where group defense is generally lower (Robertson and Norman 1977; Ortega 1991) and parasitism rates are generally higher (Robertson and Norman 1976; Krapu 1978). Several host species are known to avoid or reduce parasitism by acting aggressively toward cowbirds (Robertson and Norman 1976, 1977), but aggression is not always an effective host defense against cowbird parasitism, especially in habitats in which host densities are low because cowbirds may use host aggression (Robertson and Norman 1977) or vocalizations (Clotfelter 1998) to locate nests. Nonetheless, the Red-winged Blackbird is one of a few species reported to reduce parasitism by mobbing (Freeman et al. 1990; Chace et al. 2005).

The presence of Red-winged Blackbirds may be a double-edged sword for other passerines nesting in the same habitats, such as CRP grasslands. Red-winged Blackbirds are conspicuous breeding birds in CRP grasslands and thus might increase parasitism in nests of other species. Barber and Martin (1997) found that a conspicuous, co-occurring species in a breeding bird community can increase the risk of cowbird parasitism on alternative host species. Alternatively, other species may benefit from nesting near Red-winged Blackbirds if (1) the defensive behavior of blackbirds toward cowbirds reduces cowbird activity in the area, or (2) higher cowbird parasitism of blackbird nests reduces parasitism pressure on other species. Fretwell (1972) noted higher rates of cowbird parasitism in Dickcissel nests that were built near Red-winged Blackbird nests, whereas Clark and Robertson (1979) found the opposite for Yellow Warblers. Woolfenden et al. (2004) speculated that Red-winged Blackbirds might have increased the risk of parasitism on Yellow Warblers in their Manitoba study sites. The influence of Red-winged Blackbird presence and abundance on cowbird parasitism rates of other species requires further study.

Mayfield (1965b) suggested that grassland birds may have evolved defenses against brood parasitism because of their long evolutionary history of co-occurrence with the Brown-headed Cowbird in the Great Plains. To date, however, the species that have shown the strongest anti-parasite behaviors (i.e., egg ejection) have not been the grassland species but rather have been the species associated with woody vegetation (Peer and Sealy 2004, Table 2). Our overall rate of cowbird parasitism for grassland bird nests (16.4%) was much lower than those reported in some studies (e.g., Elliott 1978 [57.7%]; Davis and Sealy 2000 [32.6%]; Jensen and Finck 2004 [42.9%]) but comparable to or higher than those reported in other studies (e.g., Strausberger and Ashley 1997 [0%]; Kershner and Bollinger 1998 [1.7%]; Robinson et al. 2000 [7.8%]; Granfors et al. 2001 [14%]; Davis 2003 [19.9%]; Winter et al. 2004 [6.7%]). Nonetheless, we found a higher frequency of parasitism in nests of grassland species than in nests of species that nest in edge and woodland habitats (9.5%). In contrast to our results, in Illinois, Robinson et al. (1999, 2000) and Strausberger and Ashley (1997) found a higher frequency of parasitism in species nesting in edge and woodland habitats than in nests of grassland species. Although the difference between the two regions for grassland birds is consistent with the pattern that cowbird parasitism declines with distance from the center of the cowbird's range in the northern Great Plains, the difference for species associated with woody vegetation is contrary to this generalization. Again, these patterns emphasize the complexity and variability of cowbird parasitism in North America (Hahn and Hatfield 1995). Robinson and Smith (2000) and others (Peer et al. 2000; Jensen and Finck 2004) have suggested that the higher levels of parasitism in grasslands in the Great Plains than those in the Midwest might reflect the near absence of large forested areas, where more tolerant hosts can absorb cowbirds and cowbird parasitism from grasslands. Seemingly, our data support this contention. In our most-forested county in the CRP grassland study (Grant County in west-central Minnesota; Igl and Johnson, unpublished data), the density of female cowbirds (and cowbird parasitism) was much lower than would be expected given the density of breeding birds in the avian community (Figure 4a). Moreover, Minnesota typically is lumped with midwestern states rather than with Great Plains states. In the other eight counties, there are few, if any, large forested areas that could absorb cowbird parasitism from the open grasslands. Trees and shrubs in these eight counties occur largely in small, often linear, patches, where cowbird egg ejectors (e.g., kingbirds, thrashers, catbirds, robins) dominate the breeding bird community. The low parasitism rates of edge and woodland species in our study may reflect the predominance of ejector species in woody habitats in the northern Great Plains (Igl and Johnson 1997) and the avoidance by cowbirds of a habitat that may contain many less-tolerant hosts (Sealy and Bazin 1995).

In Illinois, Peer et al. (2000) recently found that Western Meadowlarks rejected (i.e., ejected or damaged) 78% of artificial and real cowbird eggs experimentally added to nests. In contrast, in the northern Great Plains, some Western Meadowlark populations are moderately to heavily parasitized (23–67%: Davis and Sealy 2000; 19–47%: Koford et al. 2000), and the species often experiences extreme levels of multiple parasitism in this region (Davis and Sealy 2000; Davis 2003; this study). It is unclear why some meadowlark individuals or populations experience heavy or intense parasitism (e.g., average of 3.4 and 3.1 cowbird eggs per parasitized nest in this study and Davis and Sealy 2000, respectively), whereas others apparently experience little or none. Davis and Sealy (2000) suggested that the apparent geographic variation in parasitism levels in Western Meadowlark populations in the northern Great Plains and elsewhere might reflect differences in the size of suitable grassland patches and the availability of other host species in the community. Peer et al. (2000) suggested that geographic differences in parasitism levels in the northern Great Plains and the Midwest might reflect geographic variation in egg rejection by Western Meadowlarks. Egg rejection behavior in the Western Meadowlark should be tested in more geographic locations or landscapes to resolve these issues. Moreover, the Western Meadowlark and its congener, the Eastern Meadowlark (*Sturnella magna*), use a similar tactic to destroy eggs or clutches of other birds (Creighton and Porter 1974; Schaef and Picman 1988; Picman 1992). The function of this egg-destroying behavior has been speculative (e.g., predation, interference competition for limited resources), but in view of the similarities (e.g., egg removal, puncture) between this egg-destroying behavior at nests of other birds and cowbird egg ejection at their own nests, experiments are needed to evaluate the relationship between general egg destruction and cowbird egg rejection by meadowlarks.

In our CRP grassland study, female cowbird densities varied greatly among the nine counties in the northern Great Plains, and rates of cowbird parasitism were higher in the counties in which densities of female cowbirds were higher. Our results support the interpretation of Miles and Buehler (2000) and Chace et al. (2005) that female cowbird densities are a reasonable predictor of the frequencies of cowbird parasitism. Our results also support the contention that cowbird parasitism declines with distance from the center of the cowbird's range, although on a smaller scale (Hoover and Brittingham 1993; Smith and Myers-Smith 1998; Thompson et al. 2000).

Few studies have evaluated the relationship between cowbird abundance and parasitism levels using cowbird and nest data collected concurrently at the same study sites over a large region (e.g., Robinson et al. 2000; Jensen and Cully 2005a, 2005b). Large-scale evaluations of this relationship typically have relied on data from unconnected sources, such as abundance data from the North American Breeding Bird Survey (BBS) and nest data from the Cornell Laboratory of Ornithology or from multiple studies (e.g., Hoover and Brittingham 1993; Basili 1997; Smith and Myers-Smith 1998; Herkert et al. 2003). Most evaluations of this relationship have focused on single species (Hoover and Brittingham 1993; Basili 1997; Smith and Myers-Smith 1998; Herkert et al. 2003). Nonetheless, many studies have found similar positive relationships between cowbird densities and cowbird parasitism levels. For example, Basili (1997) and Herkert et al. (2003) showed that cowbird densities on BBS routes were positively related to frequencies of cowbird parasitism of Dickcissel nests from multiple studies across several states. Jensen and Cully (2005a,b) found a similar, positive relationship between female cowbird densities and parasitism levels of Dickcissel nests at eight study sites in Kansas and Oklahoma. In a meta-analysis of nest and cowbird data from six studies from four midwestern states, Thompson et al. (2000) similarly found that cowbird abundance and parasitism levels of multiple species were positively correlated across study areas. In contrast, Woolfenden et al. (2004) found that female cowbird abundance was not related to parasitism frequency among three species in an avian community in Manitoba, and Robinson et al. (2000) found that the percentage of nests parasitized was not related to cowbird abundance in multiple forest sites across Illinois.

In CRP grasslands, we also found a positive relationship between cowbird abundance and all five levels of the avian community, including all avian species, all passerine species, all passerines that are non-ejectors, all passerines known to raise cowbird young, and a single, preferred host (i.e., Red-winged Blackbird). The abundance and richness of all avian species were the strongest predictors of cowbird abundance, which suggests that cowbirds might use the overall breeding bird community as a settlement cue for optimal areas to breed rather than more specific passerine or host categories (e.g., all passerines that are known to have raised cowbird young). The number of individuals and the number of species represent different components of a cowbird's breeding resource. The presence of more individuals and more species with different breeding chronologies ensures a larger number of potential hosts within the breeding bird community throughout the cowbird's breeding season (Farmer 1999). Although we evaluated these relationships using only data from the CRP grassland study, cowbirds also might use other cues (e.g., vegetation or landscape factors) as an indicator of the richness or abundance of the avian community (Chace et al. 2005).

Chace et al. (2005) tabulated 16 published studies and one unpublished study that evaluated the relationship between different measures of the avian community and cowbird abundance or occurrence. As with our results, many studies found positive relationships between cowbirds and different measures of avian densities and richness. To our knowledge, Farmer (1999) is the only other published study to have evaluated multiple host and avian community measures using both abundance and richness data. Farmer (1999) found positive relationships for nearly every level of the avian community, including abundance and richness categories. Because host species are necessary for cowbirds to be reproductively successful, most studies have evaluated these relationships at the host level. Results of such evaluations have been inconsistent. Moreover, comparisons among studies using host categories are difficult because a variety of definitions of host communities were used (Chace et al. 2005). For example, Thompson et al. (2000) found that cowbird abundance was significantly correlated with host abundance (i.e., hosts included species that bred on the study area and accepted cowbird eggs), whereas Robinson et al. (2000)

found no relationship between cowbird abundance and host abundance (i.e., hosts included species that accept cowbird eggs regularly but excluding cavity nesters, cowbird egg ejectors, and large species). Evans and Gates (1997) found that cowbird abundance was positively related to the abundance of all avian species combined, but the relationship was non-significant for richness of all avian species and richness and abundance of host species (i.e., known cowbird hosts).

In summary, our data show that, even within the northern Great Plains, there is considerable variation in parasitism rates among species and across space and time. Our results demonstrate that parasitism rates overall are moderate in the northern Great Plains, although some individual species, counties, years, and weeks experience heavier rates of parasitism or multiple parasitism than others. Our study is one of the first to show a strong, positive relationship between regional cowbird abundance and nest parasitism rates using both cowbird abundance and nest data collected at the same study sites. We also found a clear, positive relationship between female cowbird densities and the overall breeding bird communities in CRP grasslands in the northern Great Plains. More studies are needed to determine if these relationships hold elsewhere in the northern Great Plains with different host communities or within other habitats.

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