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Brown-headed Cowbirds in Grasslands: Their Habitats, Hosts, and Response to Management

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ABSTRACT -- The brown-headed cowbird (*Molothrus ater*) is an obligate brood parasite whose numbers have increased in recent decades to the potential detriment of the species that they parasitize. Thus, most management efforts focus on discouraging brown-headed cowbird parasitism or controlling brown-headed cowbird populations. Keys to discouraging brown-headed cowbird parasitism or controlling populations of brown-headed cowbirds in the Great Plains are maintaining large expanses of grassland, eliminating foraging areas (e.g., feedlots) and perch sites, and reducing the extent of overgrazed pastures.

Key words: brood parasitism, brown-headed cowbird, grassland, management, *Molothrus ater*.

The brown-headed cowbird (*Molothrus ater*), hereafter cowbird, is an obligate brood parasite, whose activities often are detrimental to the reproductive output of some host species (Rothstein 1975, 1990; Payne 1977; Sealy 1992). Although the cowbird originated in the Great Plains, it has spread eastward and westward (Mayfield 1965, Rothstein et al. 1980, Lowther 1993), and much of the attention focused on this species emphasizes areas outside of the Great Plains. Here we describe the current breeding distribution and breeding biology of the cowbird, with emphasis on the Great Plains and on grassland birds. We identify

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other grassland species that are cowbird hosts and include rates of brood parasitism (Table 1), many of which were previously unpublished. We indicate how cowbirds respond to land management practices, such as burning, mowing, and grazing, as well as to management techniques specifically aimed at controlling cowbird numbers.

BREEDING RANGE

Cowbirds breed from the Northwest Territories of Canada to central Mexico. They breed in southeastern Yukon, eastern British Columbia, Alberta, southern Saskatchewan, southern Manitoba, southern Ontario, southern Quebec, New Brunswick, Nova Scotia, Prince Edward Island, southern Newfoundland, throughout the 48 conterminous United States, and across northern Mexico (Lowther 1993). The northern Great Plains has the greatest abundance of cowbirds in the United States and Canada, according to BBS data (Price et al. 1995, Peterjohn et al. 2000, Rothstein and Robinson 2000, Wiedenfeld 2000). More regionally, cowbird abundance is influenced by the composition of the landscape or availability of hosts (Robinson 1999). For example, in forested areas, cowbirds may be limited by the amount of agricultural area available as feeding sites, whereas in agricultural areas (such as pastures, cropland, and rangeland), cowbirds may be limited by host availability. At a landscape scale (e.g., within 10 km of a study site), cowbird abundance may be limited by availability and proximity to feeding sites. At a local level (e.g., a particular tract of land), the amount of and distance to habitat edge, habitats present, tract size, host availability, and vegetation structure may influence cowbird abundance (Robinson 1999).

SUITABLE HABITAT

Before settlement by Europeans, cowbirds inhabited open grasslands in central North America but expanded their breeding range into new habitats as forests were cut and agricultural activities were established (Mayfield 1965, Lowther 1993). Cowbirds or host nests containing cowbird eggs have been found in shortgrass, mixed-grass, and tallgrass prairies; pastures; hayland; planted grassland cover (e.g., Conservation Reserve Program [CRP] fields, Permanent Cover Program [PCP] fields, and fields with dense nesting cover [DNC]); sagebrush (*Artemisia* spp.); cropland; road rights-of-way; flooded roadside ditches; wetlands; cranberry (*Vaccinium macrocarpon*) beds; grassed waterways; riparian areas; aspen parkland; shelterbelts and hedgerows; oldfields; wooded draws; forests and forest edges; and residential areas (Silloway 1904, Saunders 1914, Hergenrader 1962, Graber and Graber 1963, Wiens 1963, Mayfield 1965, Salt and Salt 1976, Lowther and Johnston 1977, Blankespoor 1980, Hubbard 1982, Brittingham

Table 1. Rates of brood parasitism in nests of grassland bird species that are known hosts of brown-headed cowbirds.¹ For each species, entries are ordered by increasing parasitism rate. For commonly parasitized species, only reports of 10 or more nests are included. For rarely parasitized species, reports are included regardless of the number of nests to indicate that parasitism has been documented.

Species	Parasitism rate (%)	No. nests	Location	Source
Ferruginous hawk (<i>Buteo regalis</i>)	1 record		North Dakota	A. Eastgate in Friedmann 1929
Greater prairie-chicken (<i>Tympanuchus cupido</i>)	1 record		Minnesota	Svedarsky 1979
Upland sandpiper (<i>Bartramia longicauda</i>)	0	28	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	1	189	North Dakota	Higgins and Kirsch 1975
	5	43	Nebraska	Faanes and Lingle 1995
Wilson's phalarope (<i>Phalaropus tricolor</i>)	0	21	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	1	386	Saskatchewan	M. A. Colwell and D. Delehanty, personal communication in Colwell and Jehl 1994
	5	43	Nebraska	Faanes and Lingle 1995
Loggerhead shrike ² (<i>Lanius ludovicianus</i>)	< 1	1661	Manitoba	K. D. De Smet, Manitoba Conservation, Melita, Manitoba, personal communication
	1	261	Iowa	De Geus and Best 1991
Horned lark (<i>Eremophila alpestris</i>)	0	163	Saskatchewan	Maher 1973
	2	201	Quebec	Terrill 1961
	3	161	Ontario	Peck and James 1987
	4	119	Ontario	Ontario nest records in Friedmann et al. 1977
	9	11	Illinois	Robinson et al. 2000
	16	32	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	19	16	Kansas, Missouri, Nebraska	Lowther 1977
	19	26	North Dakota	R. E. Stewart in Friedmann et al. 1977
	45	31	Kansas	Hill 1976
	53	15	Saskatchewan	S. K. Davis, Saskatchewan Watershed Authority, Regina, Saskatchewan, personal communication
	60	84	North Dakota	Koford et al. 2000
Sprague's pipit (<i>Anthus spragueii</i>)	0	24	Saskatchewan	B. Dale, unpublished data in Robbins and Dale 1999
	0	33	Saskatchewan	Maher 1973
	0	50	Saskatchewan	G. C. Sutter, Royal Saskatchewan Museum, Regina, Saskatchewan, personal communication
	12	58	Saskatchewan	S. K. Davis, personal communication
	15	20	Manitoba	De Smet 1992
	18	17	Manitoba	Davis 1994, Davis and Sealy 2000
Clay-colored sparrow ³ (<i>Spizella pallida</i>)	5	793	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	10	135	Minnesota	Johnson and Temple 1990
	11	204	Manitoba	Hill and Sealy 1994
	14	492	North Dakota	Granfors et al. 2001
	16	118	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	20	20	Alberta	Salt 1966
	21	44	Saskatchewan	S. K. Davis, personal communication
	23	13	Ontario	Ontario nest records in Friedmann et al. 1977

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	24	49	North Dakota	Koford et al. 2000
	24	275	Alberta, Manitoba, Saskatchewan	Prairie Nest Records Scheme in Friedmann et al. 1977
	33	40	Minnesota	Buech 1982
	36	232	Manitoba	Knapton 1978
	38	29	Ontario	Peck and James 1987
	38	42	North Dakota	Romig and Crawford 1995
	39	33	North Dakota	Stewart 1975
Field sparrow ³	<1	371	Pennsylvania	M. Carey in Carey et al. 1994
(<i>Spizella pusilla</i>)	3	32	Michigan	Evans 1976
	3	36	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	3	66	Indiana	Nolan 1963
	7	122	California, Oklahoma, Texas	Western Foundation Collection in Friedmann et al. 1977
	11	36	Michigan	Batts 1958
	11	147	Illinois	Best 1978
	11	443	Missouri	Burhans et al. 2000
	14	86	Illinois	Robinson et al. 2000
	16	57	Pennsylvania	Norris 1947
	18	33	Michigan	Berger 1951
	19	334	Ontario	Peck and James 1987
	20	25	Illinois	Best 1979

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	20	179	Ontario	Ontario nest records in Friedmann et al. 1977
	21	52	Michigan	Sutton 1960
	27	667	Michigan	Walkinshaw 1978
	30	10	Minnesota	Buech 1982
	32	72	Michigan	Evans 1978
	32	159	Ohio	Hicks 1934
	36	14	Kansas, Missouri, Nebraska	Lowther 1977
	52	71	Illinois	Strausberger and Burhans 2001
	53	19	Illinois	Strausberger and Ashley 1997
	59	29	Illinois	Strausberger 1998
	80	20	Iowa	Crooks 1948, Crooks and Hendrickson 1953
Vesper sparrow	0	10	Iowa	Frawley 1989
<i>(Pooecetes gramineus)</i>	0	12	Saskatchewan	Maher 1973
	0	18	Michigan, Pennsylvania, Wisconsin	Harrison 1975
	0	19	Saskatchewan	Prairie Nest Records Scheme in Maher 1973
	0	28	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	0	53	North Dakota	Granfors et al. 2001
	1	85	Michigan	Evans in Berger 1968
	3	107	California, Oklahoma, Texas	Western Foundation Collection in Friedmann et al. 1977
	4	74	Quebec	Terrill 1961

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	8	112	Quebec	Hicks 1934
	10	89	Michigan	Southern and Southern 1980
	11	45	Iowa	Rodenhous and Best 1983
	11	442	Ontario	Peck and James 1987
	12	195	Alberta, Manitoba, Saskatchewan	Prairie Nest Records Scheme in Friedmann et al. 1977
	15	110	Saskatchewan	McMaster et al. 1999
	15	242	Ontario	Ontario nest records in Friedmann et al. 1977
	16	25	Michigan	Ponshair in Berger 1968
	17	18	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	26	94	North Dakota	Koford et al. 2000
	61	41	Iowa	Stallman and Best 1996
Lark sparrow ³	6	17	Oklahoma	Ely 1957
(<i>Chondestes grammacus</i>)	7	228	California, Oklahoma, Texas	Western Foundation Collection in Friedmann et al. 1977
	8	25	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	13	15	Manitoba	Walley 1985
	18	11	Illinois	Robinson et al. 2000
	20	15	Alberta, Manitoba, Saskatchewan	Prairie Nest Records Scheme in Friedmann et al. 1977
	27	22	Kansas	R. F. Johnston in Friedmann 1963
	46	33	Oklahoma	Newman 1970

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	82	11	Kansas	Hill 1976
Lark bunting ³	0	30	Kansas	Shane 2000
(<i>Calamospiza</i>	16	142	Kansas	Hill 1976
<i>melanocorys</i>)	20	85	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	21	77	Kansas	Wilson 1976
	28	18	Montana, North Dakota, South Dakota	Allen 1874
	55	22	Saskatchewan	Sealy 1999
	61	23	North Dakota	Koford et al. 2000
Savannah sparrow	2	54	Michigan	Potter 1974
(<i>Passerculus</i>	4	140	Quebec	Terrill 1961
<i>sandwichensis</i>)	7	14	Saskatchewan	Prairie Nest Records Scheme in Maher 1973
	7	531	Ontario	Peck and James 1987
	7	687	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	11	44	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	13	240	Ontario	Ontario nest records in Friedmann et al. 1977
	16	111	Alberta, Manitoba, Saskatchewan	Prairie Nest Records Scheme in Friedmann et al. 1977
	21	24	Manitoba	De Smet 1992
	21	150	North Dakota	Granfors et al. 2001
	28	69	Saskatchewan	S. K. Davis, personal communication
	32	31	Manitoba	Davis 1994, Davis and Sealy 2000

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	37	46	Minnesota	Johnson and Temple 1990
Grasshopper sparrow ³	0	23	Missouri	Winter 1998
(<i>Ammodramus</i>	2	100	Ohio	H. F. Price in Friedmann 1963
<i>savannarum</i>)	2	21	North Dakota	Granfors et al. 2001
	6	48	Minnesota	Johnson and Temple 1990
	8	13	Illinois	Robinson et al. 2000
	8	39	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	8	74	Ontario	Peck and James 1987
	9	62	Iowa	Patterson 1994, Patterson and Best 1996
	21	28	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	22	18	Kansas	Hill 1976
	26	58	North Dakota	Koford et al. 2000
	27	48	Manitoba	Davis 1994, Davis and Sealy 2000
	30	40	Manitoba	De Smet 1992
	34	61	Kansas	Jensen 1999
	50	18	Kansas	Elliott 1978
	58	12	Kansas	Klute 1994, Klute et al. 1997
Baird's sparrow	0	11	Saskatchewan	Maher 1973
(<i>Ammodramus bairdii</i>)	3	11	North Dakota	Granfors et al. 2001
	15	13	Manitoba	De Smet and Conrad 1991

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	16	68	Manitoba	De Smet 1992
	21	138	Saskatchewan	S. K. Davis, personal communication
	36	76	Manitoba	Davis and Sealy 1998
Henslow's sparrow	5	59	Missouri	Winter 1999
(<i>Ammodramus henslowii</i>)	8	12	Ontario	Peck and James 1987
	8	24	Oklahoma	Reinking et al. 2000
	9	22	Oklahoma	D. Reinking, Sutton Avian Research Center, Bartlesville, Oklahoma, personal communication in Winter 1999
Le Conte's sparrow	2	51	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
(<i>Ammodramus leconteii</i>)	29	14	Minnesota	Peabody 1901
Nelson's sharp-tailed sparrow	1 record		Manitoba	J. Lane in Hill 1968
(<i>Ammodramus nelsoni</i>)				
McCown's longspur	0	74	Saskatchewan	Maher 1973
(<i>Calcarius mccownii</i>)	67	3	North Dakota	L. B. Bishop in Friedmann 1963
Chestnut-collared longspur	0	36	Saskatchewan	Fairfield 1968
(<i>Calcarius ornatus</i>)	0	38	Saskatchewan	Regina Museum of Natural History Nest Record Cards in Fairfield 1968
	0	111	Saskatchewan	Maher 1973
	0	254	Alberta	Hill and Gould 1997
	3	71	North Dakota	Granfors et al. 2001

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	4	23	Manitoba	Harris 1944
	4	27	Saskatchewan	Smith and Smith 1966
	8	26	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	12	26	Manitoba	De Smet 1992
	14	57	Manitoba	Davis 1994, Davis and Sealy 2000
	14	363	Saskatchewan	S. K. Davis, personal communication
	18	22	Saskatchewan	Prairie Nest Records Scheme in Maher 1973
	22	37	North Dakota	R. E. Stewart in Friedmann et al. 1977
	23	62	North Dakota	Stewart 1975
Dickcissel ^{3,4}	0	29	Illinois	Robinson et al. 2000
(<i>Spiza americana</i>)	1	22	Texas	Fretwell et al. 1974
	3	143	Texas	Steigman 1993
	8	12	Oklahoma	Ely 1957
	8	24	Kansas, Missouri, Nebraska	Lowther 1977
	9	241	Missouri	Winter 1999
	20	71	Kansas	Schartz 1969
	21	34	Iowa	Frawley 1989
	26	23	Kansas	R. F. Johnston in Friedmann 1963
	31	61	Oklahoma	Overmire 1962
	33	15	Oklahoma	Wiens 1963
	33	39	Iowa	Patterson 1994, Patterson and Best 1996

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	50	28	Kansas	Hill 1976
	53	17	Nebraska	Hergenrader 1962
	56	124	Kansas	Jensen 1999
	60	186	Kansas	Hughes 1996
	65	23	Kansas	Fleischer 1986
	69	620	Kansas	Zimmerman 1983
	78	55	Kansas	Zimmerman 1966
	82	34	Kansas	Klute 1994, Klute et al. 1997
	91	65	Kansas	Hatch 1983
	95	19	Kansas	Elliott 1978
Bobolink	0	20	Wisconsin	Martin 1967
(<i>Dolichonyx oryzivorus</i>)	5	184	Ohio	Hicks 1934
	6	136	Ontario	Peck and James 1987
	11	36	North Dakota	Granfors et al. 2001
	11	315	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	20	41	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	25	12	North Dakota	Koford et al. 2000
	34	47	Minnesota	Johnson and Temple 1990
Eastern meadowlark ^{3,4}	0	27	Ohio	S. D. Hull, Ohio Division of Wildlife, Ashley, Ohio, personal communication
(<i>Sturnella magna</i>)	2	52	Quebec	Terrill 1961

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	2	57	Illinois	Robinson et al. 2000
	2	370	Ontario	Peck and James 1987
	4	26	Ontario	Ontario nest records in Friedmann et al. 1977
	6	244	unspecified region	Cornell nest records in Friedmann et al. 1977
	10	47	Missouri	Winter 1998
	10	69	Kansas, Nebraska, Missouri	Lowther 1977
	16	38	Wisconsin	Lanyon 1995
	31	69	Kansas	Jensen 1999
	49	71	Kansas	Granfors 1992
	50	10	Kansas	Fleischer 1986
	50	14	Kansas	Francq 1972
	70	40	Kansas	Elliott 1978
Western meadowlark ⁴	7	29	Kansas	Hill 1976
(<i>Sturnella neglecta</i>)	11	71	Minnesota, North Dakota	M. Winter and D. H. Johnson, unpublished data
	18	76	Minnesota	Johnson and Temple 1990
	19	43	Minnesota, Montana, North Dakota, South Dakota	L. D. Igl and D. H. Johnson, unpublished data
	20	20	Saskatchewan	Prairie Nest Records Scheme in Maher 1973
	22	41	Wisconsin	Lanyon 1957
	22	81	Saskatchewan	S. K. Davis, personal communication
	44	65	Manitoba	Davis 1994, Davis and Sealy 2000

Table 1, continued.

Species	Parasitism rate (%)	No. nests	Location	Source
	45	320	North Dakota	Koford et al. 2000
	46	24	Manitoba	De Smet 1992

¹The following grassland bird species are not known hosts of brown-headed cowbird brood parasitism: American bittern (*Botaurus lentiginosus*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), lesser prairie-chicken (*Tympanuchus pallidicinctus*), mountain plover (*Charadrius montanus*), willet (*Catoptrophorus semipalmatus*), long-billed curlew (*Numenius americanus*), marbled godwit (*Limosa fedoa*), burrowing owl (*Athene cunicularia*), short-eared owl (*Asio flammeus*), and sedge wren (*Cistothorus platensis*).

²Rothstein (1982) demonstrated that loggerhead shrikes ejected red-winged blackbird (*Agelaius phoeniceus*) and tri-colored blackbird (*A. tricolor*) eggs that were experimentally placed in shrike nests.

³Occasionally abandons nests due to cowbird brood parasitism.

⁴Peer et al. (2000) found that dickcissels ejected 11% of 9 artificial, cowbird-sized eggs; eastern meadowlarks ejected 36% of 14 artificial, cowbird-sized eggs; and western meadowlarks ejected 78% of a combination of 14 artificial, cowbird-sized eggs, and four real cowbird eggs.

and Temple 1983, Faanes 1983, Zimmerman and Finck 1983, Biermann et al. 1987, Bryan and Best 1991, Cable et al. 1992, Zimmerman 1992, Camp and Best 1993, Daub 1993, Delphey and Dinsmore 1993, Jorgensen and Nauman 1993, Davis 1994, Patterson 1994, Faanes and Lingle 1995, Haas 1997, Prescott 1997, Koford 1999, Koford et al. 2000).

Cowbirds may commute among different habitats for feeding, breeding, and roosting. For foraging, cowbirds require areas of short vegetation and prefer habitats created by large, grazing mammals (Mayfield 1965). Individual cowbirds may leave their breeding sites to join foraging groups of other cowbirds; in the evening, they may then return to their breeding sites or locate suitable roosting areas (Rothstein et al. 1980). Where cowbirds do commute between feeding and breeding sites, females are most active on breeding areas in the morning and can commute up to 17 km to feeding sites in the afternoon (Rothstein et al. 1980, 1984; Goguen and Mathews 1999; Curson et al. 2000; Raim 2000). Cowbirds may commute up to 21 km from feeding to roosting sites (Curson et al. 2000). If breeding sites also provide feeding and roosting opportunities, cowbirds may not commute between breeding and feeding or roosting sites (Rothstein et al. 1980, Raim 2000). On their breeding sites, cowbirds may roost in coniferous forests, riparian woodlands, or in cattail (*Typha* spp.) marshes (Curson et al. 2000).

Perch sites are a major habitat component for displaying and singing cowbirds, as well as for observation posts from which female cowbirds watch host activity (Friedmann 1929, Norman and Robertson 1975, Elliott 1976, Lowther and Johnston 1977, Kahl et al. 1985). Suitable cowbird perches include trees, shrubs, and other structures that exceed the average height of the surrounding vegetation (Kahl et al. 1985, Davis 1994, Romig and Crawford 1995, Hauber and Russo 2000). In Alberta, cowbirds were observed perching in trees up to 4 m tall and were not observed in a treeless area dominated by sagebrush (Biermann et al. 1987).

Abundance of cowbirds may be affected by vegetation characteristics. In Nebraska, numbers of cowbirds in tallgrass prairie and in CRP fields were related positively to vegetation height (King and Savidge 1995). Within CRP fields in Minnesota, Montana, North Dakota, and South Dakota, densities of cowbirds were associated negatively with coverage of grasses and legumes (Johnson and Schwartz 1993a). Within burned mixed-grass prairie in northwestern North Dakota, cowbird abundance was associated positively with forb cover, live vegetation, and plant associations of western snowberry (*Symphoricarpos occidentalis*) and tame grasses such as quackgrass (*Elytrigia repens*) and smooth brome (*Bromus inermis*) (Madden 1996). Cowbird abundance was associated negatively with litter depth and vegetation density. Cowbird presence was associated positively with forb and grass cover and associated negatively with vegetation density. Within grazed areas in southcentral and northwestern North Dakota, cowbird abundance was associated positively with percent grass cover, litter depth, and vegetation communities dominated by a mixture of Kentucky bluegrass (*Poa pratensis*) and

native grasses (Schneider 1998). Cowbird abundance was associated negatively with shrub density and percent spikemoss (*Selaginella densa*) cover, and abundance was low in areas dominated solely by native grasses. The strongest predictor of the presence of cowbirds was low visual obstruction (vegetation height and density). In Colorado, Montana, Nebraska, North Dakota, South Dakota, and Wyoming, high densities of cowbirds were found in moderately grazed native grasslands with typic ustoll soils and with Kentucky bluegrass and white sage (*Artemisia ludoviciana*) (Kantrud and Kologiski 1982). In central North Dakota, cowbirds were more abundant in areas with 30% to 80% coverage of western snowberry and silverberry (*Elaeagnus commutata*) than in areas with less than 10% shrub coverage (Arnold and Higgins 1986). In Iowa, cowbird abundance in roadside vegetation was related inversely to vegetation height and vertical density (Camp and Best 1993). In riparian habitats, cowbird density was correlated negatively to tree density and species richness of deciduous trees, and correlated positively to sapling size, vertical stratification of vegetation less than 3 m, and species richness of all life forms (Stauffer and Best 1980). Life forms were categorized as grass-like vegetation, forbs, shrubs, deciduous trees, evergreen trees, and vines.

In an Illinois study, Robinson et al. (1999) found grassland habitats had a lower ratio (about 1.25) of female cowbirds per 100 hosts of acceptor species (those that do not reject cowbird eggs or abandon parasitized nests) than forests (3.75), savannas (12.5), or shrubland (5). Young and Hutto (1999) found in Montana and Idaho that cowbirds were more common in open areas, such as grasslands and agricultural areas, and in riparian areas, than in forests. Topography was a strong predictor of cowbird occurrence in western Montana (Tewksbury et al. 1999). Cowbirds occurred more frequently in level than in steep topography, partially because canyons were farther from agricultural areas and host density was lower in canyons than in level areas. Topography was more influential in predicting cowbird occurrence than was host density or vegetation type. Young and Hutto (1999) reported that cowbirds in Montana and Idaho were less likely to occur in high-elevation grasslands; cowbirds were not found above 2,318 m above sea level. Elsewhere, however, cowbirds have been reported at higher elevations: Colorado (2,895 m above sea level, Hanka 1985) and California (found at 41% of 114 sites greater than 2,400 m above sea level, Rothstein et al. 1980).

BREEDING BIOLOGY

The breeding season for cowbirds generally extends from early May to late July (Ortega 1998), a period that includes or overlaps with the breeding seasons of many North American grassland birds (Stewart 1975). In North Dakota, Stewart (1975) reported that the cowbird's breeding season extended into mid-August but

peaked from late May to mid-July. Cowbirds arrive in the northern United States from early April to early May and depart between August and November (Batts 1958, Bent 1965, Knapton 1979, Johnsgard 1980).

Fidelity to breeding sites has been observed in both males and female cowbirds (Friedmann 1929; Shake and Mattsson 1975; Elliott 1976; Kennard 1978; Montgomery 1979; Darley 1982, 1983; Dufty 1982; Lowther 1993; Raim 2000). In Manitoba, 64% of 337 banded male cowbirds and 46% of 173 banded female cowbirds exhibited breeding-site fidelity (Woolfenden et al. 2001). Shake and Mattsson (1975) reported that 40% of 119 males and 9% of 81 females banded in northcentral Michigan returned to within 4.8 km of the banding site the year after banding. In an Illinois study, Raim (2000) found that 47% of 79 breeding areas occupied by color-banded females in June of one year were reoccupied by the same birds the following year. During a seven-year period, 15 females held similar breeding areas for at least two years, 7 females for at least three years, and 2 females for at least five consecutive years. Four females occupied territories adjacent to those of the previous year.

Friedmann and Kiff (1985) reported 220 host species of cowbird brood parasitism, with 144 species known to have reared cowbird young. Taxonomic splitting of species and new data have increased the number of cowbird hosts to 227, 151 of which are now known to raise cowbird young (Svedarsky 1979; Davis and Sealy 1998, 2000; Ortega 1998). Of 36 North American grassland species, 24 have been parasitized by cowbirds (Table 1).

Cowbirds typically lay eggs before sunrise (Scott 1991, Neudorf and Sealy 1994, Burhans 2000, Strausberger and Burhans 2001). Scott (1991) estimated that laying time ranged from 2 to 11 min before sunrise. In a Manitoba study, 13 cowbirds laid eggs in host nests an average of 31 min before sunrise (D. G. McMaster, Saskatchewan Watershed Authority, Regina, Saskatchewan, personal communication). Strausberger and Burhans (2001) estimated that the average arrival time of female cowbirds to field sparrow (*Spizella pusilla*) nests was 15 min (6 nests) before sunrise in Missouri and 22 min (3 nests) before sunrise in Illinois.

FACTORS INFLUENCING NEST PARASITISM

Parasitic activities are influenced by nest substrate, height, location (e.g., habitat type, distance to habitat edge and to perches), and concealment (Wiens 1963, Zimmerman 1983, Romig and Crawford 1995, Davis and Sealy 2000, S. K. Davis, Saskatchewan Watershed Authority, Regina, Saskatchewan, personal communication); by characteristics of host species such as abundance, group defense (Freeman et al. 1990, Strausberger 2001), and breeding-season phenology (Fleischer 1986, Davis 1994); and by distance from grazed areas (Goguen and Mathews 2000). Our account will deal primarily with parasitism of grassland-

nesting birds, including certain raptors and gallinaceous birds, that breed in the Great Plains.

Investigators have found mixed effects of nest substrate or height on parasitism. Wiens (1963) found no differences in nest substrate or height between parasitized and unparasitized nests located in tallgrass prairie, upland woodlands, or bottomland woodlands in Oklahoma. Both parasitized and unparasitized nests were found in saplings and brush. Parasitized nests were located in edge habitat, such as low, brushy thickets bordering fairly open tallgrass, whereas most nests in open tallgrass were not parasitized. In a Kansas study, small differences in nest substrate did not appear to affect parasitism rates on red-winged blackbird (*Agelaius phoeniceus*) nests, whereas nest height did affect parasitism rates (Fleischer 1986). Parasitized nests of red-winged blackbirds and dickcissels (*Spiza americana*) were located significantly higher in the nest substrate than unparasitized nests. In a Nebraska study, cowbirds parasitized nests in woodland edges, brushy thickets, and areas containing scattered trees or shrubs (Johnsgard 1980). In Kansas, Zimmerman (1983) found that dickcissel nests in tallgrass prairie were more heavily parasitized (85% of 125 nests) than dickcissel nests in oldfields (60% of 385 nests). In southern Saskatchewan, parasitized nests of Baird's sparrows (*Ammodramus bairdii*) were concealed significantly less well than unparasitized nests; the opposite was true for clay-colored sparrows (*Spizella pallida*) (S. K. Davis, personal communication). There was no significant difference in concealment between parasitized and unparasitized nests for chestnut-collared longspur (*Calcarius ornatus*), Savannah sparrow (*Passerculus sandwichensis*), Sprague's pipit (*Anthus spragueii*), or western meadowlark (*Sturnella neglecta*).

Nests closer to edges of habitat patches appear to be more vulnerable to parasitism by cowbirds than interior nests. Highest parasitism frequency in Manitoba grasslands occurred in areas with a higher proportion of edge than other sites (Davis 1994, Davis and Sealy 2000). Close proximity of cowbird foraging areas to host nesting sites also might have resulted in higher parasitism frequencies near edges (Davis and Sealy 2000). In Illinois, frequencies of parasitism were higher in woodland edges and woodlands than in shrub/grassland or grassland habitats (Best 1978, Strausberger and Ashley 1997). In Minnesota tallgrass prairies, higher rates of parasitism occurred near (< 45 m) wooded edges of tallgrass patches than far (\geq 45 m) from edges for clay-colored sparrows and western meadowlarks (Johnson and Temple 1990, also see Johnson 2001). In Kansas, parasitism rates for eastern meadowlarks (*Sturnella magna*), grasshopper sparrows (*Ammodramus savannarum*), and dickcissels were higher for nests located within 100 m of a woodland edge than for nests located farther than 100 m from woodland edge (Jensen 1999). For those three species, there were no differences in parasitism rates for nests located near agricultural edges and nests located away from agricultural edges. Parasitism rates of Brewer's blackbird (*Euphagus*

cyanocephalus) nests in Colorado and Wyoming were higher for nests located close (≤ 300 m) to water than for nests located farther (> 300 m) from water (Hanka 1979). In Wisconsin tallgrass prairies, Clotfelter et al. (1999) found that the probability of cowbird parasitism on red-winged blackbirds increased with proximity to habitat edge or road but with increasing distance from a burned area. Habitat edge was defined as the interface between prairie and agricultural fields or woodlots. Distance to edge was not a predictor of nest success or number of fledglings.

Some edge habitats provide perches for cowbirds to use to find nests. Perches often are associated with higher parasitism rates. In Iowa, red-winged blackbird nests in restored wetlands had lower parasitism rates than nests in natural wetlands, possibly because of the paucity of trees to serve as perches near restored wetlands (Delphey and Dinsmore 1993). In a study in eastern Washington, cowbirds parasitized inactive nests of red-winged blackbirds; the parasitism rate was lower in wetlands with trees than in wetlands without trees (Freeman et al. 1990). The authors suggested that the trees provided perches that allowed female cowbirds to better assess whether nests were active or deserted.

The proximity of perches to a nest may influence the likelihood of a nest being parasitized. In eastern North Dakota, clay-colored sparrow nests that were parasitized by cowbirds were significantly closer to perches than were unparasitized nests (Romig and Crawford 1995). Perches were defined as any shrub, tree, or human-made structure standing at least 1 m above the surrounding vegetation. No nest greater than 52 m from a perch was parasitized. In Manitoba, nests located within 150 m of a perch were more likely to be parasitized than nests located farther from a perch (Davis 1994). Perches were defined as fences, shrubs, or other structures at least 1 m tall. However, some nests were parasitized even though they were far (≥ 340 m) from any such perch (Davis and Sealy 2000). In Saskatchewan, 28 parasitized chestnut-collared longspur nests were significantly closer to potential cowbird perches than were 174 unparasitized nests (mean distances were 34 m versus 50 m); the same trend was exhibited for vesper sparrows (77 m versus 159 m) (S. K. Davis and D. G. McMaster, personal communication). Perches were defined as fences, shrubs, or other structures at least 50 cm tall. Parasitized nests of the following three species were, on average, closer but not significantly, to perches than unparasitized nests: Baird's sparrow (25 m based on 21 nests versus 36 m based on 58 nests), Savannah sparrow (34 m based on 18 nests versus 36 m based on 32 nests), and western meadowlark (33 m based on 13 nests versus 38 m based on 34 nests). In New York, parasitized nests of song sparrows (*Melospiza melodia*) were significantly closer to potential perches, such as trees and other structures (e.g., fences) that were at least 2 m tall, than were unparasitized nests (Hauber and Russo 2000).

Host group defense may deter parasitism (Freeman et al. 1990, Carello and Snyder 2000). In Washington, dense colonies of red-winged blackbirds had

lower parasitism rates than more sparsely populated colonies, possibly due to group defense (Freeman et al. 1990). Parasitism rates in a Colorado area were correlated negatively with the number of red-winged blackbird nests per pond (Carello and Snyder 2000). The authors suggested that parasitism rates were lower due to the clumped distribution of nests. However, Fretwell (1972) found that dickcissels nesting in close proximity to nesting red-winged blackbirds experienced high parasitism rates; he suggested that blackbirds attracted cowbirds. In Wisconsin, Clotfelter and Yasukawa (1999) examined the effect of aggregated nesting on red-winged blackbirds. A significant positive relationship existed between the number of nests initiated per day and the proportion of nests parasitized, which suggested that the aggregation of nesting birds did not result in a decrease in parasitism. No significant differences existed in the distances to nearest neighbor for parasitized and unparasitized nests. However, synchronized egg-laying apparently helped reduce the risk of parasitism. Egg-laying periods of parasitized nests were less synchronized with their nearest neighbors than were unparasitized nests, and parasitized nests were farther from their nearest simultaneously active nests (i.e., they were more isolated) than were unparasitized nests. The mean distance between 39 parasitized nests and their nearest simultaneously active nests was 79 m, compared to 54 m for 119 unparasitized nests.

In riparian areas in western Montana, parasitism rate increased with increasing host density and with proximity to human habitations, such as farmsteads and houses (Tewksbury et al. 1999). In addition, hosts nesting in large riparian woodland patches were at greater risk of parasitism than hosts nesting in smaller riparian woodlands and coniferous areas. Many large riparian areas were near agricultural areas and had high cowbird abundance. Landscape features more than 1 km from study sites had little influence on parasitism rates.

Nesting phenology of host species may influence parasitism frequency. In Manitoba, chestnut-collared longspurs were parasitized infrequently, possibly because they initiated clutches in two distinct time periods, several weeks before and several weeks after cowbirds began egg-laying (Davis 1994). Cowbirds increasingly parasitized grasshopper sparrow nests as the breeding season progressed. In a North Dakota study, none of 24 early nests (found by 15 May) of horned larks (*Eremophila alpestris*) was parasitized, whereas 83% of 60 late nests (found after 15 May) were parasitized (Koford et al. 2000). Cowbirds parasitized red-winged blackbird nests in Kansas early in the season (prior to 25 May) and began parasitizing dickcissel nests later in the season (after 25 May) as the availability of the latter increased (Fleischer 1986). Nests of red-winged blackbirds in Washington that were built earlier in the nesting season (20-60 days into the breeding season, based on the date when the first red-winged blackbird egg was laid) were parasitized less than nests initiated later (60-80 days into the breeding season) (Freeman et al. 1990).

HOME RANGE SIZE AND AREA SENSITIVITY

Female cowbirds in an Illinois area characterized by mowed grass, wooded areas, and shrubs were flexible and opportunistic in maintaining and expanding territory size and in occupying new areas (Raim 2000). Breeding areas increased from an average of 9.2 ha in May through mid-June to 21.5 ha in late June through July as the number of breeding females decreased. Whereas some breeding areas remained stable in size and location throughout the breeding season, other areas were vacated, new areas occupied, or existing areas expanded to fill vacated areas. Breeding areas of 12 females overlapped by an average of 12%.

Territorial behavior has been observed in some cowbirds, although it may vary among habitat types (Elliott 1980). It was not observed in a grazed tallgrass prairie in Kansas (Elliott 1976), whereas it was reported among cowbirds in certain eastern studies (Dufty 1982, Darley 1983, Teather and Robertson 1985). Host abundance in grasslands may be lower than that in deciduous forests, and female cowbirds in grasslands may need to expand the area in which they search for nests to such an extent that territorial defense is uneconomical. Moreover, males may be unable to defend females over such a large range. In contrast, in deciduous forest, potential hosts may be so plentiful that territorial defense is more economical. Darley (1982) found that home ranges of monogamous males overlapped their mates' home ranges; males did not defend their home ranges but did defend their mates. In Illinois, female cowbirds were aggressive toward other female cowbirds (Raim 2000). Dufty (1982) observed that males guarded their mates and that females defended their nonfeeding ranges from other females.

The size of a habitat patch may influence brood parasitism. Daub (1993) found that parasitism occurred only in nests in wetlands less than 2.9 ha in size, possibly due to the ease in which female cowbirds could observe nesting female red-winged blackbirds and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) in smaller wetlands (Daub 1993). In Minnesota, Montana, North Dakota, and South Dakota, the density of cowbirds in CRP fields varied inversely with the size of the grassland patch that embedded the field (Johnson and Igl 2001). Similarly, in southern Saskatchewan, abundance of cowbirds and parasitism rates were two to four times higher in small (< 256 ha) pastures than in large (\geq 256 ha) pastures (S. K. Davis, personal communication).

EVIDENCE OF MANAGEMENT EFFECTS ON COWBIRDS

Few studies have found a strong effect of burning of grassland on the abundance (Zimmerman 1993, Madden 1996) or parasitism (Clotfelter et al. 1999) of cowbirds. However, Best (1979) reported that parasitism rates decreased after a burn, and Camp and Best (1993) reported that cowbirds were more abundant in

roadsides after burning. In central North Dakota, cowbird densities were depressed about one year after a burn but showed no longer-term responses (Johnson 1997). In northeastern South Dakota (Huber and Steuter 1984) and northwestern North Dakota (Madden 1996, Madden et al. 1999), cowbirds showed no significant response in abundance to burning. In Kansas, cowbirds were nonsignificantly more abundant in unburned tallgrass prairie than in annually burned prairie (Zimmerman 1993). There was no difference in the production of cowbird young per nest among unburned/grazed, burned/ungrazed, and burned/grazed treatments of tallgrass prairie (Zimmerman 1997). In a Kansas study of native-seeded CRP fields, abundance of cowbirds was nonsignificantly higher on unburned than burned fields (Robel et al. 1998). Clotfelter et al. (1999) examined effects of prescribed burning on red-winged blackbirds in a tallgrass prairie in Wisconsin. Proportion of parasitized red-winged blackbird nests and number of cowbird eggs per nest were not affected by season (spring versus fall) of burn, time elapsed since last burn, area burned, or quality of burn (burn quality depended on number and size of unburned patches, extent of burn on woody vegetation, whether head-fires were necessary, and quality of back-burn). In Minnesota tallgrass prairie, time since last burn had no significant impact on parasitism rates for field sparrow, Savannah sparrow, grasshopper sparrow, bobolink (*Dolichonyx oryzivorus*), or western meadowlark (Johnson and Temple 1990). In Illinois, both nest parasitism and nest desertion caused largely by parasitism declined in a field sparrow population in the breeding season following an April burn (Best 1979).

Very little is known about the effects of mowing on cowbirds. However, cowbird eggs and young would suffer the same fate as host eggs and young during mechanical farm operations. In Iowa, cowbirds parasitized nests before mowing operations in both the first (mowed early to mid-June) and second (mowed mid-July) alfalfa (*Medicago sativa*) crops (Frawley 1989). In Saskatchewan alfalfa hayland, 12% of 148 songbird nests were parasitized (McMaster et al. 1999). Cowbirds were observed foraging in alfalfa stubble in Nebraska after fields had been mowed (Ducey and Miller 1980). Cowbirds were common in native hayland in North Dakota the year after mowing (Kantrud 1981). Another North Dakota study found no difference in cowbird abundance in the year following haying between hayed and idled portions of CRP fields (Horn and Koford 2000). In Alberta, cowbirds were not observed in tame, delayed-cut haylands (cut once after 15 July during the previous summer) or in tame haylands (cut before 15 July) (Prescott et al. 1995).

Cowbirds generally are common in moderately to heavily grazed areas (Knapton 1978, Kantrud 1981, Kantrud and Kologiski 1982, Klute 1994, Prescott et al. 1995, Morris 1996), but see Dale (1984) and Messmer (1990). Distance to agricultural areas, such as pastures, strongly influences cowbird occurrence (Goguen and Mathews 1999). In New Mexico, cowbird abundance and rates of parasitism in plumbeous vireo (*Vireo plumbeus*) nests declined with increasing

distance from actively grazed pastures (Goguen and Mathews 2000). Parasitism rates declined from 81% (of 58 nests) in grazed pastures to 33% (of 24 nests) located 8 to 12 km from grazing areas. In Missouri, cowbirds were observed near cattle on short, heavily grazed tallgrass prairie (45% cover at 1 cm above ground and 10% cover at 25 cm above ground) (Skinner et al. 1984). In an agricultural landscape in Missouri, density of foraging cowbirds was highest in feedlots, followed by short (2 to 20 cm) grazed grass, tall (5 to 30 cm) grazed grass, and ungrazed habitats (Morris 1996, Morris and Thompson 1998). Ungrazed habitats were mowed lawns, haylands with grass 2 to 10 cm tall, or unmowed haylands with grass exceeding 30 cm tall. The parasitism rate was higher in a lightly grazed pasture (58% of 93 nests) than in an ungrazed wildlife management area (22% of 139 nests) in Manitoba (Knapp 1978). Numbers of cowbirds on the pasture declined after grazing ceased. Prescott and Wagner (1996) reported the presence of cowbirds in a variety of grazing treatments in Alberta, with highest frequency (observed in 12.5% of 24 count circles) occurring in native pastures that were grazed in early summer. Prescott et al. (1995) reported that cowbirds were present in continuously grazed native grassland, continuously grazed native parkland, and tame pastures grazed throughout the growing season, but were absent from native and tame pastures where grazing was deferred until after 15 July. In a Kansas study, cowbirds were significantly more abundant in moderately grazed, annually spring-burned tallgrass prairie than in ungrazed, annually spring-burned CRP fields planted to native grasses, but rates of parasitism were high in both habitats (71% of 42 nests in prairie and 100% of 11 nests in CRP) (Klute 1994, Klute et al. 1997). Also in Kansas, cowbirds were common in burned/ungrazed, burned/grazed, unburned/grazed, and unburned/ungrazed tallgrass treatments (Eddleman 1974). In Nebraska, cowbirds were present in cattle-grazed areas and in areas both grazed by American bison (*Bos bison*) and burned (Griebel et al. 1998). In a North Dakota study, cowbird densities did not differ significantly among several rotational grazing systems and idle pastures (Messmer 1990). The rotational systems were season-long pasture, short-duration (1 week grazed and 1 month ungrazed, repeated throughout the season), and twice-over rotation (pastures grazed twice per season, with about a 2-month rest between grazing). Kantrud and Kologiski (1982) found no consistent effect of grazing intensity on cowbird densities in Colorado, Montana, Nebraska, North Dakota, South Dakota, or Wyoming. Densities of cowbirds in Saskatchewan did not differ between grazed and ungrazed mixed-grass prairie (Dale 1984). In Alberta aspen parkland, cowbirds were present in low numbers in tame pastures of crested wheatgrass (*Agropyron cristatum*) grazed from late April to mid-June (Prescott et al. 1993) but were absent in native pastures that were grazed in early summer, grazed after 15 July (deferred), or grazed continuously throughout the growing season.

Goguen and Mathews (1999) reviewed four hypotheses that attempted to explain the association between cowbirds and livestock: 1) livestock act as

perches or protective cover, 2) livestock or livestock-holding facilities are used as places for social interactions, 3) livestock facilitate foraging opportunities, and 4) cowbirds evolved with ungulates and their association with cattle is an artifact of that association. The third hypothesis, referred to as the foraging site hypothesis, is currently the most popular among cowbird researchers. Livestock enhance foraging for cowbirds in the following ways: 1) grazing creates microhabitats, that is, short vegetation, favored for foraging by cowbirds; 2) grazing increases invertebrate abundance; 3) livestock increase invertebrate abundance through body parasites or insects and seed in manure; 4) cowbirds feed on forage provided by humans to livestock, such as spilled grain; and 5) livestock flush up insects as they move along and graze. Goguen and Mathews' (1999) data supported the final explanation.

Determining the influence of livestock on cowbird abundance and parasitism may be difficult due to issues of scale (Goguen and Mathews 1999). Cowbirds are highly mobile and attempting to determine whether cowbirds are more abundant on grazed or ungrazed pastures may be confounded by distance between treatments. Goguen and Mathews (1998) found no difference in nesting success between grazed pastures and pastures ungrazed for 20 years, but ungrazed areas were only about 4 km from grazed areas. As cowbirds have been known to commute 7 to 16 km between feeding and breeding areas (Rothstein et al. 1984, Curson et al. 2000), the ungrazed areas might have been indirectly influenced by grazing. The presence of cattle is a major factor influencing the presence of cowbirds, especially in areas where foraging sites for cowbirds would otherwise be rare (Goguen and Mathews 1999). When cattle were removed from pastures, cowbirds shifted their feeding location to other grazed locations, even if the new locations were farther from breeding areas.

Cowbirds are present in a number of agricultural habitats. In Indiana, Iowa, Kansas, Missouri, and Nebraska, cowbirds were abundant in reduced-tillage rowcrops and in both native and tame CRP fields (Best et al. 1997); some CRP fields had been mowed and some had been burned, but no details were given concerning cowbird abundance in these treatments. Cowbirds were not abundant in either rowcrops or CRP in Michigan (Best et al. 1997). In Iowa, cowbirds were observed in CRP fields planted to tame grasses (Patterson 1994, Patterson and Best 1996). Koford (1999) reported that cowbirds were more abundant in Waterfowl Production Areas (WPAs; tracts of grassland and wetland managed by the U.S. Fish and Wildlife Service to provide nesting and brood-rearing habitat for waterfowl) than in CRP grasslands in North Dakota, but the opposite was true in Minnesota. In North Dakota, cowbirds were observed in idle mixed-grass, mixed-grass pasture, and tame DNC (Renken 1983). They also were found in a field one year after grazing. Dhol et al. (1994) reported that cowbirds were observed in both native and tame fields of DNC in Manitoba. Jones (1994), however, found cowbirds in Manitoba in native but not in tame DNC. In Alberta, cowbirds were absent from DNC fields seeded to

native or tame grasses and from idle native or idle tame grasslands (Prescott et al. 1995). In Saskatchewan, cowbirds were present in three- to five-year-old DNC (Hartley 1994). DNC fields were planted to native grasses, tame grasses, or a mixture of native and tame grasses, or were idle brome hayland, but it was not clear which type of DNC supported cowbirds. In Alberta, Manitoba, and Saskatchewan, cowbirds were more common in grasslands enrolled in the PCP than in cropland; there was no difference in frequency of occurrence between PCP grasslands that were hayed and those that were grazed (McMaster and Davis 2001).

Cowbirds, or host nests containing cowbird eggs, have been reported as common in cropland (including fallow, organic, reduced-tillage, and conventional tillage) in Iowa and Michigan (George 1952, Bryan and Best 1991, Camp and Best 1993, Patterson 1994, Patterson and Best 1996, Stallman and Best 1996). Cowbirds were present in low numbers in cropland in Alberta, Minnesota, Montana, North Dakota, and South Dakota (Johnson and Schwartz 1993b, Hartley 1994, Johnson and Igl 1995, Lokemoen and Beiser 1997, Prescott 1997, Koford et al. 2000). In a Saskatchewan study, cowbirds were absent from upland habitats (defined as wheat or other cereal crop, hayland, or native or planted grassland vegetation) and were present in wetlands in conventional, minimum-tillage, and organic farmland, and in DNC (Shutler et al. 2000). Presence was related positively to percent woody vegetation around wetland margins and related negatively to area of open water in wetlands. In South Dakota, cowbirds commonly used restored grasslands, which formerly had been cropland, two to four years after being seeded to native grasses (Blankespoor 1980).

In Montana, Young and Hutto (1999) found that the strongest predictor of cowbird presence in point counts was proximity to agricultural lands (e.g., pastures and rowcrops). The median distance between agricultural areas and the 653 point counts in which cowbirds were detected was 5.3 km, compared to 11.6 km for all 7,153 point counts conducted during the study. In another Montana study, Tewksbury et al. (1999) found that the strongest predictor of cowbird occurrence was proximity to agriculture (e.g., pastures and rowcrops). In areas of level topography, cowbirds were more likely to occur in areas within 2 km of agricultural land than in areas 2 to 4 km from agriculture; no cowbirds were found in point counts located more than 4 km from agriculture. In canyons, cowbirds were more likely to be in areas within 1 km of agricultural land than farther than 1 km from agriculture. Relative abundance of cowbirds also decreased with increasing distance from agriculture.

Chemicals used to kill insects also may kill cowbirds. In New Mexico, toxaphene applied to a 71,600-ha tract of shortgrass prairie caused a decline in cowbird numbers (McEwen et al. 1972). Diazinon that was sprayed on a lawn and a baseball field in Connecticut in September killed dozens of cowbirds (Anderson and Glowa 1985).

Techniques aimed at reducing numbers of cowbirds include poisoning,

trapping, and shooting (Shake and Mattsson 1975, Dolbeer 1988, Robinson et al. 1993, Ortega 1998, De Groot et al. 1999, Rothstein and Cook 2000, De Groot and Smith 2001). In Arkansas, 4-aminopyridine was used to kill birds that damaged agricultural crops (Dolbeer 1988). Birds were baited in February with one part 4-aminopyridine diluted with nine parts of untreated feed. Baiting resulted in the deaths of over 5,400 cowbirds and European starlings (*Sturnus vulgaris*) (Dolbeer 1988). The effectiveness of 4-aminopyridine was short-term, as the numbers of birds returned to prebaiting levels within 8 days. Trapping often is used in local areas where populations of threatened or endangered host species occur (Shake and Mattsson 1975, Ortega 1998, Rothstein and Cook 2000). Permits must be obtained before trapping or shooting can be initiated.

Other techniques aimed at reducing parasitism by cowbirds include adding artificial or infertile cowbird eggs to nests (Ortega et al. 1994) and removing cattle during avian breeding times from areas where host species breed (Goguen and Mathews 1999). The addition of artificial eggs or infertile cowbird eggs to nests of red-winged blackbirds discouraged cowbirds from parasitizing those nests. Removal of real cowbird eggs may promote further parasitism by creating the impression to a cowbird that a nest has not been parasitized. However, the removal method may have less impact in areas with high frequencies of multiple parasitism; in these areas cowbirds are known to parasitize nests that already contain cowbird eggs. Removing cattle from areas where host species breed or rotating use of pastures at critical avian breeding times may reduce parasitism (Goguen and Mathews 1999). The presence of livestock provides high-quality cowbird foraging sites, especially in areas undeveloped by humans, where food sources are rare.

METHODS FOR REDUCING COWBIRD PARASITISM

Some of the most common hosts of cowbird brood parasitism occur in the Great Plains and in grasslands (Table 1). The following are recommendations from the literature for discouraging brood parasitism or controlling cowbird populations in the Great Plains or grasslands through habitat and livestock management.

- 1) Provide large blocks of grassland to decrease rates of parasitism by cowbirds. Acquire and manage large, simple-shaped tracts rather than small or irregular-shaped tracts to reduce amount of edge (Robinson et al. 1993, Saskatchewan Wetland Conservation Corporation 1997, Ortega 1998, Clotfelter et al. 1999, Davis and Sealy 2000). Discourage agricultural and suburban development that fragments remaining prairie; if prairie remnants must be created, compact shapes are preferred over shapes with greater edge habitat.

- 2) In areas with severely fragmented landscapes, reduce cowbird parasitism by maintaining and restoring grasslands, shrublands, and savannas, because cow-

birds may use these habitats less than forests, and birds in non-forest habitats typically have lower parasitism rates than birds in forests (Robinson et al. 1999).

3) Protect large wetlands to reduce amount of habitat edge (Daub 1993). Maintain large colonies of red-winged blackbirds and manipulate nesting distribution from linear to clumped shapes to protect other wetland-nesting species from brood parasitism (Carello and Snyder 2000).

4) Remove potential perches, such as woody vegetation or unnecessary fences. Implement controlled burns, mowing, and rotational grazing to reduce perches (Stauffer and Best 1980, Robinson et al. 1993, Davis and Sealy 2000).

5) Restrict agriculture (e.g., pastures and cropland) to areas already dominated by agricultural uses because expansion of agricultural areas facilitates range expansion of the cowbird (Young and Hutto 1999).

6) Reduce potential feeding areas, such as campgrounds, livestock feedlots, corrals and pack stations, bare ground, mowed roadsides, and areas of short grass near woodland edges (Herkert et al. 1993, Robinson et al. 1993, Morris 1996, Morris and Thompson 1998, Ortega 1998). During peak breeding periods of cowbird host species, remove cattle or rotate use of pastures (Goguen and Mathews 1999).

7) Maintain grass at taller heights (> 5 cm) by rotating use of pastures by cattle (Robinson et al. 1993, Morris 1996, Morris and Thompson 1998).

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