

Parasitism in shrubsteppe-*Vander Haegen and Walker*

**PARASITISM BY BROWN-HEADED COWBIRDS IN THE SHRUBSTEPPE OF  
EASTERN WASHINGTON**

W. Matthew Vander Haegen  
Washington Department of Fish and Wildlife  
Wildlife Research Division  
600 Capitol Way North  
Olympia, WA 98501

Brett Walker  
Department of Biological Sciences  
University of Montana  
Missoula, MT 59812

W. Matthew Vander Haegen  
Washington Department of Fish and Wildlife  
Wildlife Research Division  
600 Capitol Way North  
Olympia, WA 98501  
Phone: 360.902.2516  
Fax: 360.902.2162  
vademwv@dfw.wa.gov

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**Abstract:** Shrubsteppe communities within the Intermountain West have been reduced in area and fragmented by agricultural conversion and land development, yet we know little about the effects of Brown-headed Cowbirds (*Molothrus ater*) on reproductive success of birds that breed in these communities. As part of ongoing research examining landscape effects on avian productivity in eastern Washington, we collected data on parasitism rates and cowbird occurrence. During 1996 and 1997 we surveyed birds using point-counts and searched for nests in big sagebrush (*Artemisia tridentata*) stands in eastern Washington. Cowbirds were common on our study area and were recorded on point-counts at 26 of 29 sites surveyed. Cowbirds arrived on the study area in late April, attaining greatest abundance in May and June. We located and monitored a total of 779 nests of 8 species; only the Brewer's Sparrow (*Spizella breweri*), Sage Sparrow (*Amphispiza belli*), and Vesper Sparrow (*Pooecetes gramineus*) showed evidence of parasitism. Overall parasitism rates were lower than those reported for other bird communities in fragmented landscapes and for other bird communities in shrubsteppe. Low parasitism levels (<10 %) in our study area partly resulted from arrival of cowbirds after initiation of first nests by hosts. Over 40% of Sage Sparrow nests were initiated before cowbirds were observed laying on the study area. Low levels of parasitism also may be related to low availability of elevated observation perches or long distances from study plots to cowbird feeding areas. Determining why parasitism is low in this fragmented landscape may have important implications for managing cowbirds in other areas.

**Key Words:** *Amphispiza belli*, Brewer's Sparrow, Brown-headed Cowbird, *Molothrus ater*, Parasitism, Sage Sparrow, Shrubsteppe, *Spizella breweri*, Washington.

Parasitism by Brown-headed Cowbirds (*Molothrus ater*) has been found to depress significantly the reproductive output of some passerines, particularly in fragmented landscapes (Brittingham and Temple 1983, Robinson et al. 1995). Shrubsteppe communities within the Intermountain-west have been reduced in area and fragmented by agricultural conversion and land development (Quigley and Arbelbide 1997), particularly within the Columbia River Basin in eastern Washington (Dobler et al. 1996). Moreover, these communities have a long history of use as rangeland, providing feeding habitat for cowbirds in the form of feedlots, pastures, and lawns. A recent analysis of data from the Breeding Bird Survey for the Columbia River Basin reported significant, declining trends for populations of numerous shrubsteppe-associated species, with more species declining than increasing (Saab and Rich 1997). We know little about the effects of cowbirds on reproductive success of birds that breed in shrubsteppe communities (Rich 1978, Reynolds 1981, Rich and Rothstein 1985, Biermann et al. 1987).

As part of an ongoing research project examining landscape effects on avian productivity in eastern Washington, we collected data on parasitism levels and cowbird occurrence. Here we present a preliminary assessment of cowbird parasitism on the more common nesting passerines in Washington's shrubsteppe.

## **STUDY AREA AND METHODS**

The study took place in the Columbia River Basin of eastern Washington, in vegetation zones classified as shrubsteppe (Daubenmire 1988). The region is primarily semi-arid desert, with cold winters and hot summers. Most of the native vegetation communities in the region have been converted to agriculture, with an estimated 40% of the historical shrubsteppe remaining (Dobler et al. 1996).

Study plots were established in 29 sites in eight different counties. All sites were dominated by big sagebrush (*Artemisia tridentata*) and native bunch grasses (primarily blue-bunch wheatgrass [*Pseudoreginaria spicatum*], *Poa* spp., and *Stipa* spp.) and forbs. Study sites included both large (>10,000 ha) expanses of continuous shrubsteppe and smaller patches (<100 ha) surrounded by agriculture. All but one of the 29 sites were >50 km from the nearest forest community. Study plots ranged in size from 8 to 20 ha and were flagged at 50-m intervals on a quasi-grid defined by a series of adjacent, 100-m diameter point-count circles.

We surveyed birds at each plot in mid-April, mid-May, and mid-June of 1996 and 1997, using 10-minute point-counts. Birds were recorded as either within 100m of the point, or beyond 100 m but within the *Artemisia* stand containing the plot. For the present analysis, cowbirds observed during point-counts within the stand of interest (perched or flying) were counted as present.

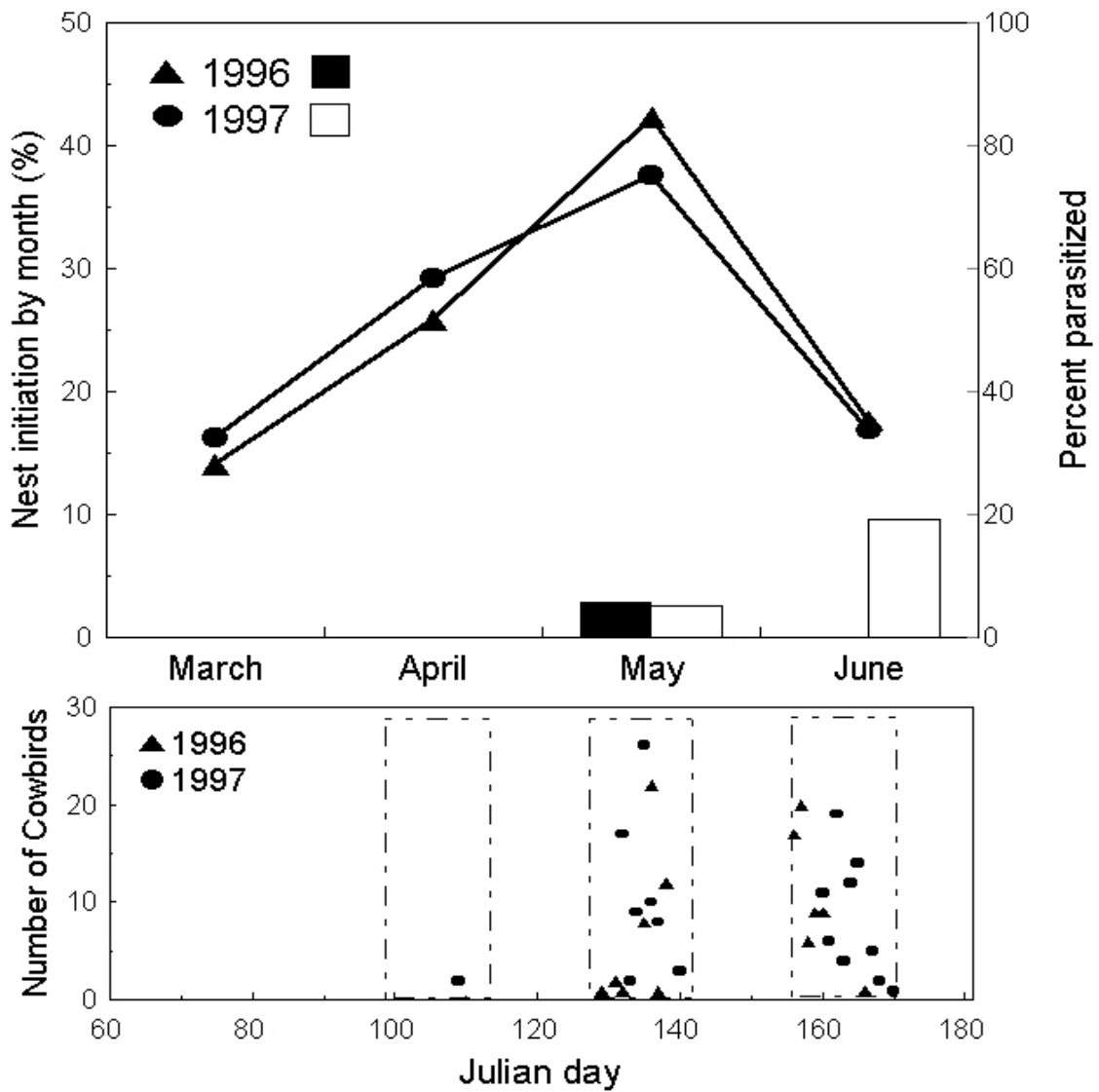
Nests of potential cowbird hosts were located by searching study plots, by following territorial males that were color-banded as part of a productivity study, and by flushing birds from nests while conducting related field work on the plots. Nests were flagged at a distance of >6m and visited every 2-5 days until fledging or failure. The number of host eggs and young and cowbird eggs and young were recorded at each visit. Nest success was calculated using the Mayfield (1975) method.

## **RESULTS**

Cowbirds were common on the study area, recorded on point-counts at 26 of 29 sites surveyed. Cowbirds arrived on the study area in late April, attaining greatest abundance in May

and June (Fig. 1). Most (81%) of the 172 cowbirds of known gender on point-counts were males; the sex of 88 birds was not determined.

**Figure 1. Relationship between nesting by Sage Sparrows and parasitism by Brown-headed Cowbirds in eastern Washington. Upper graph shows timing of nest initiation (symbols) by Sage Sparrows in 1996 (n=85) and 1997 (n=154), and percent of nests parasitized by cowbirds (bars). Lower graph shows point-count results for cowbirds on study plots in 1996 and 1997. Dotted rectangles show survey period in April, May, and June.**



We located and monitored a total of 779 nests of eight species thought to be potential cowbird hosts (Table 1). Of these eight species, only the Brewer's Sparrow, Sage Sparrow, and Vesper Sparrow showed evidence of parasitism (Table 1). These were the most common species on our study plots and provided the largest sample size of nests. Other shrubsteppe-associated species that occurred on the plots but represented by few nests included Savannah Sparrow (*Passerculus sandwichensis*) and Grasshopper Sparrow (*Ammodramus savannarum*).

**Table 1. Levels of nest parasitism by Brown-headed Cowbirds for potential hosts in eastern Washington, 1996-97.**

Species	Number of nests <sup>a</sup>	Nests initiated before 01 May (%)	Parasitism level (%)
Brewer's Sparrow ( <i>Spizella breweri</i> )	281	5	5.0
Sage Sparrow ( <i>Amphispiza belli</i> )	244	43	4.1
Sage Thrasher <sup>b</sup> ( <i>Oreoscoptes montanus</i> )	95	17	0
Vesper Sparrow ( <i>Pooecetes gramineus</i> )	77	23	2.6
Western Meadowlark <sup>b</sup> ( <i>Sturnella neglecta</i> )	36	51	0
Lark Sparrow ( <i>Chondestes grammacus</i> )	24	0	0
Horned Lark ( <i>Eremophila alpestris</i> )	12	42	0
Loggerhead Shrike <sup>b</sup> ( <i>Lanius ludovicianus</i> )	10	20	0

<sup>a</sup> Table includes only species with 10 or more nests

<sup>b</sup> Species known to reject cowbird eggs in some populations.

The proportion of nesting attempts initiated before cowbird arrival (01 May) varied from >40% for early nesting species such as Sage Sparrows, Horned Larks, and Western Meadowlarks, to  $\leq$ 5% for late-arriving species such as Brewer's Sparrows and Lark Sparrows (Table 1). Sage Sparrows began nesting in March, reaching a peak of nesting in May of both years (Fig. 1). Parasitism of Sage Sparrow clutches occurred only during May and June, reaching a peak of 20% in June of 1997 (Fig 1). In both years, first nesting attempts for Sage Sparrows were well underway before cowbirds arrived on the study area. Vesper Sparrows initiated > 40% of nests before 01 May in 1996, and < 10% in 1997 (Fig. 2). No Vesper Sparrow clutches showed evidence of parasitism in 1996, whereas in 1997 one clutch each in May and June was parasitized. Brewer's Sparrows began nesting in mid- to late April, and nesting reached its peak in May of both years (Fig. 3). Cowbirds were present on the study area for the bulk of the Brewer's Sparrow's nesting period, with parasitism levels reaching their peak in June of both years (Fig. 3).

**Figure 2. Relationship between nesting by Vesper Sparrows and parasitism by Brown-headed Cowbirds in eastern Washington. Symbols show timing of nest initiation by Vesper Sparrows in 1996 (n=32) and in 1997 (n=45). Bars show percent of nests parasitized by cowbirds in 1997 (no Vesper Sparrow nests were parasitized in 1996).**

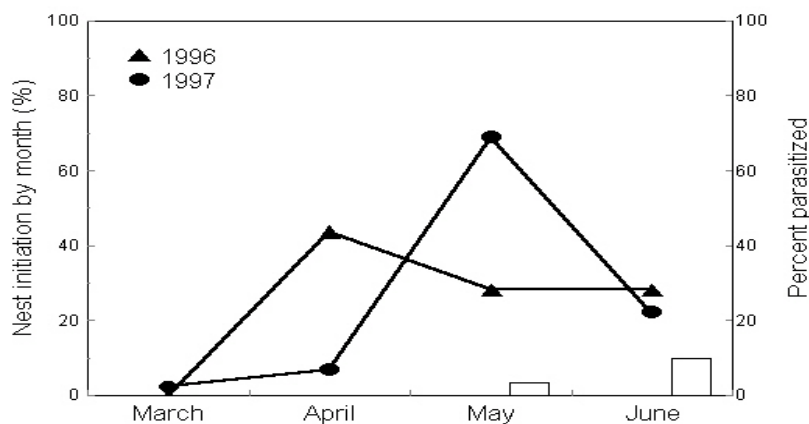
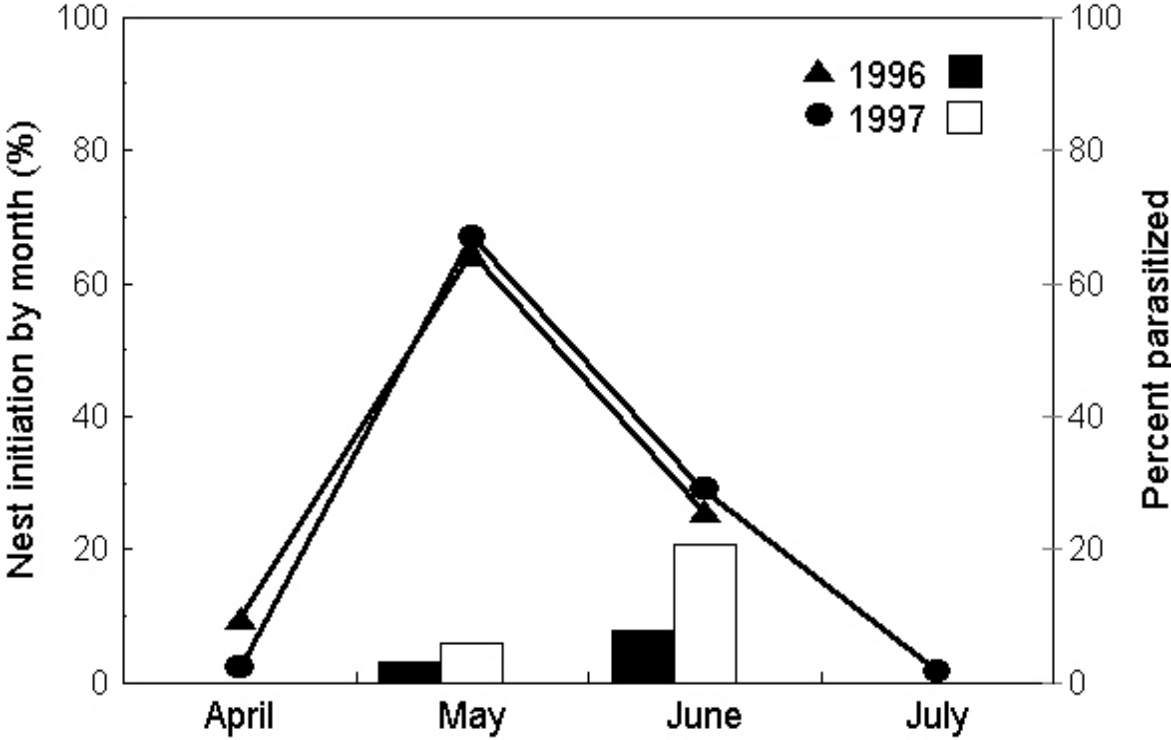


Figure 3. Relationship between nesting by Brewer's Sparrows and parasitism by Brown-headed Cowbirds in eastern Washington. Symbols show timing of nest initiation by Brewer's Sparrows in 1996 (n=93) and in 1997 (n=179). Bars show percent of nests parasitized by cowbirds in 1996 and 1997.





Brewer's Sparrows successfully fledged their own young from 31% ( $n = 135$  exposure days) of parasitized clutches, compared with 51% ( $n = 2851$  exposure days) for non-parasitized clutches.

Sage Sparrows fledged their own young from 20% ( $n = 115$  exposure days) of parasitized clutches, compared with 31% ( $n = 2320$  exposure days) for non-parasitized clutches.

Considering only nests where cowbird eggs hatched, host young fledged from 2 of 2 Brewer's Sparrow nests and from 1 of 4 Sage Sparrow nests.

Abandonment rates were greater for parasitized than for non-parasitized clutches.

Brewer's Sparrows abandoned 4 of 14 [29%] parasitized clutches, compared with 1.8% ( $n = 267$ ) of non-parasitized clutches. Sage Sparrows abandoned 1 of 10 (10%) parasitized clutches, compared with 1.2% ( $n = 234$ ) of non-parasitized clutches. In two instances, cowbirds laid a single egg in the empty, abandoned nest of Sage Sparrows.

Cowbird eggs hatched in 2 of 7 (29%) parasitized Brewer's Sparrow clutches and in 4 of 5 (80%) parasitized Sage Sparrow clutches that successfully hatched any eggs. Cowbirds fledged from 1 of 6 (17%) parasitized Brewer's Sparrow broods and from 2 of 3 (67%) parasitized Sage Sparrow broods that successfully fledged any young. Cowbirds fledged from 2 of 4 Sage Sparrow broods and from both Brewer's Sparrow broods that successfully hatched cowbird eggs.

## **DISCUSSION**

The most definitive result from our analysis was the low level of nest parasitism in this altered landscape. Although cowbirds were present on almost all of our study sites, overall parasitism rates were substantially lower than those from some other fragmented landscapes (Robinson et al. 1995) and from other populations in shrubsteppe (20%,  $n = 20$ , Rich 1978; 29%,  $n = 7$ , Reynolds 1981; 52%,  $n = 25$ , Biermann et al. 1987). Ellison (*this volume*) also reported a similar, low level of parasitism for Sage Sparrows in southern California. Most

previous reports of parasitism rates in shrubsteppe, however, were based on relatively small sample sizes.

Parasitism levels on our sites also were lower than those reported in structurally similar habitats such as continuous coastal scrub, grasslands, and prairies. Parasitism in grassland and open prairie habitats is extremely variable geographically, ranging from 3-85% (Elliott 1978, Buech 1982, Zimmerman 1983, Johnson and Temple 1990, Hill and Sealy 1994, Fondell 1997, Koford et al. 1998, Peer et al. *this volume*, Robinson et al. *this volume*, and S. Davis *this volume*). Parasitism in contiguous, open habitats is generally lower than parasitism in many eastern fragmented forests as well as western riparian habitats (Hergenrader 1962, Wiens 1963, Hill 1976, Elliott 1978, Brown 1994, Rothstein and Robinson 1994, several authors in this volume).

Parasitism rates may not be homogeneous across a landscape (Hahn and Hatfield 1995), and cowbirds observed on our surveys in shrubsteppe may focus on hosts in other communities. Several studies have reported lower rates of nest parasitism in grasslands than in adjacent forested habitats (Hahn and Hatfield 1995, Robinson et al. 1998, *this volume*). Our study sites were far from the nearest forests, but wooded riparian zones occurred irregularly across the region. Two studies of Red-winged Blackbird (*Agelaius phoeniceus*) populations within riparian communities in our study area reported parasitism rates of 54% (Orians et al. 1989) and > 30% (Freeman et al. 1990) at the height of cowbird laying activity. Red-winged Blackbirds do not reject cowbird eggs but are aggressive in defending their nests against parasitism (Freeman et al. 1990). Parasitism rates for other potential hosts in these riparian communities have not been examined.

Rates of parasitism reported for our study plots likely underestimate the actual parasitism experienced by host species. Sage Thrashers and Loggerhead Shrikes are known to reject cowbird eggs (Rothstein 1982, Rich and Rothstein 1985) and it is unlikely that we would have observed parasitism in these species. Western Meadowlarks also reject cowbird eggs in some populations (Peer et al. *this volume*), although parasitism rates can be high in others (Davis and Sealy 1998). Our parasitism rates for species that abandon (e.g., Sage and Brewer's Sparrows) also may be underestimates, as some nests that were parasitized and then abandoned likely went undetected.

#### **TIMING OF ARRIVAL AND REPRODUCTIVE PHYSIOLOGY**

Low parasitism rates in our study area were due, in part, to timing of cowbird arrival relative to initiation of first nests by hosts. Cowbirds arrived in late April and early May, by which time the first nesting attempts of Sage Sparrows, Western Meadowlarks, Horned Larks, and Vesper Sparrows (in 1996) were well underway. This finding corresponds well with information on arrival dates and timing of parasitism at this latitude in the literature. Biermann et al. (1987) reported that cowbirds did not arrive on sites in Alberta's shrubsteppe until May 10. Even though nesting by Brewer's Sparrows in Alberta did not start until May 26, early Brewer's Sparrow nests were not as heavily parasitized (1 of 5 in May) as later attempts (9 of 12 in June). Near our study sites in eastern Washington, Freeman et al. (1990) documented substantially higher parasitism of Red-winged Blackbirds later in the season compared with earlier broods. Brown (1994) reported similar results for species breeding at a lower latitude. Early nesting species (before May) in the Grand Canyon had parasitism rates below 10% whereas those species whose nesting coincided with peak laying of cowbirds in May and June were parasitized much more heavily. Completion of a significant portion of a potential host's nesting effort prior to

laying activity by Brown-headed Cowbirds has been documented in other populations (Ortega and Cruz 1991, Peer and Bollinger 1997).

Female cowbirds present early in the season may not be capable of parasitizing first broods because of physiological limitations or socio-ecological constraints, such as time involved in initial territory establishment, mate selection, or host selection. The physiological limitation hypothesis is supported by studies of reproductive timing of cowbirds. In Ontario, female cowbirds are physiologically capable of laying in late April/early May and remain active until early July (Scott 1963, Scott and Ankney 1980, 1983). Cowbirds in the central Sierra Nevada mountains of California did not have eggs in their oviducts until the second week of May (Fleischer et al. 1987). Brown (1994) indicated that peak cowbird laying seasons along the Colorado River in the Grand Canyon occurred during the latter half of May and first half of June, despite the early breeding season of hosts at that latitude. Although cowbird populations are known to shift laying dates earlier or later to synchronize with host nesting (Payne 1973, Fleischer et al. 1987, Trail and Baptista 1993), cowbirds may avoid early-nesting hosts because of high rates of nest failure reported in some populations at this time (Freeman et al. 1990). In the present study, success rates of parasitized species were similar for early and mid-season nests, with only Sage Sparrows showing a higher success rate in June (Washington Department of Fish and Wildlife, unpub. data).

## **HOST QUALITY**

Some species may be unsuitable hosts, resulting in selection against parasitism by cowbirds (Rothstein 1975). From a diet and nest-accessability standpoint, the shrubsteppe species considered here would seem to be suitable hosts. Indeed, both Brewer's and Sage Sparrows successfully fledged cowbirds, although high rates of abandonment, particularly for

Brewer's Sparrows, depressed the overall success rate. Brewer's Sparrows in Alberta experienced high parasitism and also had high abandonment rates and low cowbird fledging success compared with some other host populations (Biermann et al. 1987). Sage Sparrows also abandon parasitized nests (Rich 1978, Reynolds 1981). Abandonment is clearly a common occurrence among many host species (Rothstein 1976, Graham 1988, Hill and Sealy 1994, Goguen and Mathews 1996) and may become more common in a species after increased exposure to cowbirds (Trail and Baptista 1993). This latter phenomenon may be important from a conservation stand point, particularly if cowbirds are capable of shifting laying dates to synchronize with early-nesting hosts. It is important to note that we cannot necessarily interpret abandonment of nests as an anti-parasitism adaptation (Rothstein 1975), as it might instead be caused by a reaction to the presence of an unfamiliar egg, alteration of clutch size, or even violent physical displacement of the host by the cowbird (Rothstein 1975, Graham 1988, Hill and Sealy 1994, Rothstein and Robinson 1994, J. Tewksbury pers. comm.). Possibly, certain behaviors of shrubsteppe birds, such as incubating when female cowbirds attempt to lay (Neudorf and Sealy 1994) or remaining on and/or defending the nest against cowbirds, make these species prone to nest desertion.

Increased host defense is suggested to reduce cowbird parasitism among Least Flycatchers (*Empidonax minimus*) and Red-winged Blackbirds (Robertson and Norman 1976, Robertson and Norman 1977, Briskie et al. 1990, Freeman et al. 1990). Alternatively, host defense also may facilitate nest-finding by Brown-headed Cowbirds (nest-cue hypothesis), although this has recently received mixed support from experiments by Gill et al. (1997) and Banks (1997). In our study, anecdotal observations of Brewer's Sparrows mobbing female

cowbirds as they hopped through the sagebrush suggest that cowbirds are recognized as a threat by this species, but it is unknown whether mobbing influences parasitism success.

### **DISTANCE TO FEEDING AREAS**

Our study sites may have been too far from cowbird feeding areas to support sufficient densities of breeding cowbirds. Cowbirds require both host-rich laying areas in the morning for successful reproduction and suitable feeding areas (feedlots, livestock pastures, corrals, bird feeders) during the afternoon (Rothstein et al. 1980, Dufty 1982, Rothstein et al. 1984). In fact, cowbirds may be more limited by foraging habitat than by host availability (Hamilton and Orians 1965). Biermann et al. (1987) suggested that the proximity of one of their Alberta study sites to riparian areas, pastures, and feedlots was probably responsible for its high parasitism rates (59%), whereas their study site without any parasitism was >10 km from the nearest feedlot. In Idaho, parasitized Sage and Brewer's Sparrow nests were found within 3 km of a neighboring cattle ranch from which cowbirds dispersed in the mornings (Rich 1978).

Distance to feeding areas also may have played a part in the skewed sex ratio of cowbirds recorded on our surveys. The preponderance of male cowbirds on our surveys may indicate that our sites were too far from foraging areas for female cowbirds, suggesting that many of the males on our surveys were unpaired. Point count surveys elsewhere have revealed sex ratios for cowbirds close to 50% (S. K. Robinson, pers. comm.). Identification of cowbird feeding areas on our study area may help to explain the observed patterns of parasitism.

### **AVAILABILITY OF PERCHES**

It may be difficult for cowbirds to find and determine activity levels of host nests in the shrubsteppe due to the low, dense, homogenous vegetation, and the sparsity of elevated observation perches (Norman and Robertson 1975, Gates and Gysel 1978, Gochfeld 1979). These ideas have been suggested by many other researchers, but to our knowledge have not been tested rigorously. Limited correlative data support the perch-limitation hypothesis. In Alberta, sites with parasitized Brewer's Sparrow nests had perches up to 4m in height located in a nearby riparian strip, whereas sites without parasitism had none (Biermann et al. 1987). In Arizona, parasitism rates for Black-throated Sparrows (*Amphispiza. bilineata*) were greater in areas with high (>2 m) perches provided by crucifixion thorn (*Canotia holacantha*) and power lines, compared with sites with only creosote bush (*Larrea divaricata*) (Johnson and van Riper, *this volume*). In Minnesota, Johnson and Temple (1990) found that prairie-nesting birds experienced lower parasitism farther from wooded edges.

Cowbirds are known to lay in inactive nests, regardless of the presence or absence of host eggs (Norman and Robertson 1975, Lowther 1979, Freeman et al. 1990), indicating that they cannot always accurately assess the status of nests. On our sites, we identified at least two instances of cowbird eggs laid in recently depredated nests of Sage Sparrows. Presumably, elevated perches make it easier for cowbirds to track the status of active nests and therefore, when perches are absent, they lay eggs more often in inactive nests. Freeman et al. (1990) reported that 21.5% of all cowbird eggs found in their study of Red-winged Blackbirds were in inactive nests and that this occurred more frequently in areas without nearby perches. Moreover, the low hatching rate of cowbird eggs in our study suggests that cowbirds frequently were unable to track nest development and therefore laid in nests that were too advanced for the cowbird eggs to receive sufficient incubation.

## WHICH SUBSPECIES?

Mobbing of cowbird females, high abandonment rates of parasitized Brewer's Sparrow nests, and the likely ejection of cowbird eggs by Sage Thrashers suggest that shrubsteppe birds in eastern Washington have been exposed to cowbird parasitism long enough to develop defensive responses. Cowbirds in shrubsteppe habitats of Washington may be of the native subspecies *artemisiae*, rather than the subspecies *obscurus*, the more recent arrival that is presumed to be responsible for recent widespread parasitism in the northwestern states (Rothstein et al. 1980, Laymon 1987, Rothstein 1994). Ward and Smith (1998) provided morphological evidence that cowbirds have been present in British Columbia's Okanagan Valley, 100 km north of our study area, long enough to become morphologically differentiated from the *artemisiae* and *obscurus* subspecies. Low observed parasitism of shrubsteppe birds in Washington may result from coevolved defenses on the part of the host species (Mayfield 1965 [but see also Rich 1978 and Robinson et al. *this volume*]).

## CONCLUSIONS

Parasitism levels of shrubsteppe species in eastern Washington were low compared with those reported for other bird communities in shrubsteppe and for bird communities in some other fragmented landscapes. Based on analysis of data from the first two years of this study, there appears to be no substantial effect of parasitism on avian reproduction within the big sagebrush communities of Washington's shrubsteppe, at least among the species considered here. Several shrubsteppe-associated species were not represented well in our sample, nor did we sample populations in communities other than big sagebrush. Parasitism levels have been found to vary considerably among years within a host population (Smith and Arcese 1995), so more long-term data will be of considerable value.



Determining why parasitism is low in this fragmented landscape may have important implications for managing cowbirds in other areas. Further analysis of data from this continuing study in eastern Washington may help to elucidate factors influencing parasitism rates. For now, we suggest that future research on cowbird parasitism in shrubsteppe focus on 1) determining effects of distance, distribution, and size of cowbird feeding areas on rates of nest parasitism, 2) examining how cowbirds find nests in shrubsteppe, focusing on experiments of perch availability, and 3) comparisons of host quality, both through observational studies to determine parasitism, hatching, and fledging rates, and through experiments to further define abandonment and ejection rates as well as host ability to raise cowbird young.

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## **LITERATURE CITED**

- Banks, A. J. 1997. Variation among host species in probability of parasitism by Brown-headed Cowbirds: the role of everyday host activity. M. S. Thesis, University of Montana, Missoula.
- Biermann, G. C., W. B. McGillivray and K. E. Nordin. 1987. The effect of cowbird parasitism on Brewer's Sparrow productivity in Alberta. *Journal of Field Ornithology* 58: 350-354.
- Briskie, J. V., S. G. Sealy, and K.A. Hobson. 1990. Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. *Behavioral Ecology and Sociobiology* 27: 403-410.
- Brittingham, M. C. and Temple, S. A. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience*. 33:31-35.
- Brown, B. T. 1994. Rates of brood parasitism by brown-headed cowbirds on riparian passerines in Arizona. *Journal of Field Ornithology* 65(2): 160-168.
- Buech, R. R., 1982. Nesting ecology and cowbird parasitism of Clay-colored, Chipping and Field sparrows in a Christmas tree plantation. *Journal of Field Ornithology* 53: 363-369.
- Daubenmire, R. F. 1988. *Steppe vegetation of Washington*. Wash. State Univ., Pullman. 131pp.

- Davis, S. K. and S. G. Sealy. 1998. Cowbird parasitism and nest predation in fragmented grasslands of southwestern Manitoba. *In* J. N. M. Smith, T. Cook, S. I. Rothstein, S. G. Sealy, and S. K. Robinson (editors). Ecology and management of cowbirds. University of Texas Press, Austin (in press).
- Dobler, F. C., J. Eby, C. Perry, S. Richardson, and M. Vander Haegen. 1996. Status of Washington's shrubsteppe ecosystem: extent, ownership, and wildlife/vegetation relationships. Research Report. Washington Department of Fish and Wildlife, Olympia. 39pp.
- Dufty Jr., A. 1982. Movements and activities of radio-tracked brown-headed cowbirds. *Auk* 99: 316-327.
- Elliott, P. F. 1978. Cowbird parasitism in the Kansas tallgrass prairie. *Auk* 95: 161-167.
- Fleischer, R. C., A.P. Smyth and S. I. Rothstein. 1987. Temporal and age-related variation in the laying rate of the parasitic brown-headed cowbird in the eastern Sierra Nevada, California. *Canadian Journal of Zoology* 65: 2724-2730.
- Fondell, T. F.. 1997. Nest density and nest success of ground-nesting grassland birds relative to grazing in western Montana. M. S. Thesis, University of Montana, Missoula.
- Freeman, S., D. F. Gori, and S. Rohwer. 1990. Red-winged blackbirds and brown-headed cowbirds: Some aspects of host-parasite relationship. *Condor* 92: 336-340.
- Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59(5): 871-883.
- Gill, S. A., P. M. Grieff, L. M. Staib and S. G. Sealy. 1997. Does nest defense deter or facilitate cowbird parasitism? A test of the nesting-cue hypothesis. *Ethology* 103: 56-71.
- Gochfeld, M. 1979. Brood parasite and host coevolution: interactions between shiny cowbirds and two species of meadowlarks. *American Naturalist*. 113: 855-870.
- Goguen, C. B. and N. E. Mathews. 1996. Nest desertion by blue-gray gnatcatchers in association with brown-headed cowbird parasitism. *Animal Behaviour* 52: 613-619.
- Graham, D. S. 1988. Responses of five host species to cowbird parasitism. *Condor* 90:588-591.
- Hahn, D. C. and J. S. Hatfield. 1995. Parasitism at the landscape scale: Cowbirds prefer forests. *Conservation Biology* 6:1415-1424.
- Hamilton, W.J., III and G.H. Orians. 1965. Evolution of brood parasitism in altricial birds. *Condor* 67: 361-382.
- Hergenrader, G. L. 1962. The incidence of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) on roadside nesting birds in Nebraska. *Auk* 79: 85-88.
- Hill, R. A. 1976. Host-parasite relationships of the Brown-headed Cowbird in a prairie habitat of West-central Kansas. *Wilson Bulletin* 88:555-565.
- Hill, D. P. and S. G. Sealy. 1994. Desertion of nests parasitized by cowbirds: have clay-coloured sparrows evolved an anti-parasite defense? *Animal Behaviour* 48: 1063-1070.
- Johnson, R. G. and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106-111.
- Koford, R. R., B. S. Bowen, J. T. Lokemoen, and A. D. Kruse. 1998. Cowbird parasitism in grassland and cropland in the northern Great Plains. *In* J. N. M. Smith, T. Cook, S. I. Rothstein, S. G. Sealy and S. K. Robinson, (editors). Ecology and management of cowbirds. Univ. Texas Press, Austin. (In press).
- Laymon, S. A. 1987. Brown-headed cowbirds in California: historical perspectives and management opportunities in riparian habitats. *Western Birds* 18:63-70.

- Lowther, P. E. 1979. Nest selection by brown-headed cowbirds. *Wilson Bulletin* 91:118-122.
- Mayfield, H. 1965. The brown-headed cowbird, with old and new hosts. *Living Bird* 4:13-28.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin*. 87:456-466.
- Neudorf, D. L. and S. G. Sealy. 1994. Sunrise nest attentiveness in cowbird hosts. *Condor* 96:162-169
- Norman, R. F. and R. J. Robertson. 1975. Nest-searching behavior in the brown-headed cowbird. *Auk* 92:610-611.
- Orians, G. H., E. Roskaft, and L. D. Beletsky. 1989. Do brown-headed cowbirds lay their eggs at random in the nests of red-winged blackbirds? *Wilson Bulletin* 101:599-605.
- Ortega, C. P. and A. Cruz. 1991. A comparative study of cowbird parasitism in yellow-headed blackbirds and red-winged blackbirds. *Auk* 108:16-24.
- Payne, R. B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird. *Condor* 75: 80-89.
- Peer, B. D. and E. K. Bollinger. 1997. Explanations for the infrequent cowbird parasitism on common grackles. *Condor* 99:151-161.
- Quigley, T. M. and S. J. Arbelbide (Tech. eds.) 1997. An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins: Volume 2. General Technical Report PNW-GTR-405. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station Portland, Oregon.
- Reynolds, T. D. 1981. Nesting of the Sage Thrasher, Sage Sparrow and Brewers Sparrow in southeast Idaho. *Condor* 83: 61-64.
- Rich, T. 1978. Cowbird parasitism of Sage and Brewers Sparrows. *Condor* 80: 438.
- Rich, T. and S. I. Rothstein. 1985. Sage Thrashers reject Cowbird eggs. *Condor*. 87:561-562.
- Robertson, R. J. and R. F. Norman. 1976. Behavioral defenses to brood parasitism by potential hosts of the brown-headed cowbird. *Condor* 78: 166-173.
- Robertson, R. J. and R. F. Norman. 1977. The function and evolution of aggressive host behavior towards the brown-headed cowbird (*Molothrus ater*). *Canadian Journal of Zoology* 55: 508-518.
- Robinson, S. K., J. Hoover, J. R. Herkert, and R. Jack. 1998. Cowbird parasitism in a fragmented landscape: Effects of tract size, habitat, and abundance of cowbirds and hosts. *In* J. N. M. Smith, T. Cook, S. I. Rothstein, S. G. Sealy, and S. K. Robinson (editors). *Ecology and management of cowbirds*. University of Texas Press, Austin (in press).
- Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995. Ecology and behavior of cowbirds and their impact on host populations. Pages 428-460 *in* T. E. Martin and D. M. Finch (Editors). *Ecology and Management of neotropical migratory birds*. Oxford University Press, New York, NY.
- Rothstein, S. I. 1975. Evolutionary rates and host defenses against avian brood parasitism. *American Naturalist* 109: 161-176.
- Rothstein, S. I. 1976. Experiments on defenses Cedar Waxwings use against Cowbird parasitism. *Auk* 93: 675-691.
- Rothstein, S. I., J. Verner and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the brown-headed cowbird in the Sierra Nevada. *Auk* 97: 253-267.
- Rothstein, S. I. 1982. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. *American Zoologist* 22:547-560
- Rothstein, S. I., J. Verner and E. Stevens. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. *Ecology* 65:77-88

- Rothstein, S. I. 1994. The cowbirds invasion of the far west: history, causes and consequences experienced by host species. *Studies in Avian Biology*. 15: 301-315.
- Rothstein, S. I. and S. K. Robinson. 1994. Conservation and coevolutionary implications of brood parasitism by cowbirds. *TREE* 9: 162-164.
- Saab, V. A. and T. D. Rich. 1997. Large-scale conservation assessment for neotropical migratory land birds in the interior Columbia River Basin. General Technical Report PNW-GTR-399. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station Portland, Oregon.
- Scott, D. M. 1963. Changes in the reproductive activity of the brown-headed cowbird within the breeding season. *Wilson Bulletin* 75:123-129.
- Scott, D. M. and C. D. Ankney. 1980. Fecundity of the brown-headed cowbird in southern Ontario. *Auk* 97:677-683.
- Scott, D. M. and C. D. Ankney. 1983. The laying cycle of brown-headed cowbirds: passerine chickens? *Auk* 100:583-592.
- Smith, J. N. M., and P. Arcese. 1995. Brown-headed Cowbirds and an island population of Song Sparrows: a 16-year study. *Condor* 96:916-934.
- Trail, P. W. and L. F. Baptista. 1993. The impact of brown-headed cowbird parasitism on populations of the Nuttalls White-Crowned Sparrow. *Conservation Biology* 7:309-315.
- Ward, D. and J. N. M. Smith. 1998. Morphological differentiation of brown-headed cowbirds in the Okanagan Valley, British Columbia. *Condor* 100:1-7.
- Wiens, J. A. 1963. Aspects of cowbird parasitism in southern Oklahoma. *Wilson Bulletin* 75: 130-138.
- Zimmerman, J. L. 1983. Cowbird parasitism of dickcissels in different habitats and at different host densities. *Wilson Bulletin* 95:7-22.

