

BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) PARASITISM ON WARBLING VIREOS (*VIREO GILVUS*) IN SOUTHWEST COLORADO

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ABSTRACT.—From May through July, 1993–1998 and 2001, effects of Brown-headed Cowbird (*Molothrus ater*) parasitism on 36 Warbling Vireo (*Vireo gilvus*) nests were documented in southwest Colorado. Overall parasitism was 75.0% and was the major source of nest failure. Among vireo nests that were not depredated, a significantly lower proportion of parasitized nests (10.2%) than nonparasitized nests (85.7%) fledged host young. Significantly fewer vireos hatched and fledged per nest and per egg in parasitized nests compared with nonparasitized nests. We observed no significant differences in mortality rates during the incubation stage between parasitized and nonparasitized nests. However, during the nestling stage, mortality rate was significantly higher in parasitized nests (0.17 nests lost per observation day) than nonparasitized nests (0.01 nests lost per observation day). Cowbirds almost always hatched 3 to 5 days before vireo nestlings. In two cases, vireo nestlings fledged from parasitized nests; in one nest the cowbird egg failed to hatch, and in the other nest the vireo hatched simultaneously with the cowbird. The low vireo production at that study site suggests that that area may be a sink population for Warbling Vireos. Received 15 June 2002, accepted 5 February 2003.

RESUMEN.—Desde mayo a julio, entre 1993 y 1998 y en 2001, documentamos los efectos del parasitismo de *Molothrus ater* en 36 nidos de *Vireo gilvus* en el suroeste de Colorado. En general el parasitismo fue de 75.0% y fue la principal causa de fracaso durante la nidificación. De los nidos que no fueron depredados, los nidos parasitados emplumaron significativamente menos pollos de hospedero (10.2%) que los no parasitados (85.7%). Significativamente menos *V. gilvus* eclosionaron y emplumaron por nido y por huevo en los nidos parasitados que en los no parasitados. No observamos diferencias significativas en las tasas de mortalidad durante el periodo de incubación entre nidos parasitados y no parasitados. Sin embargo, durante el periodo de empollamiento, la tasa de mortalidad fue significativamente mayor en los nidos parasitados (0.17 nidos perdidos por día de observación) que en los no parasitados (0.01 nidos por día de observación). *M. ater* casi siempre logró eclosionar de 3 a 5 días antes que el hospedero. En dos ocasiones, los pollos del hospedero lograron emplumar en nidos parasitados; en un nido el huevo del parásito no eclosionó, y en el otro nido, huésped y hospedero eclosionaron simultáneamente. La baja producción de *V. gilvus* en este sitio de estudio sugiere que esta población podría ser una población sumidero para *V. gilvus*.

THE EFFECT OF Brown-headed Cowbirds (*Molothrus ater*) on their hosts is highly variable, both among host species and among populations of the same host species. Many hosts of equivalent size or larger than cowbirds may successfully raise their own young along with a cowbird, although the number of hosts fledged per nest or per egg is often reduced (Weatherhead 1989, Røskaft et al. 1990, Ortega and Cruz 1991, Clotfelter and Yasakawa 1999). Smaller hosts, on the other hand, frequently raise none of their own (Marvil and Cruz 1989, Chace 1995, Curson and Goguen 1998).

For smaller host species, such as most vireos (*Vireo* spp.) that also have relatively long incubation periods and essentially lack effective antiparasite defenses, cowbird parasitism may be the major source of nest failure (Marvil and Cruz 1989, Chace 1995, Curson and Goguen 1998, Ward and Smith 2000). Individual Warbling Vireos (*V. gilvus*) in the eastern United States and Canada, however, appear to eject cowbird eggs, whereas the western population apparently does not respond to cowbird eggs (Sealy 1996, Sealy et al. 2000). Recent declines in vireo populations and the listing of Least Bell's (*V. belli pusillus*) and Black-capped (*V. atricapilla*) vireos as federally endangered have promoted concern for other vireo species because they ap-

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pear to be particularly vulnerable to the negative effects of cowbird parasitism (Marvil and Cruz 1989, Chace 1995, Curson and Goguen 1998, Ortega 1998, Ward and Smith 2000). For example, a high incidence of cowbird parasitism apparently has resulted in a sink population of Warbling Vireos in British Columbia (Ward and Smith 2000). Similarly, Gardali et al. (2000) and Gardali and Jaramillo (2001) reported a decline in Warbling Vireos in California and suggested that more data are needed on reproductive success. Despite broad distribution of Warbling Vireos, little is known of their breeding biology (Gardali et al. 2000, Ward and Smith 2000), in part, perhaps because their nests are often high and difficult to inspect.

Changes in cowbird abundance or changes in host use may result in population declines of hosts that are particularly vulnerable to cowbird parasitism and also suffer high frequencies of parasitism. For example, Faaborg et al. (1997) suggested that declines of Puerto Rican Vireos (*V. latimeri*) followed the invasion and subsequent increases of Shiny Cowbirds (*Molothrus bonariensis*). In contrast, from 1966–2000, Brown-headed Cowbirds significantly declined in the southern Texas brushlands ($P = 0.001$; Sauer et al. 2001) and nonsignificantly declined in the California foothills (Sauer et al. 2001). Cowbirds have, nonetheless, been implicated in the declines of Least Bell's (Goldwasser et al. 1980; Franzreb 1987, 1988) and Black-capped vireos (Grzybowski et al. 1986, 1994).

Breeding Bird Survey (BBS) data suggest that Warbling Vireos are increasing in the intermountain grassland region (Sauer et al. 2001), which includes southwest Colorado. Here, we compare nesting success of parasitized versus nonparasitized Warbling Vireos in southwest Colorado.

METHODS

From May through July, 1993–1998, and 2001 we searched for Warbling Vireo nests at the Colorado State University San Juan Basin Research Center, 8 km south of Hesperus, La Plata County, Colorado (37°14'N, 108°2'W; 2,316 m elevation). The site consisted of riparian and upland pastures grazed by cattle at various intensities (0–3.3 head ha⁻¹). Riparian pastures, approximately 5–200 m on either side along the La Plata River, were dominated by narrow-leaf cottonwoods (*Populus angustifolia*) and to a lesser degree by water birch (*Betula fontinalis*). Upland pas-

tures were dominated by Gambel oak (*Quercus gambelii*) and grasses. Shrubs and other heavy understory were scarce in the riparian and upland pastures.

Nests were visited every 1 to 3 days and contents of each nest were recorded until all young had fledged or until the nest was depredated or abandoned. We considered predation of nestlings to have occurred if all nestlings disappeared before they were 12 days old for vireos and 9 days for cowbirds. A few nests were low enough to look directly into, but most nests were monitored with the aid of a mirror mounted on extendable aluminum poles. We estimated nest height and nesting tree height using 2 m poles against the tree as a guide.

Statistical analyses.—Most data were not normally distributed; therefore, we used nonparametric statistical tests. For contingency tables, we used log-likelihood goodness-of-fit tests with William's correction, and to detect differences between mean values, we employed two-tailed Mann-Whitney *U*-tests, corrected for ties when appropriate (Zar 1996). We also determined success rates (Mayfield 1961, 1975) and used program CONTRAST (Hines and Sauer 1989, Nur et al. 1999) to analyze difference in success rates between parasitized and nonparasitized nests. We considered a *P* value of <0.05 to be significant. Standard deviations are provided with all mean values.

RESULTS

We found 36 Warbling Vireo nests; 32 (88.9%) were in riparian pastures and 4 (11.1%) were in oak pastures. Most nests (97.2%) were found during construction, laying, or early incubation. Cowbird parasitism was heavy (75% for all years combined, range: 40–100%). Most parasitized nests contained one cowbird egg (20 nests with 1 cowbird egg [74.1%], 6 with 2 cowbird eggs [22.2%] and 1 with 3 cowbird eggs [3.7%]).

Of the 35 nests with known outcomes, 8 nests (22.9%) were successful, 10 (28.6%) failed due to cowbird nestlings out-competing vireo nestlings, 9 (25.7%) were depredated, 6 (17.1%) were abandoned, 1 (2.9%) had infertile eggs, and in 1 nest (2.9%) the nestlings died. Clutch size did not differ significantly between parasitized nests (2.9 ± 0.9 eggs, $n = 26$) and nonparasitized nests (3.3 ± 0.9 eggs, $n = 9$, $Z = 1.188$, $P = 0.24$). The frequency of nest abandonment did not differ between parasitized (5 of 27, 18.5%) and nonparasitized (1 of 9, 11.1%) nests ($G_1 = 0.286$, $P = 0.59$).

Among nests that were not depredated, a significantly lower proportion of parasitized

nesses (2 of 19, 10.5%) than nonparasitized nests (6 of 7, 85.7%) fledged at least one vireo per nest ($G_1 = 13.568$, $P < 0.001$). Mean number of vireos fledged per nest and per egg also differed significantly between parasitized and nonparasitized nests (Table 1). During incubation, the mortality rate of parasitized nests (0.04 nests lost per observation day) did not differ from the mortality rate for nonparasitized nests (0.02 nests lost per observation day, $\chi^2 = 0.989$, $P = 0.32$; CONTRAST). However, during the nestling stage, the mortality rate of parasitized nests was significantly higher (0.17 nests lost per observation day) than the mortality rate for nonparasitized nests (0.01 nests lost per observation day, $\chi^2 = 14.78$, $P = 0.0001$; CONTRAST).

The incubation period for Warbling Vireos was 13.9 ± 1.4 days ($n = 9$ nests, range = 12–15 days) from the last laid egg. In parasitized Warbling Vireo nests, cowbirds almost always hatched 3–5 days before vireos, and Warbling Vireo nestlings almost never survived more than 2–3 days in those situations. Only two parasitized Warbling Vireo pairs fledged some of their own. In one nest, the cowbird egg did not hatch. In the other nest, one vireo hatched on the same day the cowbird hatched, and the other vireo hatched two days later; the vireo that hatched simultaneously with the cowbird fledged along with the cowbird. However, in another parasitized nest, the vireos hatched at the same time as the cowbird and were present at 10 days when the nest was depredated.

Most (75%) Warbling Vireos placed their nests in narrow-leaf cottonwoods, but some were in water birch (8.3%), Gambel oak (5.6%), quaking aspen (*Populus tremuloides* 8.3%), and choke cherry (*Prunus virginiana* 2.8%). Neither nesting tree height nor nest height differed between parasitized (tree height: 5.9 ± 3.8 m, $n = 27$; nest height: 2.9 ± 1.3 m, $n = 27$) and nonpara-

sitized nests (tree height: 5.9 ± 1.9 m, $n = 9$, $Z = 0.86$, $P = 0.39$; nest height: 3.3 ± 1.5 m, $n = 9$, $Z = 0.60$, $P = 0.55$).

Eighteen cowbirds hatched from the 27 parasitized nests (66.7%), and 11 cowbirds fledged (42.3%) from the 26 parasitized nests with known outcomes. The mean number of cowbirds hatched per egg was 0.62 ± 0.47 ($n = 35$ eggs in 27 nests), and mean number of cowbirds fledged per egg was 0.38 ± 0.48 ($n = 34$ eggs in 26 nests of known outcome).

DISCUSSION

Clutch size did not differ significantly between parasitized and nonparasitized nests, and failure rates during the incubation stage were similar between parasitized and nonparasitized nests. The egg loss we observed was considerably lower than Ward and Smith (2000) found in their study of Warbling Vireos and than Marvil and Cruz (1989) found in their study of Plumbeous Vireos (*Vireo plumbeus*) in north-central Colorado. Most losses occurred during the nestling stage. The consistent failure of Warbling Vireos to raise their own young in the company of a cowbird nestling appeared to be due almost entirely to cowbirds hatching before vireos. That is similar to what Ward and Smith (2000) found and is also consistent with the pattern in Plumbeous Vireos (Marvil and Cruz 1989, Curson and Goguen 1998).

Frequencies of parasitism on Warbling Vireos in this study were high compared with other studies of Warbling Vireos, such as 0% in Michigan (Southern and Southern 1980), 3.6% in Manitoba (Sealy 1996), and 16.7% in California (Verner and Ritter 1983), and closer to the parasitism frequencies in British Columbia (50–70%) reported by Ward and Smith (2000). Parasitism in our study was also higher than reported for

TABLE 1. Mean number (\pm SD) of Warbling Vireos hatched and fledged per nest and per egg among parasitized nests and nonparasitized nests, San Juan Basin Research Center, La Plata County, Colorado, 1993–1998, 2001.^a

	Parasitized (n)	Nonparasitized (n)	P ^b	Z
Hatched/nest	1.15 \pm 1.03 (27)	2.44 \pm 1.67 (9)	*	2.268
Fledged/nest	0.08 \pm 0.27 (26)	1.67 \pm 1.58 (9)	**	3.752
Hatched/egg	0.38 \pm 0.36 (26)	0.69 \pm 0.43 (9)	*	2.061
Fledged/egg	0.02 \pm 0.09 (26)	0.48 \pm 0.42 (9)	**	3.8

^aSample sizes vary for hatched and fledged per nest and per egg because we did not know the clutch size for one nest that was found during the nestling stage.

^bTwo-tailed Mann-Whitney U-test, corrected for ties * $P < 0.05$; ** $P < 0.001$.

the eastern slope of Colorado (48.3%, Chace and Cruz 1996). The eastern Warbling Vireo population ejects cowbird eggs, whereas the western population apparently does not (Sealy et al. 2000). If ejection occurs before investigators discover parasitism, that could partially explain the lower frequency of parasitism on the eastern population.

Warbling Vireos were parasitized at a much higher frequency (75%) than other host species at our site even though other hosts were more common. For example, parasitism on Yellow Warblers (*Dendroica petechia*) was 36.4% (Ortega and Ortega 2000), and parasitism on Chipping Sparrows (*Spizella passerina*) was 22% (Ortega and Ortega 2001). Similarly, in Texas, Barber and Martin (1997) found a higher frequency of parasitism among Black-capped and White-eyed vireos (*Vireo griseus*) than among other more common hosts.

Both predation and abandonment occurred infrequently in our study, and abandonment was distributed equally between parasitized and nonparasitized nests. Fewer parasitized nests in our study were abandoned than other vireo species: Red-eyed Vireos (*Vireo olivaceus*, 34% compared with 12% in nonparasitized nests; Graham 1988) and Bell's Vireos (73% compared with 42% in nonparasitized nests, Parker 1999; 51% compared with 4% in nonparasitized nests, Budnik et al. 2001). Furthermore, nest failure, whether because of predation or parasitism, will not necessarily lead to re-nesting. For example, conceding that some pairs may have re-nested outside their site, Ward and Smith (2000) recorded only two pairs of Warbling Vireos that re-nested after their nests had been depredated, and none re-nested after abandonment ($n = 58$ nests).

Our results supported the expectation of Briskie et al. (1990) that cowbirds should preferentially select hosts with the highest probability of raising their young. Not only were vireo nests conspicuous and perhaps relatively easy for cowbirds to discover, but predation rates were low relative to other potential hosts. For example, at the same site during most of the same years, predation on nests of Chipping Sparrows was 52.6% and Yellow Warblers was 39.1% (Ortega and Ortega 2000, 2001) compared to 25% in Warbling Vireos. The relatively low level of predation undoubtedly contributed to the high cowbird production, with 38% of eggs

producing fledglings. At the same site, only 18% of cowbird eggs in Chipping Sparrow nests produced fledglings (Ortega and Ortega 2001).

Ward and Smith (2000) suggested that the high frequency of cowbird parasitism resulted in a sink population for Warbling Vireos in the Okanagan Valley, southern British Columbia, despite the indication from BBS of a significant increase of Warbling Vireos in that region from 1980 to 1996 (Sauer et al. 1997). Those authors further suggested that the apparently conflicting results may have reflected their investigation on a small population in a valley where cowbirds were abundant as opposed to the BBS, which covered a larger area and included higher elevations where cowbirds were not as abundant. D. Ward (pers. comm.) suggested that that pattern may be predictable elsewhere in the western United States. Although we did not band Warbling Vireos as Ward and Smith did, with the extreme frequency of parasitism and the almost certain failure to raise hosts in parasitized nests, we assume that that small population is probably a sink. Breeding Bird Survey data, however, indicated a significant increase in Warbling Vireos of 9.7% per year ($P = 0.04$) from 1966 to 1998 and a nonsignificant increase of 8.4% per year ($P = 0.11$) from 1980 to 1999 (Sauer et al. 1999) in the intermountain grassland region (the region which includes our study site; J. Sauer pers. comm.). Our study site may be considered high elevation by most standards, but cowbirds are abundant there and in the surrounding area. At yet higher elevations, where Warbling Vireos also exist, cowbirds may be less abundant than they are at the elevation of our site (C. P. Ortega pers. obs.). We believe that the same phenomenon may be occurring in southwest Colorado that apparently is occurring in Ward and Smith's (2000) study—that is, the Warbling Vireo population at our site may be supplied by populations at higher elevations where cowbirds are not as abundant.

Alternatively, BBS data may not reflect actual Warbling Vireo population trends in our study area. Indeed, Sauer et al. (1999) suggested that data for Warbling Vireos in the intermountain grassland area reveal an important deficiency (low abundance, small sample size, imprecise, or inconsistency in trend over time). Therefore, it is important to continue monitoring nesting success and populations of Warbling Vireos and other hosts in Colorado and elsewhere to distinguish between sink and source populations.

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