

EFFECTS OF BROWN-HEADED COWBIRDS AND PREDATORS ON THE NESTING SUCCESS OF YELLOW WARBLERS IN SOUTHWEST COLORADO

JOSEPH C. ORTEGA AND CATHERINE P. ORTEGA

Department of Biology, Fort Lewis College, Durango, Colorado 81301-3999

Abstract.—We studied the effects of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and predators on the reproductive biology of Yellow Warblers (*Dendroica petechia*) in La Plata County, Colorado, 1992–1996. Overall, 36.4% of Yellow Warbler nests ($n = 66$) were parasitized by Brown-headed Cowbirds. Although parasitized and nonparasitized nests were equally likely to fledge at least one warbler, in nonparasitized nests, warblers had larger clutches, hatched more young, and tended to fledge more young. Frequency of parasitism was not influenced by nest height and, on a weekly basis, was not correlated with number of warbler nests initiated. Overall, 39.1% of Yellow Warbler nests were lost to predators, but complete predation was not affected by nest height. On a weekly basis, percent complete predation of warbler nests increased with number of active nests. No significant relationship existed between frequency of complete predation and frequency of parasitism in Yellow Warbler nests.

EFFECTOS DEL PARASITISMO POR *MOLOTHRUS ATER* Y DE DEPREDADORES EN EL ÉXITO DE ANIDAJE DE *DENDROICA PETECHIA* EN EL SUROESTE DE COLORADO

Sinopsis.—Estudiamos los efectos de el parasitismo de nido por *Molothrus ater* y de los depredadores sobre la biología reproductiva de *Dendroica petechia* en el Condado de La Plata en tre 1992 y 1996. En general, el 36.4% de los nidos de *Dendroica petechia* ($n = 66$) fue parasitado por *Molothrus ater*. Aunque los nidos parasitados y los no parasitados tuvieron la misma posibilidad de producir al menos un volanton de *Dendroica petechia*, los nidos no parasitados produjeron camadas mayores, empollaron más crías y tendían a producir más volantones. La frecuencia de parasitismo no fué influenciada por la altura del nido y, semanalmente, no se correlacionó con la cantidad de nidos de *Dendroica petechia* comenzados. Un total del 39.1% de los nidos de *Dendroica petechia* se perdió a los depredadores, pero la depredación completa no fué afectada por la altura de los nidos. El porcentaje de nidos de *Dendroica petechia* depredados aumentaron con el número de nidos activos en términos semanales. No se halló una relación significativa entre la frecuencia de nidos depredados completamente y la frecuencia de nidos parasitados en los nidos de *Dendroica petechia*.

Although Yellow Warblers (*Dendroica petechia*) have an extensive geographic range, their reproductive biology is known primarily from the central, eastern, and more northern parts of their range (Clark and Robertson 1981, Goossen and Sealy 1982, Folkers and Lowther 1985, Burg-ham and Picman 1989, Weatherhead 1989, Briskie et al. 1990, Sealy 1992, 1995, Prather and Cruz 1995). Only a few studies exist on the reproductive biology of Yellow Warblers from the intermountain or western part of their range (Frydendall 1967, Taylor and Littlefield 1986, Knopf and Sedgewick 1992). This is unfortunate because there is some evidence that populations of Yellow Warblers are declining in this region (listed as a species of special concern in Colorado; Webb 1985).

Loss of riparian habitat is a likely principal threat to western populations of the Yellow Warbler. However, quantifying the impact of parasitism

by Brown-headed Cowbirds (*Molothrus ater*) and nest predation is also critical to understanding the dynamics of these populations. Therefore, the purpose of this paper is to report on the reproductive biology of Yellow Warblers and their relationship with Brown-headed Cowbirds and predators in an area of their geographic range lacking any previous research.

METHODS

We studied the interaction between Brown-headed Cowbirds and Yellow Warblers from 1992 to 1996 along the La Plata River at the Colorado State University, San Juan Basin Research Center, La Plata County, Colorado (37°14'N, 108°3'W). Narrow-leaf cottonwood (*Populus angustifolia*) was the dominant plant species at our site; riverbirch (*Betula fontinalis*) and Gambel oak (*Quercus gambelii*) were also common and, in some areas, thinleaf alder (*Alnus tenuifolia*) and willows (*Salix* spp.) were present. Understory cover was scarce, and the area was typically grazed by an average of 0.4 head/ha of cattle. Nest sites were marked with flagging tape placed near the nest tree at a height of 1.5–2 m. We examined nests every 1–3 d either by direct observation or by use of mirror and pole.

Of 66 nests included in this study, only eight (12.1%) were discovered after incubation. Therefore, we believe the following analyses accurately estimate frequency of parasitism by Brown-headed Cowbirds and nesting success of Yellow Warblers. Nests were defined as successful if they fledged at least one warbler (Goossen and Sealy 1982, Weatherhead 1989, Ortega et al. 1997).

We quantified mean clutch size, number of eggs hatched, number of chicks successfully fledged, and nest height. We used two-tailed Kruskal-Wallis tests to compare these variables among years for complete nonparasitized and parasitized nests, respectively, because our data were not normally distributed (Zar 1984). To determine potential effects of parasitism by Brown-headed Cowbirds, these variables were compared between nonparasitized and parasitized nests using Mann-Whitney *U*-tests (Zar 1984). We examined frequency of complete predation (i.e., predation in which all nest contents were eaten) among years and between nonparasitized and parasitized nests using appropriate *G*-tests (Sokal and Rohlf 1981), and all correlation analyses were completed using Spearman Rank Correlation tests (Zar 1984). We used $P \leq 0.05$ to indicate statistical significance for all tests.

RESULTS

We examined 8 Yellow Warbler nests in 1992, 16 in 1993, 15 in 1994, 16 in 1995, and 11 in 1996. In nests that were not depredated, there were no significant differences among years in mean clutch size, number of eggs hatched, and number of young fledged from nonparasitized and parasitized Yellow Warbler nests ($P_s \geq 0.105$). Therefore, data for these variables from nonparasitized and parasitized warbler nests, respectively, were pooled among years.

TABLE 1. Mean clutch size, number of eggs hatched, number of chicks fledged, and nest height (\pm SD) for Yellow Warblers in nonparasitized and parasitized nests by Brown-headed Cowbirds in La Plata County, Colorado, 1992–1996. All comparisons two-tailed Mann-Whitney U -test corrected for ties (Zar 1984).

Variable	Nonparasitized	Parasitized	P
clutch size	3.79 \pm 0.64	3.37 \pm 0.68	0.051
n	34	19	
number of eggs hatched	3.28 \pm 1.02	2.31 \pm 1.44	0.027
n	25	13	
number of chicks fledged	2.56 \pm 1.26	1.93 \pm 1.21	0.153
n	25	14	
nest height (m)	3.89 \pm 1.70	4.08 \pm 1.68	0.694
n	42	24	

We observed (or determined by backcounting from the day of hatching) that first egg laying dates ranged from 24 May 1996 to 4 Jun. 1995. Final egg laying dates ranged from 22 Jun. 1992 to 30 Jun. 1995. Nonparasitized warbler nests had larger mean host clutches, number of host eggs hatched, and number of host young fledged than did parasitized nests (Table 1), but this was statistically significant only for number of host eggs hatched (Table 1).

Frequency of parasitism by Brown-headed Cowbirds varied from 18.8% ($n = 16$ nests) in 1993 to 50.0% ($n = 8$ nests) in 1992 but did not differ significantly among years ($G_{\text{adj}} = 3.613$, $df = 4$, $P < 0.50$). Overall, 24 (36.4%) of 66 Yellow Warbler nests were parasitized. Among 42 nonparasitized nests, 22 (52.4%) were successful in fledging at least one warbler, and 11 of 24 (45.8%) parasitized nests were successful. There was no significant difference in nesting success by Yellow Warblers in nonparasitized versus parasitized nests ($G_{\text{adj}} = 0.362$, $df = 1$, $P > 0.50$). Mean nest height of nonparasitized nests did not differ significantly from that of parasitized nests (Table 1). Of those parasitized nests discovered in the egg stage or earlier, 21 (95.9%) of 22 had one Brown-headed Cowbird egg; one had two cowbird eggs. When warbler nests were analyzed by week, there was no significant association between number of nests initiated and percent of nests parasitized by cowbirds (Fig. 1; $r_s = 0.169$, $n = 7$, $P > 0.50$).

Frequency of complete predation on warbler nests varied from 12.5% ($n = 8$) in 1992 to 53.3% ($n = 15$) in 1994. However, among years, there was no significant difference in the frequency of complete predation ($G_{\text{adj}} = 5.542$, $df = 4$, $P < 0.25$). Twenty-five (39.1%) of 64 nests were completely depredated; 13 (52.0%) of 25 complete predation events occurred when eggs were in the nest, and 12 (48.0%) occurred during the nestling stage. We found no significant difference in mean nest height (\pm SD) for those nests in which all eggs or chicks were lost to predators ($\bar{x} = 3.85 \pm 1.72$ m, $n = 25$, range = 1.52–7.32 m) and those not preyed upon ($\bar{x} = 4.03 \pm 1.72$ m, $n = 39$, range = 1.52–7.62 m; $P = 0.705$). There was

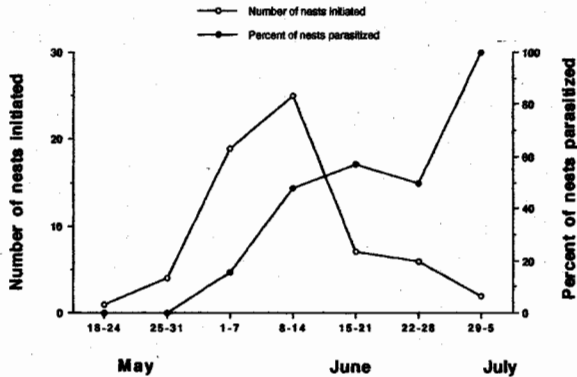


FIGURE 1. Number of nests initiated and percent of nests parasitized by Brown-headed Cowbirds according to date in the breeding season for Yellow Warblers in La Plata County, Colorado, 1992-1996. Number of warbler nests initiated and percent of nests parasitized by cowbirds were not correlated ($r_s = 0.169$, $n = 7$, $P > 0.50$).

no significant relationship between the frequency of complete predation and the frequency of parasitism (Table 2; $G_{adj} = 0.00007$, $df = 1$, $P > 0.975$). The contents of nests that were parasitized were not preyed upon more or less than those nests not parasitized. However, we found a significant correlation between number of active nests and percent complete predation of such nests (Fig. 2; $r_s = 0.757$, $n = 10$, $P = 0.023$).

Abandonment was uncommon. Only four (6.1%) of 66 nests were abandoned. Three of these cases occurred when eggs were in the nest (two of these nests had been parasitized), and one case occurred when chicks were in the nest.

DISCUSSION

Mean clutch size in nonparasitized nests from southwest Colorado was between the 2.50 eggs found in a Yellow Warbler (*D. p. gundlachi*) population in Key Largo, Florida (Prather and Cruz 1995), and the 4.1-4.63 eggs observed in studies at higher latitudes (Table 1; Clark and Robertson 1981, Goossen and Sealy 1982, Weatherhead 1989, Sealy 1992). Therefore, our data support the generalization of increasing clutch size with increasing latitude in many avian species (Skutch 1949, Lack 1968). Clark and Robertson (1981) and Sealy (1992) also reported reduced Yellow

TABLE 2. Relationship between parasitism by Brown-headed Cowbirds and complete predation of Yellow Warbler nests in La Plata County, Colorado, 1992-1996.

Complete predation	Nonparasitized	Parasitized
Yes	16 (64.0%)	9 (36.0%)
No	25 (64.1%)	14 (35.9%)

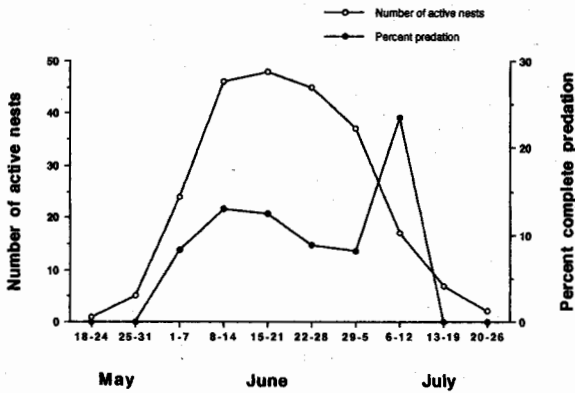


FIGURE 2. Number of active nests and percent complete predation according to date in the breeding season for Yellow Warblers in La Plata County, Colorado, 1992–1996. Number of active warbler nests and percent complete predation were significantly correlated ($r_s = 0.757$, $n = 10$, $P = 0.023$).

Warbler clutch sizes in parasitized nests; they attributed such reductions to female cowbirds removing host eggs. Smaller host clutch sizes in parasitized nests of other passerines may have also resulted from removal of host eggs by female cowbirds (Hann 1937, Nice 1937, Smith 1981, Blankespoor et al. 1982, Zimmerman 1983, Marvil and Cruz 1989, Røskaft et al. 1990). While we have yet to observe female cowbirds removing Yellow Warbler eggs from parasitized nests, our clutch size data are consistent with this explanation.

In successful nests, we found significantly more warbler eggs hatching and a tendency for more warblers to fledge from nonparasitized nests than from parasitized nests (Table 1). In eastern Ontario, Burgham and Picman (1989) similarly found successful nonparasitized nests fledging more young than nests that were either parasitized or that involved a second nesting attempt after rejection of the initial clutch because of prior parasitism. In successful nests in southern Manitoba, Weatherhead (1989) found an average of 3.56 ± 1.11 fledglings from nonparasitized Yellow Warbler nests compared to 1.89 ± 0.60 fledglings from nests with at least one cowbird fledgling. We observed a smaller negative effect on host offspring production by cowbirds in southwest Colorado. Perhaps this was partly due to the mean incubation period of 10.5 d ($n = 16$, range = 8–14) of Yellow Warblers in our study being essentially equivalent to the 10 d known for Brown-headed Cowbirds (Friedmann 1929, Ortega 1998). Other populations of Yellow Warblers had incubation periods of 11–12 d (Bigglestone 1913, Schrantz 1943, Clark and Robertson 1981, Prather and Cruz 1995). We also observed Yellow Warblers fledging from nests as early as 8–9 d, a nestling period shorter than the 10–11 d of Brown-headed Cowbirds (Woodward 1983). In contrast, Prather and Cruz

(1995) observed a nestling period of 12 d in Yellow Warblers in southern Florida, a population that was not parasitized by cowbirds.

The 36.4% overall frequency of cowbird parasitism in our study falls within the range of parasitism rates (0–70%) previously reported for Yellow Warblers (see Appendix C in Ortega [1998]). At least for nesting attempts by Yellow Warblers in our area, parasitism by cowbirds is more likely later in the breeding season (Fig. 1). Therefore, our observation of peak Yellow Warbler nest initiation occurring earlier in the breeding season may reflect an attempt to avoid cowbird parasitism (Fig. 1). Clark and Robertson (1979) also found a high degree of parasitism of Yellow Warbler nests late in the breeding season. In northcentral Colorado, the frequency of cowbird parasitism also increased after host egg-laying peaked in both Red-winged Blackbirds (*Agelaius phoeniceus*, in 1986, Ortega and Cruz 1991) and Plumbeous Vireos (*Vireo plumbeus*, Marvil and Cruz 1989). In contrast, in northeastern New Mexico, Goguen and Mathews (1996) found that cowbird parasitism of Blue-gray Gnatcatchers (*Poliioptila caerulea*) decreased later in the breeding season.

Overall, we observed a 39.1% frequency of complete predation on Yellow Warbler nest contents. In eastern Ontario, 37% of Yellow Warbler nests were depredated (Clark and Robertson 1979). However, in southern Manitoba, 63% of Yellow Warbler nest failures resulted from predation (Goossen and Sealy 1982), and in Florida, 63.6% of egg losses in Yellow Warblers were due to predators (Prather and Cruz 1995). In a review of 32 Neotropical migrants, Martin (1992) found approximately 44% of nests and eggs were lost to predation and that 80% of nestling deaths were the result of predators. Likely and known predators at our study site were Black-billed Magpies (*Pica pica*), Western Scrub-Jays (*Aphelocoma californica*), Steller's Jays (*Cyanocitta stelleri*), chipmunks (*Tamias* spp.), deer mice (*Peromyscus maniculatus*), rock squirrels (*Spermophilus variegatus*), long-tailed weasels (*Mustela frenata*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), and garter snakes (*Thamnophis* spp.; Ortega et al. 1998). This suite of predators generally preyed upon Yellow Warbler nests in direct proportion to the availability of such nests (Fig. 2). However, in eastern Ontario, Clark and Robertson (1979) found a higher proportion of Yellow Warbler nests preyed upon as the total number of all avian nests decreased.

In contrast to our observing no significant differences in nest height between nonparasitized and parasitized clutches and between those nests completely preyed upon and those nests not completely preyed upon, Briskie et al. (1990) found that Yellow Warbler nests at lower heights were more frequently parasitized in southern Manitoba. We could not find all Yellow Warbler nests on our study site partially because some narrow-leaf cottonwoods (a common nesting substrate) were known to be 27 m in height. In 1998, we found one Yellow Warbler nest that was about 12.2 m high on the side of a narrow-leaf cottonwood. The highest Yellow Warbler nest that we were able to monitor was only 7.6 m; therefore, some

potential nesting habitat was not easily examined, and this could have affected our results.

To the best of our knowledge, this study represents the first thorough examination of the reproductive biology of the Yellow Warbler in the western part of its range. The conservation status of the Yellow Warbler has raised concern (Webb 1985, Tate 1986); this may be the result of continued loss of riparian habitat (a preferred habitat type) and perhaps because of heavy grazing in certain locations. Taylor and Littlefield (1986) reported that intense grazing in a willow-dominated habitat at the Malheur National Wildlife Refuge, southeastern Oregon, negatively affected the number of Yellow Warblers counted on Breeding Bird Surveys. However, their research highlights the fact that the effects of grazing on abundance of Yellow Warblers and other Neotropical migrants depends on grazing intensity, habitat type, and the species under study (Bock et al. 1993). We have not found a strong negative effect of cattle grazing on the nesting success of Yellow Warblers at our study site, and Yellow Warblers are a species described as having mixed responses to cattle grazing (Bock et al. 1993). Therefore, future research in the west should investigate the effects of different habitats in combination with different grazing intensities on the reproductive success of Yellow Warblers and other Neotropical migrants. Also, we studied Yellow Warblers on their breeding grounds; however, future studies must also examine conditions on their wintering grounds if humans are to better understand the factors contributing to population decreases in some Neotropical migrants (Rappole and McDonald 1994).

ACKNOWLEDGMENTS

We thank David Schafer and Al Denham for allowing us full access to the Colorado State University, San Juan Basin Research Center. We also greatly appreciate Susan Allerton, Stacia Backensto, Thomas Kreykes, Donald Palmer, Cristin Rapp, Dawn Sekayumptewa, and Shawchyi Vorisek for helping to find and monitor nests. This research was funded by a Howard Hughes Medical Institute Grant to the Departments of Biology and Chemistry, Fort Lewis College, and by a Ford Foundation Fellowship (administered by the National Research Council) to J. C. Ortega. Initial preparation of this manuscript was also supported by a U.S. Forest Service Grant to William Romme in the Department of Biology, Fort Lewis College. C. Ray Chandler, Christopher C. Rimmer, and an anonymous reviewer provided helpful comments on earlier versions of this manuscript.

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Received 27 Jan. 1999; accepted 24 Jun. 1999.