mun de los páramos de la Cordillera Central de los Andes Colombianos entre 3550 y 4300 metros de altitud. A lo largo del talud de corte de los carreteables de la zona se observa su preferencia por excavar las galerìas de anidación y descanso en los estratos claros formados por mantos de cenizas volcánicas de erupciones pasadas, mas que en los estratos oscuros y densos de los paleosoles. Los mantos de cenizas volcánicas son porosos y friables siendo facilmente excavados por cinclodes. La mayoria de las galerìas han sido excavadas cerca del borde superior del talud ($n = 285$; $\bar{x} = 0.5 + 0.3$ m desde arriba). La altura media desde la base del carreteable es de 2.3 + 0.3 m. Las galerìas comprendidas entre 0.6 y 1.1 metros de longitud ascienden suavemente y terminan en una camara ligeramente mayor. En una galerìa recientemente abandonada se encontraron dos huevos (uno agrietado y otro roto).

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A HIGH INCIDENCE OF BROWN-HEADED COWBIRD PARASITISM OF WILLOW FLYCATCHERS[1]

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Key words: Willow Flycatcher; Brown-headed Cowbird; brood parasitism; Colorado; Empidonax traillii; Molothrus ater.

Brown-headed Cowbirds (*Molothrus ater*) parasitize both Willow (*Empidonax traillii*) and Alder (*E. alnorum*) flycatchers (Friedmann et al. 1977, Friedmann and Kiff 1985). These two flycatchers were considered a single species until 1973 (AOU 1973), which has masked information about the frequency with which each is parasitized. Whereas several studies of the superspecies (Traill's Flycatcher) have focused on or included details of cowbird parasitism, most were of eastern populations, and most reported frequencies of parasitism ≤21% (Hicks 1934, Berger 1951, Berger and Parmalee 1952, Walkinshaw 1966, Holcomb 1972). Friedmann et al. (1977:13) suggested that western populations (Willow Flycatchers) are parasitized only about half as much (ca. 10%) as eastern populations (Traill's Flycatcher superspecies). This note describes a high rate of cowbird parasitism within a population of Willow Flycatchers in northcentral Colorado. We include details of responses to parasitism and host vs. cowbird fledging success.

STUDY AREA AND METHODS

The study was conducted in northcentral Colorado on the Arapahoe National Wildlife Refuge (ANWR), located in North Park, a high elevation (2,500 m) intermountain glacial basin. We studied Willow Flycatchers along a 7-km stretch of the floodplain of the Illinois River. Willow Flycatchers are common in North Park, occurring wherever there are extensive stands of healthy shrub willows, *Salix* spp. (Knopf and Sedgwick, unpubl. data). Eight species of willows characterized the woody community at ANWR (Cannon and Knopf 1984) with Woods rose (*Rosa woodsii*) and golden current (*Ribes aureum*) being minor components of the woody community. Common timothy (*Phleum pratense*), blue flag (*Iris versicolor*), and several species of sedges (*Carex* spp.) dominated the herbaceous layer.

As part of a larger study of avian populations and habitats, we surveyed the avifauna of the willow community using point transects after Reynolds et al. (1980) during June of 1985 and 1986 (see Knopf et al. 1988). Population densities of common species, including Willow Flycatchers and Brown-headed Cowbirds, were calculated using program TRANSECT (Burnham et al. 1980) adapted for point transect data (K. P. Burnham, pers. comm.).

We located most nests during construction or early in the egg-laying period. Intensive nest searches were conducted daily following avian censuses. After several censuses, virtually all territories were identified and we narrowed the scope of our search to activity centers within territories. We followed females to locate most nests; other nests were found by searching individual bushes within territories. Nests were visited every 1 to 2 days during the period of maximum susceptibility to parasitism (nest building through egg laying) and at

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TABLE 1. Incidence of parasitism and nest success of Willow Flycatcher nests and pairs, Arapahoe National Wildlife Refuge, Colorado, 1985 to 1986.

Class	Total nests or pairs	Parasitized nests or pairs		Unparasitized nests or pairs	
		n (%)	Nest success (%)	*n* (%)	Nest success (%)
First nests	12	9 (75.0)	1 (11.1)	3 (25.0)	1 (33.0)
Renests	15	2 (13.3)	1 (50.0)	13 (86.7)	8 (61.5)
All nests	27	11 (40.7)	2 (18.2)	16 (59.3)	9 (56.3)
Pairs	15	11 (73.3)	6 (54.5)	4 (26.7)	2 (50.0)

least weekly thereafter. We were usually able to determine nest outcome by circumstances at the nest or by locating fledged young.

Flycatcher territories were either discrete (isolated) or adjacent but nonoverlapping, allowing us to distinguish among individual pairs. Because individuals were not marked, male or female replacement may have occurred within territories; however, territorial boundaries remained intact throughout the breeding season and we use "territories" and "pairs" interchangeably when referring to parasitism rates.

RESULTS

Brown-headed Cowbirds parasitized at least 11 of 27 (40.7%) nests (Table 1). Five additional nests may have been parasitized, but were either destroyed, or abandoned and taken apart by flycatchers during or just preceding egg laying by flycatchers; hence, parasitism may have been as high as 50% (16/32). These 27 nests were built by 15 pairs of flycatchers, so that at least 11/15 pairs (73.3%) were parasitized.

First nests were more heavily parasitized ($\chi^2 = 10.50$, df = 1, $P < 0.05$) than second or later nests (75% [9/12] vs. 13.3% [2/15], respectively; Table 1). We recorded cowbird parasitism of Willow Flycatchers only from 21 to 27 June (both years) which coincided with the average date of clutch initiation for first nest attempts (24 June ± 0.16 days). Renest attempts had an average date of clutch initiation of 9 July ± 0.65 days.

Of the 11 parasitized nests, nine contained one, and two contained two cowbird eggs. Cowbird eggs were accepted by Willow Flycatchers at only two nests. We had no evidence that flycatchers removed cowbird eggs; rather either the cowbird egg(s) became depressed into the nest lining ($n = 2$), or the flycatchers abandoned the nest ($n = 7$). Some abandoned nests were dismantled by the flycatchers, and the nesting material apparently used again in the renest. McCabe (1963) also observed this in the superspecies, and other species as well have been observed dismantling deserted nests e.g., American Goldfinch, *Carduelis tristis* (Knight, pers. comm.).

Nest success (≥ one flycatcher fledged) was 18.2% (2/11) for parasitized nests vs. 56.3% (9/16) for unparasitized nests ($\chi^2 = 3.91$, df = 1, $P < 0.05$; Table 1). Two flycatchers and one cowbird fledged from each of the two successful, parasitized nests where cowbird eggs were accepted. Three flycatcher eggs and one cowbird egg were laid in each nest; there were two and three flycatcher eggs present, respectively, in these nests at the time the cowbird egg was laid. In one nest, a flycatcher egg disappeared, and in the other, a 2-day-old flycatcher was found dead in the nest. Circumstances suggest that cowbirds were responsible for both the disappearance of the egg and mortality of the nestling. Acceptance of the cowbird egg after two and three flycatcher eggs had already been laid, and the successful fledging of both host species and parasite is similar to results reported by Rothstein (1975) and Clark and Robertson (1981) for the Yellow Warbler (*Dendroica petechia*). An average of 2.2 ± 0.3 (SE) young fledged from each successful, unparasitized nest.

Nest success for parasitized flycatcher pairs was at least 54.5% (6/11) (Table 1): two pairs accepted cowbird eggs and successfully fledged both cowbirds and flycatchers, and four second nest attempts were successful after abandonment of parasitized first nests. Two parasitized pairs were unsuccessful in producing young and full seasonal histories were incomplete for the remaining three parasitized pairs. Of only four pairs of flycatchers definitely known not to have been parasitized, at least two successfully reared young. Full seasonal histories were unknown for the other two pairs.

The percentage fledging success from all cowbird eggs laid was 15.4% (2/13). The number of cowbirds fledged per parasitized nest was 0.18 (2/11).

DISCUSSION

INCIDENCE OF PARASITISM

We found the incidence of cowbird parasitism on Willow Flycatchers in northcentral Colorado (40.7%) to be high compared to that of other studies. Friedmann (1963) reported a compiled rate of 10.7% for six studies of the superspecies, and Friedmann et al. (1977) summarized five additional studies, all finding rates of parasitism ≤17%. Only Trautman (1940) reported a higher rate of parasitism than we encountered: 56.3% from a small sample of nests (16) of the superspecies parasitized in Ohio.

We attribute the relatively high rate of cowbird parasitism of flycatchers in northcentral Colorado to three factors: (1) The population density of cowbirds was exceptionally high on our study area. Previously reported as occurring only on the plains and in the lower foothills, the Brown-headed Cowbird has recently expanded its range into higher altitude habitats in Colorado (Hanka 1985). In 1985 and 1986, we recorded cowbird densities of 1.19 ± 0.10 and 1.02 ± 0.09 birds/ha, respectively. We compared cowbird densities on our study area with those from breeding bird census records published in 1984 (Van Velzen and Van Velzen 1984). Densities reported as territories/hectare (based on the number of female cowbirds on study plots) were converted to birds/hectare using the sex ratio of 1.5

males : female cowbird (Darley 1971). Only 10/212 censuses reported cowbird densities greater than those we recorded on our study area in either 1985 or 1986. In addition, densities of cowbirds were higher on our study area than at any of five other riparian or six other upland sites in an avian survey of the Platte River drainage along an altitudinal cline in Colorado (Knopf 1985 and unpubl. data). The incidence of parasitism is a function of cowbird density (McGeen 1972) and based on high cowbird densities on our study area, we would expect high rates of parasitism.

(2) The narrow, linear nature of the willow riparian zone on our study area (width of the willow vegetation ranges from <50 to 200 m) may make the area especially attractive to cowbirds. Cowbirds avoid forest interiors, preferring open habitat (Brittingham and Temple 1983), and they feed in open, grassy areas (Mayfield 1965, Rothstein et al. 1984). Brittingham and Temple (1983) found that brood parasitism varied inversely with the distance of a nest to open habitat, and suggested that parasitism rates are influenced more by the proximity of open habitat than cover type. The narrow, willow-dominated floodplain and adjacent sagebrush-steppe uplands with open, grassy feeding sites apparently provide ideal cowbird habitat.

(3) Because the rate of parasitism is often based on a single visit per nest per season, parasitism is probably understated for many studies. To determine the incidence of parasitism accurately, nests must be found before hosts have laid (Nolan 1978), must be checked frequently, and the full seasonal history of each pair must be known. In our study, we found most nests early and therefore detected those nests abandoned or abandoned and dismantled. Failure to detect parasitized/abandoned nests (difficult to find) or parasitized/dismantled nests (present for only a short time) would bias estimates of the rate of parasitism downwards. Similarly, finding nests relatively later in the breeding cycle—after cowbird eggs have been ejected—would understate the incidence of parasitism. Parasitism rates determined from egg collections are further biased because of the preference of some early collectors for nests without cowbird eggs (Friedmann et al. 1977) as well as for the reasons given above.

RESPONSES TO PARASITISM

Nest desertion was the most common response to cowbird parasitism in this study, and was effective because renesting attempts appeared to occur after the main period of cowbird parasitic activity. The incidence of parasitism declined sharply after late June, as reported elsewhere (Hofslund 1957, Hill 1976). As a result, second or later nest attempts, initiated in July, were only infrequently parasitized.

Depressing cowbird eggs into the bottom of the nest (i.e., burying or building them into the lining) was the second type of response to parasitism we observed. Egg depression effectively prevents incubation, as any other eggs lie on top of the depressed egg(s); this also precludes turning of depressed eggs during incubation. Walkinshaw (1961) and Holcomb (1972) also observed this behavior by the superspecies.

These responses (nest desertion and egg depression) are not necessarily antiparasite adaptations. Rothstein (1975) suggested that nest desertion may not be in response to the presence of cowbird eggs per se but, alternatively, may be due to (1) visits by human observers to the nest; (2) alteration of the combined egg mass; or (3) discovery of the cowbird at the host's nest. In this study, there was no nest desertion at unparasitized nests (which were visited as frequently as parasitized nests); thus nest abandonment at parasitized nests was probably not due to visits by human observers. However, nest abandonment may have been due to alteration of the combined egg mass (which obviously occurred) or to discovery of the cowbird at the host's nest (which may have occurred) and not to the presence of a cowbird egg as such (Rothstein 1975, 1986). In at least five of the seven instances of desertion, the cowbird egg(s) was laid before flycatchers would have initiated laying. Birds are especially likely to abandon under these circumstances (Friedmann 1963, Nolan 1978) but this may be merely a response to a foreign object in the nest and not an antiparasite adaptation. Similarly, in the two cases of cowbird egg depression, the response of flycatchers may have been to a foreign object. In at least one of the two cases of egg depression, the cowbird egg was laid before flycatcher eggs, and apparently after the completion of nest construction. In both cases, additional flycatcher eggs were laid after the cowbird egg had been laid and depressed into the nest lining.

EFFECTS OF PARASITISM ON FLYCATCHER PRODUCTIVITY

Cowbird parasitism generally results in lower host reproductive output (Rothstein 1975). Whereas nest success was lower for parasitized (18.2%) vs. unparasitized (56.3%) nests, nest success for parasitized pairs was at least 54.5%. Renesting after abandonment of parasitized first nests was frequently successful and appears to be a successful antiparasite strategy for Willow Flycatchers. Clutch size is smaller for renests than first nests in Willow Flycatchers (Holcomb 1972), however, suggesting fewer fledglings per nest for renests and lowered reproductive output. Additionally, whereas later nest attempts may be less frequently parasitized than first nest attempts, those that are parasitized may be less likely to be abandoned than parasitized first nests. The growing season in northcentral Colorado is short, averaging only 46 days (Cannon and Knopf 1984); this corresponds to an equally short breeding season. Flycatchers may be less likely to abandon parasitized second nest attempts at this locale due to insufficient time remaining in the breeding season to renest successfully. Also, reproductive output may be lowered in later nests that may be out of phase with food abundance (Immelmann 1971), lowering both nestling and fledgling survival.

Whereas second nests by Willow Flycatchers appeared to occur after the period of maximum cowbird activity, even first nest attempts occurred near the end of the breeding cycle of cowbirds. Willow Flycatchers are late migrants (Bent 1942), and they initiated their nests 1 to 2 weeks later than either Yellow Warblers or Song Sparrows (*Melospiza melodia*), both common cowbird hosts in northcentral Colorado. The breeding cycle of cowbirds in northcentral Colorado is more synchronous with the breeding cycles of these more abundant species. Based on host densities and the chro-

nology of breeding cycles of cowbirds and available hosts, we speculate that parasitism of these other species is considerably higher than that of Willow Flycatchers.

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