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RATES OF BROOD PARASITISM BY BROWN-HEADED COWBIRDS ON RIPARIAN PASSERINES IN ARIZONA

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Abstract.—Active nests of passerine hosts of the Brown-headed Cowbird (*Molothrus ater*) were examined from 1982 to 1987 along the Colorado River in Grand Canyon National Park, Arizona, to examine rates of brood parasitism and to determine cowbird nesting chronology relative to host nesting chronology. Eight of 16 (50%) species and 37 of 207 (17.9%) nests were parasitized. Nests of Willow Flycatcher (*Empidonax traillii*), Common Yellowthroat (*Geothlypis trichas*) and Blue Grosbeak (*Guiraca caerulea*) experienced at least 50% cowbird parasitism. Overall rates of parasitism differed among years (range = 3.3–30.4%/yr; $P = 0.017$). The cowbird nesting season extended from 6 May to 18 July, with a peak from mid-May to mid-June when 86% of cowbird eggs were laid. Passerine hosts whose peak nesting coincided with cowbird peak nesting exhibited relatively high rates of brood parasitism.

RAZONES DE PARASITISMO DE CAMADA POR *MOLOTHRUS ATER* EN LOS PASERINOS DE ZONAS RIPARIAS DE ARIZONA

Síntesis.—Se examinaron nidos activos de los hospederos paserinos de *Molothrus ater* entre 1982 y 1987 a lo largo del Río Colorado en el Parque Nacional del Gran Cañón en Arizona para examinar las razones de parasitismo de camada y determinar la cronología de anidamiento de *Molothrus* en comparación con la de sus hospederos. Ocho de las 16 especies (50%) y 37 de los 207 de los nidos (17.9%) fueron parasitados. Por lo menos un 50% de los nidos de *Empidonax traillii*, de *Geothlypis trichas*, y de *Guiraca caerulea* fueron parasitados. Las razones totales de parasitismo diferieron en medio de los años (alcance = 3.3 a 30.4% por año; $P = 0.017$). La temporada reproductiva de *Molothrus* se extendió desde mayo 6 hasta julio 18, con un mayor número entre la mitad de mayo y la mitad de junio, donde 86% de sus huevos se depositaron. Los hospederos paserinos cuya cúspide reproductiva coincidió con la de *Molothrus* tuvieron razones de parasitismo de camada relativamente altas.

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) is known to occur in at least 220 host species (Friedmann and Kiff 1985) in a dynamic relationship influencing the immediate fitness of both parasite and host (Payne 1973). Rates of brood parasitism by Brown-headed Cowbirds, which have often increased due to anthropogenic factors such as habitat modification and livestock grazing, can strongly influence host population dynamics and even threaten hosts with extinction (Brittingham and Temple 1983, Goldwasser et al. 1980, Mayfield 1977). Rates of cowbird parasitism have been reported for diverse avian communities across much of North America (e.g., Elliott 1978, Hanka 1979, Hill 1976, Norris 1947, Payne 1973, Weatherhead 1989). Little information exists, however, on host-specific rates of cowbird parasitism in the arid southwestern United States (Finch 1982, 1983). This is particularly true for riparian bird communities, which are of special interest due to their large

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contribution to overall avian density and diversity in lowland desert ecosystems and because they support a disproportionate number of rare and endangered bird species (Johnson et al. 1987).

Here I report on long-term rates of cowbird parasitism in a community of riparian passerines along the Colorado River in Grand Canyon National Park. My objectives were to determine host-specific rates of brood parasitism, to determine if rates of brood parasitism varied by year, and to examine cowbird nesting chronology relative to host nesting chronology. This study is of interest because it documents rates of cowbird parasitism in a protected natural area that is largely free of anthropogenic factors that may influence brood parasitism.

METHODS

The study area was the 389-km riparian corridor of the Colorado River through Grand Canyon National Park and Glen Canyon National Recreation Area, Arizona, from Glen Canyon Dam to Diamond Creek (see Brown 1992, Brown and Trosset 1989). The study area was substantially modified by the 1963 completion of Glen Canyon Dam and subsequent dam operations (Turner and Karpisack 1980).

Nest searches were conducted 10 Apr.–12 Jul. 1982–1987, throughout the river corridor by up to six trained observers (Brown 1992, Brown and Trosset 1989). Intensive, non-biased searches for nests of all species were made at nine permanent study plots (Brown 1992). Data recorded on nests included species, date, number of eggs or young present, age of young (if applicable) and presence of cowbird eggs or young. All nest locations were marked by placing colored surveyor's tape a known distance and direction from nests to aid future relocation and avoid duplication.

I calculated nesting chronology from data collected on active nests during one to three visits, with 82% of nests visited once. The egg-laying period was the number of days required to lay a completed clutch (Table 1), as a single egg was assumed laid each day at dawn (Pettingill 1970). The incubation period was the number of days from laying of last egg to hatching of last egg, and the nestling period was the number of days from hatching of the first egg to fledging of the last young. The average number of days of the cowbird egg-laying period was 1 d, even though more eggs may be laid in host nests. Numbers of cowbird nestlings hatched were extrapolated from known numbers of eggs or nestlings, and did not represent percent of successfully hatched eggs. Nesting information on Lucy's Warbler (*Vermivora luciae*) was unavailable, but was assumed to be similar to that of Nashville Warbler (*Vermivora ruficapilla*). I assumed no delay occurred between termination of egg-laying and initiation of incubation.

I used the average duration of each nesting period to reconstruct the chronology of each nest, based on nest contents. Host nests containing fewer eggs than expected for a completed clutch were assumed to be at the corresponding day of the egg-laying period. Host nests containing a completed clutch were assumed to be at mid-point of the incubation period.

TABLE 1. Length of nesting period of Brown-headed Cowbirds and their known or potential hosts along the Colorado River in Grand Canyon, Arizona. Only species for which ≥ 5 active nests were located from 1982 to 1987 have been included.

Species	Average number of days/period			Reference
	Egg-laying	Incubation	Nestling	
Willow Flycatcher (<i>Empidonax traillii</i>)	4	12	14	Bent 1942
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	4	14	12	Bent 1949
Bell's Vireo (<i>Vireo bellii</i>)	4	14	11	Barlow 1962, Brown 1993
Lucy's Warbler (<i>Vermivora luciae</i>)	4	12	11	Estimated from Bent 1953
Yellow Warbler (<i>Dendroica petechia</i>)	4	11	10	Bent 1953
Common Yellowthroat (<i>Geothlypis trichas</i>)	4	12	10	Stewart 1953, Bent 1953
Yellow-breasted Chat (<i>Icteria virens</i>)	4	15	11	Petrides 1938, Bent 1953
Blue Grosbeak (<i>Guiraca caerulea</i>)	4	12	12	Bent 1968, Genung 1976
Brown-headed Cowbird (<i>Molothrus ater</i>)	1	11	10	Bent 1958, Scott 1979
House Finch (<i>Carpodacus mexicanus</i>)	4	13	15	Evenden 1957, Bent 1968
Lesser Goldfinch (<i>Carduelis psaltria</i>)	4	12	12	Linsdale 1957, Bent 1968

Presence of ≥ 1 cowbird egg in a host clutch was added to the number of host eggs to determine whether or not the nest was in the egg-laying or incubation period, as cowbirds may remove host eggs when laying (Weatherhead 1989). Nestling age was estimated to the nearest day after published descriptions of nestling development (see references in Table 1). Cowbird eggs discovered in host nests containing less than the average completed clutch (including cowbird eggs) were assumed to have been laid within the last 2 d; cowbird eggs discovered in host nests containing a completed clutch (including cowbird eggs) were assumed to have been laid approximately 8 d previously. The latter assumption was made because completed clutches were assumed to be at the mid-point of incubation. As most cowbird eggs are laid during the host's egg-laying period (Marvil and Cruz 1989), most cowbird eggs in completed clutches would have been approximately 8 d old (range = 7–9 d). The greatest source of error in reconstructing nesting chronology occurred in nests containing completed clutches. Nests discovered with completed clutches that were actually on first or last day of incubation would introduce an error of ± 5 –7 d, depending on the species, into extrapolated nesting chronology.

TABLE 2. Number of passerine nests located and percent of nests exhibiting brood parasitism by Brown-headed Cowbirds along the Colorado River in Grand Canyon, Arizona, 1982 to 1987.

Species	# nests located	% parasitized
Black Phoebe	2	0
Say's Phoebe	4	0
Willow Flycatcher	8	50.0
Blue-gray Gnatcatcher	28	32.1
Phainopepla	3	0
Bell's Vireo	57	7.0
Lucy's Warbler	13	23.1
Yellow Warbler	22	22.7
Common Yellowthroat	9	55.6
Yellow-breasted Chat	37	10.8
Black-headed Grosbeak	1	0
Blue Grosbeak	5	60.0
Indigo Bunting	2	0
Northern Oriole	1	0
House Finch	7	0
Lesser Goldfinch	8	0
Total	207	17.9

A Chi-squared goodness-of-fit test was used to compare parasitism rates among years. Significance was accepted at $P < 0.05$. Sample sizes of various analyses differed due to missing data.

RESULTS

Eight of 16 (50%) species and 37 of 207 (17.9%) nests were parasitized (Table 2). The overall rate of parasitism was 20.7% for only those eight species known to have been parasitized (Table 2). One cowbird egg was present in 26 of 37 (70%) parasitized nests; two eggs in nine (24%); and three and four eggs in one each (3% each). Species with nests containing two cowbird eggs included (n in parenthesis): Willow Flycatcher (*Empidonax traillii*) (2), Blue-gray Gnatcatcher (*Poliophtila caerulea*) (1), Bell's Vireo (*Vireo bellii*) (1), Lucy's Warbler (1), Common Yellowthroat (*Geothlypis trichas*) (3), and Blue Grosbeak (*Guiraca caerulea*) (1). Both nests containing at least three cowbird eggs were those of Yellow-breasted Chat (*Icteria virens*).

Willow Flycatcher, Common Yellowthroat and Blue Grosbeak experienced the highest rates of cowbird parasitism, with $\geq 50\%$ of nests parasitized (Table 2). Numbers of nests located and rates of cowbird parasitism by year in all passerines combined were: 1982, $n = 22$, 4.5%; 1983, $n = 30$, 3.3%; 1984, $n = 24$, 30.4%; 1985, $n = 53$, 15.1%; 1986, $n = 45$, 22.2%; and 1987, $n = 33$, 30.3%. Parasitism varied among years ($\chi^2 = 13.83$, $df = 5$, $P = 0.017$). Sample sizes were too small in most cases to examine annual variation within a species.

Thirty-five active host nests containing cowbird eggs or young were located between 18 May and 28 Jun. 1982–1987. Reconstruction of the

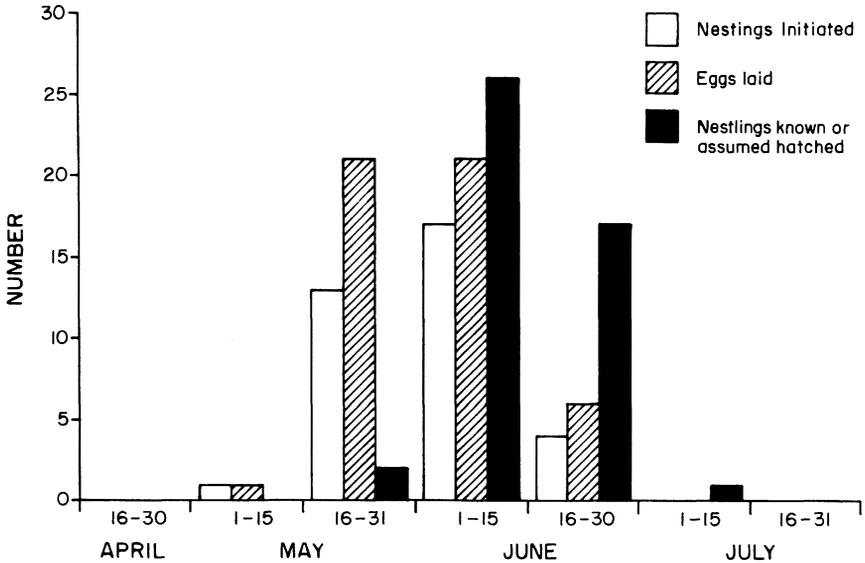


FIGURE 1. Chronology of the Brown-headed Cowbird nesting season as indicated by number of cowbird nestings initiated ($n = 35$), number of cowbird eggs laid ($n = 49$), and number of nestlings known or assumed hatched ($n = 46$) by 2-wk intervals along the Colorado River in Grand Canyon, Arizona, 1982-1987.

nesting cycle indicated that the mean date of the earliest cowbird egg laid was 23 May (SD = 10.9 d, earliest egg laid on 6 May). The mean date of latest fledging occurred on 2 July (SD = 8.1 d, latest fledging on 18 July). Peak cowbird egg-laying occurred from mid-May to mid-June, when 42 of 49 (86%) cowbird eggs were laid (Fig. 1). Peak cowbird nesting coincided with peak nesting of seven of 10 host species for which ≥ 5 active nests were discovered (Fig. 2).

DISCUSSION

The overall rate of cowbird parasitism in my study area (17.9%) was low relative to that reported from elsewhere: Kansas, 21% (Hill 1976) and 58% (Elliott 1978); Oklahoma, 37% (Wiens 1963); Nebraska, 31% (Hergenrader 1962); Pennsylvania, 31% (Norris 1947); and Michigan, 22% (Berger 1951). Overall rates of cowbird parasitism were probably underestimated because I checked most nests only once per season, and because many cowbird eggs may have been ejected by hosts before detection (Finch 1982).

Although the overall rate of cowbird parasitism was relatively low, three host species (Willow Flycatcher, Common Yellowthroat, and Blue Grosbeak) experienced parasitism rates $\geq 50\%$. High rates of parasitism for Common Yellowthroat and Blue Grosbeak, common species in the study area (Brown and Trosset 1989), may not be reliable because of

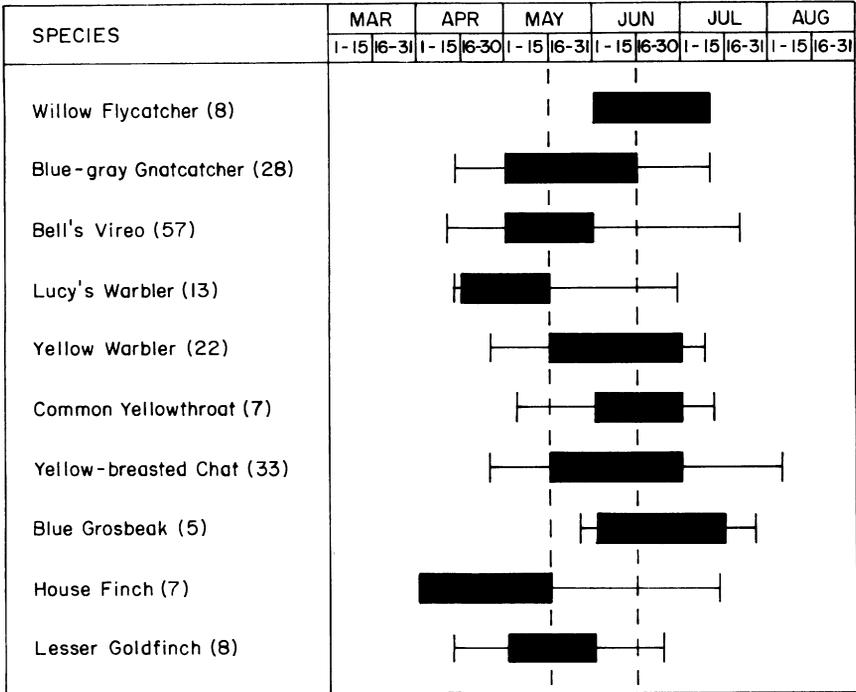


FIGURE 2. Nesting seasons of passerine hosts of Brown-headed Cowbirds along the Colorado River in Grand Canyon, Arizona, 1982-1987. Only species with ≥5 active nests located have been included (sample sizes in parenthesis). Broad horizontal lines indicate peak nesting (≥50% of nests active). Dashed vertical lines indicate peak cowbird egg-laying period.

small sample sizes of nests discovered ($n = 9$ and 5 nests, respectively), but are comparable with those reported elsewhere for the species. Parasitism rates for Common Yellowthroat have been reported as 16.7 and 26.9% in Illinois (Graber et al. 1983), 42% in the Great Plains states (Mayfield 1965), and 100% in Pennsylvania (Norris 1947), whereas a parasitism rate of 100% has been reported for Blue Grosbeaks across North America (Friedmann et al. 1977).

In contrast, Willow Flycatcher was very rare in the study area (Brown and Trosset 1989) and the small sample size of active nests discovered ($n = 8$) represented a substantial portion of the actual population, which peaked at 11 singing males in 1986 (Brown 1988). I suggest that the high rate of cowbird parasitism experienced by Willow Flycatchers was partially responsible for its decline to two singing males by 1991 (Brown 1991), especially considering that the majority of its nesting habitat was relatively unchanged. Willow Flycatcher nests in southern California experience up to 68% cowbird parasitism, which has been identified as a leading cause of nest failure there (Harris 1991). Cowbird parasitism

rates >30% have been demonstrated to lead to unstable populations susceptible to local extirpation due to stochastic events (Laymon 1987), and have been suggested to jeopardize the continued regional existence of some riparian birds (Finch 1983).

Peak cowbird nesting activity coincided with peak nesting for many local host species, as reported from California (Payne 1973). Excepting Lucy's Warbler, all host species experiencing $\geq 10\%$ cowbird parasitism were at their peak of nesting concurrently with peak cowbird egg-laying (Fig. 2). Bell's Vireo experienced relatively little cowbird parasitism (7%), in spite of its peak nesting being partially concurrent with cowbird peak egg-laying (Fig. 2). This is in sharp contrast to rates of cowbird parasitism on the endangered Least Bell's Vireo in California, where >33% of vireo nests from the late 1920s through 1979 contained cowbird eggs (Goldwasser et al. 1980). House Finch and Lesser Goldfinch also may have experienced low rates of cowbird parasitism in my study area by exhibiting nesting peaks prior to that of cowbirds (Fig. 2).

Community-wide rates of cowbird parasitism varied annually along the Colorado River for reasons that are unclear. Environmental variables that might influence annual cowbird abundance (and parasitism rates) were not measured during my study, and information on this topic is lacking. Future investigations should recognize that rates of cowbird parasitism may vary annually when attempting to explain rates and effects of brood parasitism in a host community.

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MEETINGS OF INTEREST

American Birding Association Convention '94, 13-19 June 1994, Best Western International Inn, 1505 North Broadway, Minot, North Dakota 58701.

Address inquiries to: Carol Wallace, ABA Convention Registrar, P.O. Box 6599, Colorado Springs, CO 80934 (800-850-BIRD).

American Ornithologists' Union, Cooper Ornithological Society and Wilson Ornithological Society, joint annual meetings, 21-26 June 1994, University of Montana, Missoula, Montana.

Address inquiries to: Ornithology Meeting, Center for Continuing Education, The University of Montana, Missoula, MT 59812.

14th North American Prairie Conference, 12-16 July 1994, Kansas State University, Manhattan, KS.

Address inquiries to: 14th North American Prairie Conference, Conference Office, Division of Continuing Education, College Court Building, Kansas State University, Manhattan, KS 66506-6006.

Animal Behavior Society, 24-30 July 1994, University of Washington, Seattle, Washington.

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