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RRH: Cowbird Parasitism of Riparian Passerines

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 1982-1987 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 (50%) of 16 species and 37 (17.9%) of 207 nests were parasitized. Willow Flycatcher (Empidonax traillii), Common Yellowthroat (Geothlypis trichas), and Blue Grosbeak (Guiraca caerulea) experienced at least 50% cowbird parasitism. Overall rates of parasitism differed significantly between years (3.3-30.4%/yr). 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.

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 (Mayfield 1977, Goldwasser et al. 1980, Brittingham and Temple 1983). Rates of cowbird parasitism have been reported for diverse avian communities across much of North America (e.g. Norris 1947, Payne 1973, Hill 1976, Elliot 1978, Hanka 1979, Weatherhead 1989). However, little information exists

on host-specific rates of cowbird parasitism in the arid southwestern United States (Finch 1982, Finch 1983). This is particularly true for riparian bird communities, which are of special interest due to their large 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. Study objectives were to determine host-specific rates of brood parasitism, determine if rates of brood parasitism varied by year, and examine cowbird nesting chronology relative to host nesting chronology.

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 as described previously (Brown and Trosset 1989, Brown 1992). The study area had been substantially modified by the 1963 completion of Glen Canyon Dam and subsequent dam operations (Turner and Karpiscak 1980).

Nest searches were conducted from 10 April through 12

July 1982-1987 throughout the river corridor by up to six trained observers (Brown and Trosset 1989, Brown 1992). 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.

Nesting chronology was calculated from data collected on active nests (containing eggs or young) during one to three visits, with 82% of nests visited once. Egg-laying period was number of days required to lay a completed clutch (Table 1), as a single egg was assumed laid each day at dawn (Pettingill 1970). Incubation period was number of days from laying of last egg to hatching of last egg; and nestling period was number of days from hatching of first egg to fledging of last young. Average number of days of 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 was unavailable, but assumed similar to

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Nashville Warbler (Vermivora ruficapilla). I assumed no delay occurred between termination of egg-laying and initiation of incubation.

The average duration of each nesting period was used to reconstruct 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 incubation period. Presence of ≥ 1 cowbird egg in a host clutch was added to number of host eggs to determine whether or not nest was in egg-laying or incubation period, as cowbirds often removed host eggs when laying (Weatherhead 1989). Nestling age was estimated to the nearest day after published descriptions of nestling development (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 last 2 d; cowbird eggs discovered in hosts nests containing a completed clutch (including cowbird eggs) were assumed to have been laid approximately 8 d previously. The greatest source of error in reconstructing nesting chronology occurred in nests containing a completed clutch. Nests discovered with completed clutches that were actually on first or last day of incubation would

introduce an error of \pm 5-7 d, depending on species, into extrapolated nesting chronology.

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

RESULTS

Eight (50%) of 16 species and 37 (17.9%) of 207 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 (70%) of 37 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 (2), Blue-gray Gnatcatcher (1), Bell's Vireo (1), Lucy's Warbler (1), Common Yellowthroat (3), and Blue Grosbeak (1). Both nests containing at least three cowbird eggs were those of Yellow-breasted Chat. Willow Flycatcher, Common Yellowthroat, and Blue Grosbeak experienced the highest rates of cowbird parasitism, with \geq 50% of nests parasitized (Table 2). Rates of cowbird parasitism in all passerines combined varied between years ($\chi^2 = 13.83$, $df = 5$, $P = 0.017$).

Thirty-five active host nests containing cowbird eggs

or young were located between 18 May and 28 June 1982-1987. Reconstruction of the nesting cycle indicated 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 (86%) of 49 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). The overall rate of cowbird parasitism in this study would have been 16.1% if I had included 23 unparasitized Mourning Dove (Zenaida macroura) nests discovered during the study period. However, this species is a questionable to rare host of cowbird parasitism (Friedmann and Kiff 1985). 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).

While the overall rate of cowbird parasitism was relatively low, three host species (Willow Flycatcher, Common Yellowthroat, and Blue Grosbeak) experienced parasitism rates $\geq 50\%$. However, 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 small sample sizes of nests discovered ($n = 9$ and 5 nests, respectively). 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 their decline to two singing males by 1991 (Brown 1991), especially considering that the majority of their nesting habitat was relatively unchanged. 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. 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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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 1982-87 have been included.

Species	Average number of days/period			Literature Source
	Egg-laying	Incubation	Nestling	
Willow Flycatcher				
(<u>Empidonax traillii</u>)	4	12	14	Bent 1942
Blue-gray Gnatcatcher				
(<u>Polioptila caerulea</u>)	4	14	12	Bent 1949
Bell's Vireo				
(<u>Vireo bellii</u>)	4	14	11	Barlow 1962, Brown In Press
Lucy's Warbler				
(<u>Vermivora luciae</u>)	4	12	11	Estimated from Bent 1953
Yellow Warbler				
(<u>Dendroica petechia</u>)	4	11	10	Bent 1953
Common Yellowthroat				
(<u>Geothlypis trichas</u>)	4	12	10	Stewart 1953, Bent 1953
Yellow-breasted Chat				
(<u>Icteria virens</u>)	4	15	11	Petrides 1938, Bent 1953
Blue Grosbeak				
(<u>Guiraca caerulea</u>)	4	12	12	Bent 1968, Genung 1976
Brown-headed Cowbird				
(<u>Molothrus ater</u>)	1	11	10	Bent 1958, Scott 1979

TABLE 1. Continued.

Species	<u>Average number of days/period</u>			Literature Source
	Egg-laying	Incubation	Nestling	
House Finch				
(<u>Carpodacus mexicanus</u>)	4	13	15	Evenden 1957, Bent 1968
Lesser Goldfinch				
(<u>Carduelis psaltria</u>)	4	12	12	Linsdale 1957, Bent 1968

TABLE 2. Sample size (n), number nests parasitized (#), and percent of passerine nests exhibiting brood parasitism by Brown-headed Cowbirds along the Colorado River in Grand Canyon, Arizona, 1982-87.

Species	1982		1983		1984		1985		1986		1987		1982-87		Percent Parasitized
	n	#	n	#	n	#	n	#	n	#	n	#	n	#	
Black Phoebe	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0
Say's Phoebe	0	0	0	0	0	0	2	0	2	0	0	0	4	0	0
Willow Flycatcher	1	0	0	0	2	2	3	2	2	0	0	0	8	4	50.0
Blue-gray Gnatcatcher	0	0	4	0	4	2	3	1	7	2	10	4	28	9	32.1
Phainopepla	0	0	0	0	0	0	0	0	2	0	1	0	3	0	0
Bell's Vireo	12	1	7	0	7	0	16	1	9	0	6	2	57	4	7.0
Lucy's Warbler	1	0	0	0	0	0	2	0	4	0	6	3	13	3	23.1
Yellow Warbler	1	0	1	1	2	0	9	0	7	3	2	1	22	5	22.7
Common Yellowthroat	0	0	1	0	2	1	2	2	3	2	1	0	9	5	55.6
Yellow-breasted Chat	6	0	9	0	5	1	7	1	5	2	5	0	37	4	10.8
Black-headed Grosbeak	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Blue Grosbeak	0	0	0	0	1	1	2	1	2	1	0	0	5	3	60.0
Indigo Bunting	0	0	1	0	0	0	1	0	0	0	0	0	2	0	0
Northern Oriole	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0
House Finch	1	0	2	0	1	0	1	0	1	0	1	0	7	0	0
Lesser Goldfinch	0	0	3	0	0	0	4	0	0	0	1	0	8	0	0
TOTAL	22	1	30	1	24	7	53	8	45	10	33	10	207	37	17.9
Percent Parasitized/Yr	4.5		3.3		30.4		15.1		22.2		30.3		17.9		

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FIGURE CAPTIONS

Figure 1. Chronology of 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.

Figure 2. Nesting seasons of passerine hosts of brood parasitism by 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 ($\geq 50\%$ of nests active). Dashed vertical lines indicate peak cowbird egg-laying period.

Fig 1

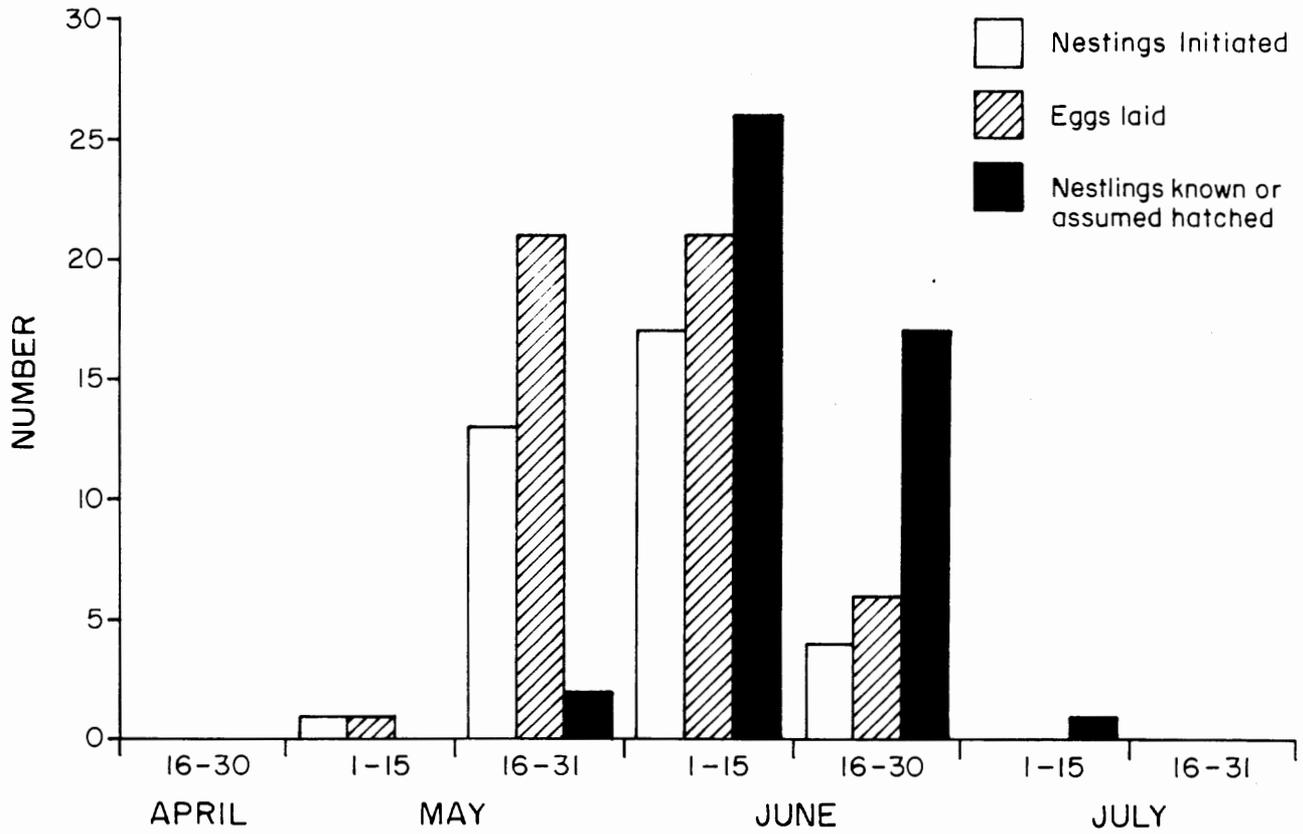


Fig 2

SPECIES	MAR		APR		MAY		JUN		JUL		AUG	
	1-15	16-31	1-15	16-31	1-15	16-31	1-15	16-31	1-15	16-31	1-15	16-31
Willow Flycatcher (8)								■	■			
Blue-gray Gnatcatcher (28)			■	■	■	■	■	■				
Bell's Vireo (57)			■	■	■	■						
Lucy's Warbler (13)			■	■	■	■						
Yellow Warbler (22)					■	■	■	■				
Common Yellowthroat (7)							■	■				
Yellow-breasted Chat (33)					■	■	■	■				
Blue Grosbeak (5)							■	■	■			
House Finch (7)			■	■	■	■						
Lesser Goldfinch (8)					■	■						