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RANGE-WIDE IMPACT OF BROWN-HEADED COWBIRD PARASITISM ON THE SOUTHWESTERN WILLOW FLYCATCHER (*EMPIDONAX TRAILLII EXTIMUS*)

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Abstract. We present datasets from long-term studies of brood parasitism of Southwestern Willow Flycatcher (*Empidonax traillii extimus*) populations at the South Fork Kern River (SFKR), California, the Grand Canyon, Arizona, and from other intensive flycatcher studies in Arizona. In the two main study areas, we recorded high parasitism rates for the flycatcher. We found that 75 % of Willow Flycatcher nests failed completely when parasitized and that an extremely low percentage of Willow Flycatcher eggs survived to fledging in parasitized nests (11% vs. 47% in unparasitized nests). Our data show that cowbird parasitism also delayed the fledging of young flycatchers. However, contrary to our expectations, we did not find a significant difference between the return rates of "early" versus "late" fledged birds. To evaluate how important cowbird parasitism is to the population decline of the endangered Southwestern Willow Flycatcher, we reviewed the current level of parasitism on this species throughout its range in six states using a large number of datasets from different sites. We also reviewed the historic pattern of increase in Brown-headed Cowbird (*Molothrus ater*) populations in the southwest between 1872–1997 using both nest record and egg collections and documentary evidence. Given the level of impacts to flycatcher productivity inflicted by cowbird parasitism that we observed at SFKR and Grand Canyon, it is likely that cowbirds played a role historically in reducing many local Southwestern Willow Flycatcher populations. Also, cowbirds continue to play a role in slowing or preventing the recovery of this subspecies.

Key Words: brood parasitism, Brown-headed Cowbird, *Empidonax traillii, Molothrus ater,* reproductive success, Willow Flycatcher.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*) once commonly bred in riparian thickets throughout the Southwest (Fig. 1; Unitt 1987). Although the flycatcher is still found in most of its former range, its numbers have been severely reduced in the last 60 years, prompting the US Fish and Wildlife Service to list this Willow Flycatcher subspecies as endangered (Unitt 1987, USFWS 1995).

Johnson and Haight (1984) estimated that only 5% of the original lowland riparian habitat in the Southwest remains, and destruction of this habitat is regarded as the main cause of the decline of this subspecies (Gaines 1974, Harris et al. 1987, Unitt 1987, Garrett and Dunn 1981, USFWS 1995). In addition, Brown-headed Cowbird (*Molothrus ater*) parasitism is considered a major factor in the subspecies' decline (Gaines 1974, Unitt 1987, Harris 1991,USFWS 1995).

Southwestern Willow Flycatchers suffer from high parasitism rates in at least two areas for which long-term data are available: the South Fork of the Kern River, California (SFKR), and in the Grand Canyon, Arizona (Brown 1988, 1994; Sogge et al. 1997, Whitfield in press). However, is cowbird parasitism a problem throughout the flycatcher's range? In this paper, we use long-term datasets to examine the impacts of cowbird parasitism on the flycatcher's reproductive success. We also review both the current and historical parasitism rates of Southwestern Willow Flycatchers in different parts of its range, as well as the pattern of increase in cowbird populations, to evaluate the contribution of cowbird parasitism to the population decline of this subspecies.

METHODS

LONG-TERM STUDY AREAS

Grand Canyon, AZ.

Data were collected from 1992 to 1996 in riparian habitat patches along the Colorado River in the Grand Canyon from just below Glen Canyon Dam, downstream to the boundary between Grand Canyon National Park and Lake Mead National Recreation Area. Some data were also collected by B. Brown from 1982 to 1986 (see Brown 1988 and Sogge et. al 1997 for more details).

South Fork Kern River, CA.

The study area is located on The Nature Conservancy's Kern River Preserve (now managed by Audubon California) and the adjoining South Fork Wildlife Area in Kern Co., California. It encompasses 500 ha of cottonwood-willow riparian forest dominated by three tree species: red willow (*Salix laeviagata*), Gooding's black willow (*Salix gooddingii*) and Fremont cottonwood (*Populus fremontii*). Data were collected in 1987 by J. Harris and from 1989 to 1997 by

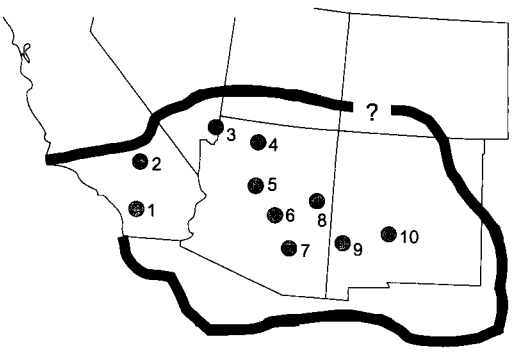

FIGURE 1. Approximate breeding range distribution (thick black line) of *Empidonax traillii extimus*, adapted from Unitt (1987) and Browning (1993). Shaded circles are approximate locations of breeding sites for which cowbird parasitism data are presented in the text. 1= San Luis Rey River, 2 = South Fork Kern River, 3 = Mesquite, Virgin River Delta, and Mormon Mesa, 4 = Grand Canyon, 5 = Verde River, 6 = Roosevelt Lake, 7 = San Pedro River, 8 = White Mtns., 9 = Gila River, 10 = Rio Grande.

M. Whitfield (see Harris 1991 and Whitfield et. al. *this volume* for more details).

Overview of Current Parasitism Rates

We obtained data on current parasitism rate and cowbird presence at Willow Flycatcher breeding locations across the subspecies range from various sources (Fig. 1, Table 1).

Long-term Datasets: Impact of Parasitism on Flycatcher Reproductive Success

We used data from our own long-term studies and four other sources (Table 1) to analyze nest outcome of parasitized nests. We used only active nests (defined as nests with at least one egg or young, cowbird or flycatcher), with known outcome, in our analyses. A successful nest was one that fledged at least one Willow Flycatcher.

Egg success data were collected at SFKR from 1989 to 1997. We used a t-test and a Mann-Whitney U test for comparing hatching success and fledging success of parasitized and unparasitized nests.

We used six sources (Table 1) for the nest success analysis. Nest success was defined as the total number of successful nests divided by the total number of active nests. We used the Chi-square test of homogeneity for comparing nest success in parasitized and unparasitized nests in California, Arizona, and New Mexico.

Return rates of early versus late nesters.

Data were collected using banded birds on the SFKR from 1989 to 1997. All nestlings used in

TABLE 1. Data sources for the various analyses conducted in this paper

State(s)	Region	Author	Citation	Type of data			
				Parasitism rates and cowbird presence	Parasitism rates by habitat types	Nest outcome	Nest success
AZ	Grand Canyon	Brown	1988	X		X	
AZ	Grand Canyon	Sogge et al.	1997 and this study	X		X	X
AZ	Various sites throughout the state	Muiznieks et al.	1994	X	X	X	X
AZ	Various sites throughout the state	Sferra et al.	1995, 1997	X	X	X	X
AZ	Various sites throughout the state	Spencer et al.	1996	X	X	X	X
CA	South Fork Kern River	Harris	1991	X		X	X
CA	South Fork Kern River	Whitfield	this study	X		X	X
CA	San Luis Rey River	W. Haas	Unpubl. data	X			
CO, NV and UT	Various sites in these states	Sogge	this study	X			
NM	Various sites throughout the state	Maynard	1994	X			
NM	Various sites throughout the state	Cooper	1996, 1997	X			
NM	Rio Grande River	Ahlers and White	1995	X			
NM	Gila River Valley	Skaggs	1996	X			
NM	Gila River Valley	S. Stoleson	Unpubl. data	X			X
NV	Virgin River	R. McKernan	Unpubl. data	X			

the analysis were banded with a USFWS band. Due to heavy cowbird parasitism and the resultant low productivity, and low return rates, we did not have a large enough sample size to test directly whether breeding delays caused by cowbirds resulted in lower fledgling survival. However, we could indirectly test whether cowbirds decreased the survivorship of fledged young by investigating differences in return rates of young fledged from early vs. late nests. The first step was to determine whether cowbird parasitism caused significant delays in Willow Flycatcher fledging dates. To do this, we standardized laying dates in relation to arrival dates by designating the date when the first Willow Flycatcher egg was laid for the breeding season as day one for that year. This method helps reduce bias due to yearly variation in arrival dates (Perrins and McCleery 1989). For nests that were found after its first egg was laid, we estimated the first egg laid date by counting backwards the appropriate number of days (15 to 17 days depending on clutch size) from the hatching date.

The comparison of return rates of early versus late nesters was made by comparing the first egg dates of successful parasitized females with successful unparasitized females. A successful female was defined as a female that fledged at least one flycatcher young. Females that had nests in which we addled cowbird eggs or removed cowbird chicks were not used in the analysis. Because the data were not normally distributed, we tested for the difference in first egg dates between parasitized and unparasitized females using the Mann-Whitney U test.

To determine if there was a difference in survivorship of young that fledged early in the breeding season versus young that fledged late, we recorded the first egg dates of recaptured Willow Flycatchers that had been banded in earlier years as nestlings. Because the return rates of hatching years birds were unusually high (averaged 32% for eight years), we assumed that recapture rates would be a good index for survivorship (Uyehara et al. in press). To mimic the delay that parasitism has on successful parasitized females, a bird was categorized as "early fledged" when the first egg date of its natal nest was before the average first egg date of successful parasitized females. A bird was categorized as "late fledged" when the first egg date of its natal nest was on or later than the average first egg date of successful parasitized females.

Historical Data on Increase in Cowbird Abundance and Parasitism Rates

To estimate historical parasitism rates of the Southwestern Willow Flycatcher, we looked through records of nest collections sent to us from 50 North American natural history museums. We classified records as *E. t. extimus* if they came from a site that was within the known *E.t. extimus* range as reported by Unitt (1987) and Browning (1993). The following museums had *E.t. extimus* nest records: Cornell University (1 record); California State University, Long Beach (1 record); Delaware Museum of Natural History (5 records); Denver Museum of Natural History (1 record); New York State Museum, Albany (1 record); Peabody Museum of Natural History (5 records); Provincial Museum of Alberta (1 record); Royal Ontario Museum (3 records); San Bernardino County Museum (16 records); Santa Barbara Museum of Natural History (12 records); Slater Museum of Natural History at the University of Puget Sound, Washington (2 records); Smithsonian National Museum of Natural History (20 records); University of Arizona Museum Collection (35 records); University of California, Berkeley (3 records); University of Nevada, Las Vegas (1 record); Western Foundation of Vertebrate Zoology (147 records).

Information on historical presence and distribution of cowbirds in California was found in Unitt (1987), Laymon (1987), and Rothstein (1994). Estimates of historical abundance elsewhere in the Southwest were derived from sources listed in Table 9.

RESULTS

Overview of Current Parasitism Rates

During the past five years, cowbirds have been detected at all known Southwestern Willow Flycatcher breeding locations in California, Arizona, New Mexico, southwestern Colorado, Utah, and Nevada. As is typical of all host species, cowbird parasitism rates of Southwestern Willow Flycatchers varied both geographically and temporally (Tables 2 and 3). In California, pre-trapping parasitism rates are known only for SFKR (1987, 1989–1992), where the rates averaged 66%. Post-trapping parasitism rates on SFKR (1993–1997) range from 11% to 38%. In Arizona, cowbird parasitism at most sites is below 25%, with a few of the smaller sites (< 5 pairs) experiencing parasitism of 100% in a given year and as much as 50% over 5–10 year periods. New Mexico parasitism data are limited to a few sites, where rates range from 18–40%. Although parasitism data are very limited or absent for Willow Flycatchers in Nevada, southern Utah, and southwest Colorado, cowbird parasitism has been documented at sites in each of these states.

Long-term Datasets: Impact of Parasitism on Flycatcher Reproductive Success

The data from our long-term studies of Willow Flycatcher populations at the SFKR and the

TABLE 2. GEOGRAPHIC VARIATION IN PARASITISM RATES OF THE SOUTHWESTERN WILLOW FLYCATCHER AT SELECTED LOCATIONS IN CALIFORNIA, NEVADA, ARIZONA, AND NEW MEXICO

Region	Years covered	No. nests	Mean annual parasitism rate[a]	SD
South Fork Kern River, CA	1987, 1989–1992	163	66%	0.11
Mesquite, NV	1997	5	40%	n/a
Virgin River Delta, NV	1997	14	21%	n/a
Mormon Mesa, NV	1997	3	0%	n/a
Grand Canyon, AZ	1982–1986,			n/a
	1992–1996	25	48%	0.50
White Mountains, AZ	1993–1996	36	19%	0.19
San Pedro River, AZ	1995–1996	61	3%	0.03
Roosevelt Lake, AZ	1995–1996	17	18%	0.04
Verde River, AZ	1996	13	46%	n/a
Gila River Valley, NM	1995, 1997	49	18%	0.09
other sites, NM	1995	10	40%	n/a

[a] No cowbird trapping was done at these sites for these dates.

Grand Canyon, and from other extensive studies in Arizona, reflect the severe impacts that parasitism has on three parameters of reproductive success: nest failure rate, hatching success, and fledging success. Nest data from Arizona and SFKR show that the majority of parasitized Willow Flycatcher nests failed (Table 4). Nests fledged cowbird young two to three times more often than flycatcher young, and fewer than 2% of the nests fledged both a cowbird and a flycatcher. In addition, SFKR egg success data show that for all years (though it is only significant in 5 of the 7 years tested), the percentage of eggs hatched per nest is lower in parasitized than unparasitized nests (Table 5). When the data are pooled, the average hatching rate for parasitized nests (20%) is significantly lower than the hatching rate for unparasitized nests (61%) ($t_{279} = 8.21$, $p < 0.001$). The number of flycatcher eggs that hatched and subsequently produced fledglings followed the same pattern as hatching success, with all years showing lower fledging rates in parasitized nests than unparasitized nests (Table 6). When the data are pooled, the fledging rate is significantly lower most years in parasitized nests (11%) than unparasitized nests (47%) ($t_{279} = 7.51$, $p < 0.001$). Nest success data showed a similar pattern as the egg success data in which the success of parasitized nests was lower than unparasitized nests in every year. An ANOVA showed that the yearly (MS error) variation was insignificant when compared to the difference between parasitized and unparasitized nests (MS effect) (AZ: ANOVA, MS effect =0.236, MS error = 0.037; CA: MS effect = 0.845, MS error = 0.018). Therefore, we pooled the data and found that nest success is significantly lower in parasitized nests than in unparasitized nests in California ($\chi^2_1 = 54.01$, $p < 0.001$), Arizona ($\chi^2_1 = 22.46$, $p < 0.001$), and New Mexico ($\chi^2_1 = 8.13$, $p = 0.004$) (Table 7).

Return rates of early versus late nesters

First egg dates of successful parasitized females were significantly later (day 27) than first egg dates of successful unparasitized females (day 16) ($Z = -3.60$, $P = 0.003$, Mann-Whitney U test). However, we did not find any significant differences in return rates of the "early fledged" (first egg date < day 27) birds when compared to the "late fledged" (first egg date ≥ 27) young) in any single year (Table 8). We did not pool the data and analyze the results, because of the substantial annual differences in the relative

TABLE 3. ANNUAL VARIATION IN COWBIRD PARASITISM RATES OF SOUTHWESTERN WILLOW FLYCATCHERS IN ARIZONA, CALIFORNIA, AND NEW MEXICO

Region	Years	Mean no. nests per year	Range of annual parasitism rates	
			No trapping	Trapping
Various sites, AZ[a]	1994–1996	76	8%–21%	
South Fork Kern River, CA	1989–1997	35	50%–80%	11%–38%
San Diego Co., CA	1994–1997	24	Unknown	0%–10%
Gila River Valley, NM	1995, 1997	24.5	14.7%–27%	

[a] Parasitism rates of Arizona were calculated from data pooled from all sites.

TABLE 4. NEST OUTCOME OF SOUTHWESTERN WILLOW FLYCATCHER NESTS PARASITIZED BY BROWN-HEADED COWBIRDS IN CALIFORNIA AND ARIZONA

Region	Years	Number of nests	Fledged cowbird	Fledged flycatcher	Fledged both	Failed
South Fork Kern River, CA	1989–1997	72	14%	9.7%	1.4%	75%
Various sites, AZ	1992–1996	40	30%	7.5%	0%	62.5%

return rate patterns for "early fledged" vs. "late fledged" birds.

HISTORICAL DATA ON INCREASE IN COWBIRD ABUNDANCE AND PARASITISM RATES

We found 254 *E. t. extimus* nest records from 16 of the 50 collections of nest records examined. None of the 36 Southwestern Willow Flycatcher nests collected between 1872 and 1899 were parasitized (Fig. 2). The first recorded parasitized Southwestern Willow Flycatcher nest was found by Herbert Brown near Yuma, Arizona, in 1900 (nest record collection of University of Arizona). The nest records show that the number of parasitized nests collected, and hence the inferred rate of parasitism increased gradually from zero before 1900 to 40% by 1997.

Our search of the literature indicated that although cowbirds were in the southwest much earlier than 1860, they apparently did not start to increase until after the 1860s or 1870s (Table 9).

DISCUSSION

THE CURRENT EXTENT AND ROLE OF PARASITISM

Observations from recent flycatcher surveys (sources listed in Table 1) indicated that cowbirds are present at all known Southwestern Willow Flycatcher breeding sites. Thus, the potential for parasitism of flycatcher nests is widespread and pervasive. Although cowbirds must obviously be at a site for parasitism to occur, mere cowbird presence does not mean that flycatchers are being parasitized at that site nor that parasitism rates are high. Indeed, we found enough geographic, temporal, and habitat-based variation in flycatcher parasitism rates to make it impossible to predict parasitism rates based simply on the presence of cowbirds.

However, Southwestern Willow Flycatchers are being parasitized throughout their range (Table 2). In southern California, pre-cowbird trapping parasitism rates are known only for the SFKR, which suffered from heavy parasitism (>50%) (Harris 1991, Whitfield 1990, in press).

TABLE 5. PERCENT EGGS HATCHED IN PARASITIZED AND UNPARASITIZED SOUTHWESTERN WILLOW FLYCATCHER NESTS ON THE SOUTH FORK KERN RIVER, CA, 1989–1997

	Unparasitized nests			Parasitized nests[a]				
		Mean percent eggs hatched			Mean percent eggs hatched		Difference	
Year	Number of nests	per nest	SE	Number of nests	per nest	SE	t-value	P-value
1989	15	68%	0.12	14	20%	0.10	3.06	0.005
1990	14	52%	0.13	17	27%	0.08	1.71	0.09
1991	9	70%	0.12	26	11%	0.05	5.60	<0.001
1992	11	54%	0.12	19	32%	0.10	1.34	0.19
1993	19	71%	0.09	11	32%	0.12	2.61	0.014
1994	25	64%	0.09	5	0%	0.00	2.62[b]	0.009
1995	21	51%	0.10	3	17%	0.17	n/a[c]	
1996	24	82%	0.08	2	0%	0.00	n/a[c]	
1997	36	45%	0.07	10	12%	0.10	2.17	0.04
Unmanipulated nest totals	n/a			57	18%	0.04		
Manipulated nest totals	n/a			50	23%	0.05		
Total	174	61%	0.03	107	20%	0.04	8.21	<0.001

[a] 1989–1991-no test manipulation (i.e. no addling of cowbird eggs or removal of cowbird chicks from nests), 1992–1997: nests manipulated.
[b] Z-value; Mann-Whitney U test used instead of t-test due to unequal variances and small sample size.
[c] Sample size too small to test.

TABLE 6. PERCENT EGGS THAT HATCHED AND FLEDGED IN PARASITIZED AND UNPARASITIZED SOUTHWESTERN WILLOW FLYCATCHER NESTS ON THE SOUTH FORK KERN RIVER, CA, 1989–1997

	Unparasitized nests			Parasitized nests[a]			Difference	
Year	Number of nests	Mean percent eggs to fledglings per nest	SE	Number of nests	Mean percent eggs to fledglings per nest	SE	t-value	*P*-value
1989	15	53%	0.13	14	2%	0.02	3.81	<0.001
1990	14	36%	0.14	17	13%	0.07	1.61	0.117
1991	9	58%	0.16	26	10%	0.05	4.05	<0.001
1992	11	54%	0.12	19	20%	0.09	2.27	0.031
1993	19	49%	0.11	11	16%	0.08	2.14	0.041
1994	25	51%	0.10	5	0%	0.00	2.08[b]	0.037
1995	21	46%	0.10	3	17%	0.17	n/a[c]	
1996	24	73%	0.09	2	0%	0.00	n/a[c]	
1997	36	26%	0.06	10	2%	0.03	1.88	0.067
Unmanipulated nest totals	n/a			57	9%	0.03		
Manipulated nest totals	n/a			50	13%	0.04		
Totals	174	47%	0.04	107	11%	0.02		

[a] 1989–1991-no nest manipulation (i.e. no addling of cowbird eggs or removal of cowbird chicks from nests), 1992–1997: nests manipulated.
[b] Z-value; Mann-Whitney U test used instead of t-test due to unequal variances and small sample size.
[c] Sample size too small to test.

The Santa Margarita River Willow Flycatcher population in San Diego County has increased from 5 birds to 24 birds after cowbird trapping started (Griffith and Griffith in press). Currently, all known southern California Willow Flycatcher populations of more than 10 pairs occur in areas where cowbirds are trapped (Unitt 1987, USFWS 1995), and mean parasitism rates of these Willow Flycatcher populations are 22% or lower. In Arizona and New Mexico, the statewide parasitism rates average 20% and 22% respectively. The overall picture that emerges in every state with intensive flycatcher monitoring is that parasitism is occurring throughout the range, often at rates exceeding those considered acceptable to most host species (Mayfield 1977, Brittingham and Temple 1983, Trail 1992).

When parasitism does occur, data from the SFKR and Arizona show that it negatively impacts the flycatcher at many different levels. Most parasitized Willow Flycatcher nests fail, and few fledge flycatchers. Cowbird parasitism significantly reduces hatching success and fledgling success leading to significantly lower reproductive success. Harris (1991) noted that some parasitized Willow flycatcher pairs on the SFKR renested several times, one as many as five times, before successfully fledging flycatcher young. He hypothesized that these cowbird-caused delays in fledging could negatively affect survival of the young. Our data show that cowbird parasitism does indeed cause delays in fledging, on average an 11-day delay in first egg dates of successful parasitized pairs when compared to successful unparasitized pairs. However, unlike other studies (e.g., Perrins and McCleery 1989, Hochachka 1990, Verhulst et al. 1995), we did not find any significant differences in the return rates of nestlings from early nests when compared to nestlings from late nests.

Although these negative impacts are widespread, it is difficult to quantify the population-level effects of this loss of productivity, and the long-term effects of parasitism will vary between sites. Parasitism rates averaging 50% in

TABLE 7. NEST SUCCESS OF PARASITIZED AND UNPARASITIZED SOUTHWESTERN WILLOW FLYCATCHER NESTS IN DIFFERENT PARTS OF ITS RANGE

		Parasitized		Unparasitized	
Region	Years	N	Nest success	N	Nest success
South Fork Kern River, CA	1989–1997	133	14%	190	54%
Various sites, AZ	1994–1996	31	13%	133	60%
Gila River Valley, NM	1997	6	0%	61	61%

TABLE 8. RETURN RATES OF BANDED NESTLING SOUTHWESTERN WILLOW FLYCATCHERS FROM EARLY VERSUS LATE NESTS ON THE SOUTH FORK KERN RIVER, KERN CO., CA

	Early			Late			
Year	No. banded	No. returned	Percent returned	No. banded	No. returned	Percent returned	Fisher's exact P
1989	16	5	31.0%	0	0	n/a	n/a
1990	8	0	0.0%	10	1	10.0%	0.56
1991	0	0	n/a	9	0	0.0%	n/a
1992	14	4	28.6%	16	1	6.0%	0.13
1993	17	5	29.4%	11	4	36.4%	0.50
1994	24	7	29.2%	11	3	27.3%	0.62
1995	23	10	43.5%	6	1	16.7%	0.24
1996	38	12	31.6%	0	0	n/a	n/a
Total	140	43	30.7%	63	10	15.8%	n/a

the Grand Canyon have created a "population" that is not stable, but is maintained only by an influx of individuals from other areas (Sogge et al. 1997). A demographic analysis conducted on the SFKR Willow Flycatcher population by Uyehara et al. (in press) suggests that parasitism levels over 10% reduce population growth. On the other hand, the Gila River Valley population in New Mexico appears to be stable or increasing over the last few years while experiencing on average an 18% parasitism level (Skaggs 1996, S. Stoleson, pers comm.). However, this population of flycatchers appears to be well over 100 pairs and thus may be able to tolerate higher levels of parasitism than the smaller SFKR population (Hall and Rothstein *this volume*). Although population-level effects vary and are not widely studied, high rates of parasitism threaten the stability of at least some Willow Flycatcher populations and probably limit potential rates of increase for others.

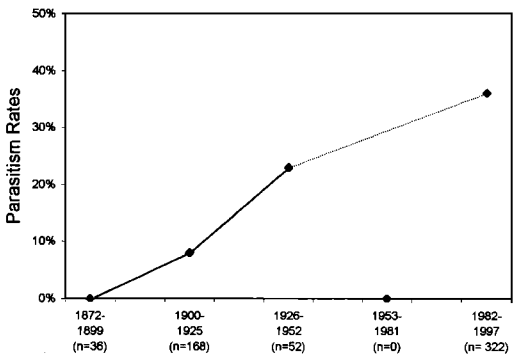

FIGURE 2. Historical cowbird parasitism rates of Southwestern Willow Flycatchers in Arizona and California, 1872–1997 (no data available 1953–1981).

THE ROLE OF PARASITISM IN THE FLYCATCHER'S DECLINE

Cowbird parasitism may have contributed to the Southwestern Willow Flycatcher's population decline, but because cowbird parasitism is strongly influenced by habitat destruction and degradation, as well as nearby human land-use patterns, it is not possible to show how much of the decline was due to cowbird parasitism as opposed to habitat destruction (Rothstein 1994). However, we believe that cowbird parasitism may have played a role in at least some local flycatcher declines and probably reduced the capability of flycatcher populations to recover after habitat was lost.

Several lines of evidence support this conclusion. First, flycatcher population declines occurred concurrently with increasing parasitism. Unitt (1987) summarizes the historical status of the Southwestern Willow Flycatcher, and found it to be widespread and abundant until the early 1900s. Historical data sources (Table 9) and Rothstein (1994) show that Brown-headed Cowbirds were uncommon in the Southwest prior to the 1860s, but had become fairly common by 1925.

Historical flycatcher nest data reflect an association between increasing size of regional cowbird populations and increasing rates of flycatcher parasitism; cowbird parasitism was very rare prior to the turn of the century, but increased thereafter. It is possible that nest collectors were biased towards or against parasitized nests; however, most modern (i.e., twentieth century) egg collectors and collections were not biased, and data from these sources probably present an accurate overview of the frequency of host parasitism at the time they were collected (L. Kiff, pers. comm.).

Thus, regional cowbird abundance increased as sympatric Southwestern Willow Flycatcher

TABLE 9. HISTORICAL ACCOUNTS OF COWBIRD PRESENCE IN THE SOUTHWEST (1858 TO 1945)

Author(s)	Year	States	Comments
Baird	1858	NV, UT, CA, CO, NM, and AZ	Compilation of zoological collection records from over a dozen survey parties exploring the West. Fewer than a dozen cowbird specimens were collected in the Southwest through the mid-1850's.
Linsdale	1936	NV	Information about Ridgeway collecting a male and female cowbird in 1867 in the Humboldt Valley at Oreana, Pershing Co., NV. The only other individual seen by him was an adult male collected by him in 1868 at Truckee Reservation, Wahoe, Co., NV.
Henshaw	1875	NV, UT, CA, CO, NM, and AZ	Report on the ornithological collections for Nevada, Utah, California, Colorado, New Mexico, and Arizona. He found that in Utah and Colorado, the cowbird was in "about the same abundance as in the eastern states" (meaning common, given data presented by Mayfield 1965). He also found that the cowbird did not appear to occur in great numbers in portions of Arizona.
Ridgeway	1880	UT	Found only two adult and one juvenile cowbirds during an expedition that covered major portions of three years and included a wide geographic region including the Great Basin/central Utah.
Fisher	1893	UT and CA	Report on the biological survey for The Death Valley Expedition. The author only mentions finding several cowbirds in the Lower Santa Clara Valley, Utah, a few in Pahranagat Valley, Utah, and shooting one male at Furnace Creek, Death Valley, California.
Bailey	1923	AZ	Author notes that in 1903, Swarth found cowbirds to be fairly abundant in the Santa Rita Mountains in southern Arizona but not as common as in the lowlands.
Swarth	1914	AZ	Author found that cowbirds were common and widespread along the Colorado and Gila Rivers and associated tributaries.
Woodbury and Russell	1945	AZ, NM, CO and UT (four corners area)	The authors state: "This cowbird nowhere appears to be common, but seems to be well distributed in small numbers in the lower altitudes."

populations decreased. This correlation, however, does not address how heavy the impact of parasitism has been on the flycatcher. As noted above, cowbird parasitism negatively impacts flycatcher reproductive success at many current breeding sites. It is reasonable to assume that, historically, parasitism had the same negative influence on the flycatcher's reproductive success as it does today. By the late 1920s, Willow Flycatchers in some areas in southern California suffered from heavy parasitism. Hanna (1928: 162) referring to an area in San Bernardino Co., writes, "The Traill Flycatcher, California Least Vireo and California Yellow Warbler suffer even more than this report would indicate. They not only have the most parasitized nests and the most Cowbird eggs per nest, but a large number of nests of these species were absolutely destroyed by the Cowbirds (at least I blame the destruction to them), and such nests were not considered in making the survey." In 1937, M.C. Badger commented on an identification card for an egg set collected at the Santa Clara River mouth (Ventura Co., CA), that cowbird eggs were "nearly always found in the nests of this species" (Unitt 1987). Cowbird parasitism almost certainly reduced flycatcher populations such as those described above.

Unfortunately, quantitative data do not exist to document the degree to which cowbird parasitism contributed to and/or prolonged the historical decline of the Southwestern Willow Flycatcher. However, increased cowbird parasitism coincided with decreasing flycatcher populations, some local populations were heavily parasitized, and parasitism probably affected flycatcher productivity then as it does now. Given this, we believe that cowbird parasitism, at the very least, played a role in the reduction of some local flycatcher populations and reduced the capacity for some flycatcher populations to recover once they were reduced due to habitat destruction or degradation.

MANAGEMENT OF PARASITISM

Cowbird control programs have reduced parasitism rates and stabilized or increased popu-

lations of several endangered species and can be an important tool in Willow Flycatcher management and recovery (Kepler et al. 1996, Rothstein and Cook in press, Whitfield et al. *this volume*). However, it is important to keep in mind that habitat destruction and modification are the primary causes of the decline of the Willow Flycatcher, and that high cowbird parasitism is a symptom of this problem (Unitt 1987; Robinson et al. 1993; Rothstein 1994; USFWS 1993b, 1995; Whitfield in press). Therefore, habitat acquisition, improvement and restoration must be given high priority and, wherever possible, be implemented along with cowbird control measures. Also, given the high variability of parasitism rates, it is important to evaluate each site separately before initiating a cowbird control program. Furthermore, because parasitism rates vary geographically and temporally, the degree of cowbird parasitism at one site cannot be predicted based on only a single year's data, or by extrapolating from other sites.

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