EFFECTS OF BROOD PARASITISM BY BROWN-HEADED COWBIRDS ON WILLOW FLYCATCHER NESTING SUCCESS ALONG THE KERN RIVER, CALIFORNIA

JOHN H. HARRIS, Biology Department, Mills College, 5000 MacArthur Blvd., Oakland, California 94613

Alteration and loss of riparian habitat have played a central role in the decline of riparian bird species (Gaines 1974, Remsen 1978, Laymon et al. 1987). However, the absence of certain species from seemingly suitable habitat (Gaines 1974) suggests that other factors may also be important. In his review of the historical riparian avifauna of the Sacramento Valley, Gaines (1974) suggested that 9 of 12 of the declining species, including the Willow Flycatcher (*Empidonax traillii*), were susceptible to and had probably been adversely affected by Brown-headed Cowbird (*Molothrus ater*) brood parasitism.

Brood parasitism by Brown-headed Cowbirds has been implicated in the decline of songbirds in eastern deciduous forests (Mayfield 1965, 1977a, Brittingham and Temple 1983) and in western riparian habitats (Gaines 1974, 1977, Goldwasser et al. 1980, Laymon 1987). Brown-headed Cowbirds increased their range with the clearing of forests and spread of intensive grazing and agriculture. These changes increased the amount of suitable foraging habitat available to cowbirds and rendered their host populations more vulnerable by reducing their numbers and fragmenting their habitat (Mayfield 1977a, Rothstein et al. 1980, Brittingham and Temple 1983, Laymon 1987). Riparian birds are especially susceptible to brood parasitism because their habitat is linear, ecotonal, often patchy, and frequently near pastures, stockyards, or agricultural fields. Thus the cowbird's favored feeding areas (heavily grazed pasture, stubblefields, livestock concentrations) are near its potential hosts in the riparian vegetation. Brown-headed Cowbirds commute from feeding areas to habitats with high host density (Rothstein et al. 1980, 1984, Stafford and Valentine 1985).

The Willow Flycatcher is one of many riparian bird species that have suffered serious declines in the southwestern United States (Gaines 1974, Serena 1982, Harris et al. 1987a,b). In recent years the Willow Flycatcher has been included on the Audubon Blue List (Arbib 1979, Tate 1981, 1986, Tate and Tate 1982), the U.S. Forest Service's Region 5 (California) Sensitive Species List, the U.S. Fish and Wildlife Service's Region 1 (California, Oregon, Washington, Idaho, Nevada) Sensitive Species List, and it was considered a Species of Special Concern by the California Department of Fish and Game beginning in 1978 (Remsen 1978). In California, where all Willow Flycatchers occur in isolated remnant populations (Serena 1982, Harris et al. 1987b, Unitt 1987), the species was recently listed as endangered by the California Fish and Game Commission. The Willow Flycatcher also is listed as an endangered species in Arizona. The southwestern subspecies (*E. t. extimus*) has been reduced to an estimated 500-1000 pairs in California, Arizona, New Mexico, Utah, Nevada and Baja California (Unitt 1987).

Early studies in lowland southern California showed that the Willow Flycatcher is a host for Brown-headed Cowbirds (Hanna 1928, Rowley 1930, Friedmann 1963). Friedmann (1963) reported 150 instances of parasitism of Willow Flycatchers, 41 of them in southern California. Hanna (1928) found more parasitized nests of Willow Flycatchers than of any other species, and commented on the difficulty of finding an unparasitized Willow Flycatcher nest. The decline of the Willow Flycatcher in central and coastal California coincided with the cowbird's range expansion in the 1920s and 1930s (as summarized by Gaines 1974, Garrett and Dunn 1981, Laymon 1987). Unfortunately, early studies did not report parasitism rates for Willow Flycatchers, nor did they follow nests through the breeding season; thus the responses of Willow Flycatchers to parasitism and the fledging success rate under parasitism remain poorly known for southwestern riparian habitats (Brown 1988). The incidence of parasitism observed in recently studied California montane meadow populations is low (Stafford and Valentine 1985, Valentine et al. 1988, Sanders and Flett 1989), suggesting that parasitism rate could be related to elevation or habitat differences.

The purpose of this investigation was to study the characteristics and success rate of Willow Flycatcher nests in a habitat representative of the former core, and remaining lowland portions, of the flycatcher's range in California. The study population (on the Kern River, Kern County, California), is the largest remaining Willow Flycatcher population documented in California (Harris et al. 1987b) and is one of the largest populations in the total range of the subspecies *E. t. extimus* (Unitt 1987).

METHODS

I conducted the study from 1 June through 15 August 1987 on The Nature Conservancy's Kern River Preserve, on the south fork of the Kern River upstream from Lake Isabella, Kern County, California. It includes a large area of mature riparian forest dominated by cottonwoods (*Populus fremontii*) and willows (*Salix laevigata* and *S. gooddingii*). I studied nesting success of Willow Flycatchers at two locations on the preserve: Mariposa Marsh, a marsh and willow thicket draining into the Kern River, and Slough Channel No. 4, a willow-lined slough near the preserve headquarters. Both sites are at 822 m (2630 feet) elevation.

At both sites the home ranges of singing males were searched for females and nests daily. I identified 12 territories based on daily observations of locations of singing males and the consistent use of specific singing perches throughout the breeding season. I checked nests three or four times weekly, minimizing the duration of nest checks. I noted the activities of the nesting pair (nest construction, brooding, response to parasitism, feeding of young) and observed the nest contents by using a small automobile side-mirror mounted on a pole. If an adult was sitting on a nest, I did not disturb the nest. I noted the plant species in which each nest was located, nest construction material, height of the nest over ground or water, distance to the edge of the willow clump, distance to the canopy top, and the percentage of ground covered with standing water in the pair's home range. I

collected these data after nesting was completed or the nest was abandoned.

RESULTS

Nests

Moist, low-lying areas and sloughs with dense willow thickets were the Willow Flycatcher's preferred nesting habitat. Many nests were around the ponds created by beaver dams. The nesting and foraging activities of Willow Flycatchers were frequently concentrated in openings within the canopy of willow thickets.

I located nests on 8 of the 12 territories. On three of the other territories, no nests or females were located despite repeated, intensive searching. Males in these territories also disappeared from the area earlier in the season than did males with nests, suggesting that the former were unmated. On the remaining territory, movements and vocalizations of the male suggested the presence of a female, but no nest was found. In addition to the nests at my two principal sites, I located another nest adjacent to the main river channel near the preserve headquarters and monitored the nest for the final three weeks of the study.

Table 1 Characteristics of Willow Flycatcher Nests

Subspecies[a]	Location	Nest Substrate	Mean and Range of Nest Height (m)	*N*	Source
E.t. traillii	Michigan	Dogwood (48%) Willow (15%) Elderberry (12%)	1.33 (0.61–2.82)	93	Walkinshaw (1966)
E.t. traillii	Ohio/ Nebraska	Dogwood (39%) Hawthorn (18%) Willow (12%)	1.37 (0.72–2.78)	80	Holcomb (1972)
E.t. brewsteri	British Columbia	Willow, Rose, Dogwood[b]	1.14 (0.68–2.62)	26	Stein (1963)
E.t. brewsteri	California	Willow (100%)	1.14 (0.70–1.75)	20	Sanders and Flett (1989)
E.t. brewsteri	California	Willow, Dogwood, Azalea[b]	1.49 (0.77–2.18)	22	Valentine et al. (1988, pers. comm.)
E.t. extimus	Entire range[c]	Willow (86%)	2.3 (0.60–5.50)	172	Unitt (1987)
E.t. extimus	Arizona	Tamarisk (100%)	3.3[d] (1.50–4.50)	12	Brown (1988)
E.t. extimus	California	Willow (100%)	2.52 (1.00–6.40)	19	This study

[a]Subspecific identity where not provided by the source was determined with reference to the review of Unitt (1987).
[b]Listed in order of importance from most frequently used to least frequently used.
[c]Review of nest characteristics from egg collection data throughout the subspecies' range in the southwestern U.S.
[d]Median nest height.

Table 2 Rates of Brood Parasitism and Acceptance of Cowbird Eggs by Willow Flycatchers[a]

Subspecies[b]	Location	Habitat	Parasitism Rate	Acceptance Rate	Source
E.t. adastus	Washington	Riparian willow/ Floodplain forest	4.5% (2/44)	50.0% (1/2)	King (1955)
E.t. adastus	Colorado	Riparian willow	40.7% (11/27)	18.2% (2/11)	Sedgwick and Knopf (1988)
E.t. traillii	Ohio Nebraska	Oldfields, hedges/ Riparian thickets	8.0% (7/88)	42.9% (3/7)	Holcomb (1972)
E.t. traillii	Michigan	Cornus/Elderberry/ Willow thickets	5.3% (5/94)	40.0% (2/5)	Walkinshaw (1966)
E.t. traillii	Michigan	Cornus/Elderberry/ Willow thickets	10.1% (33/325)	72.7% (24/33)	Berger (1967)
E.t. brewsteri	California	Montane meadow/ Willow thickets	0% (0/20)	—	Valentine et al. (1988)
E.t. brewsteri	California	Montane meadow/ Willow thickets	4.8% (1/21)	100% (1/1)	Sanders and Flett (1989)
E.t. extimus	Arizona	Riparian tamarisk	50.0% (4/8)	0% (0/4)	Brown (1988)
E.t. extimus	California	Riparian willow	68.0% (13/19)	46.2% (6/13)[c]	This study

[a]Studies conducted before the split of Willow and Alder Flycatchers are included only if the author clearly indicated that birds of the "fitz-bew" song type were involved.
[b]Subspecific identity where not provided by the source was determined with reference to the review of Unitt (1987).
[c]Cowbird eggs appeared in two of these nests after the hatching of Willow Flycatcher young.

I found 19 nests on the 8 territories, an average of 2.4 (range 1–6) nests per territory. Incidences of multiple nests within territories were all due to renesting attempts. All nests were in willows, mostly between forked branches (nesting has been reported recently in other plant species on the preserve, M. Whitfield pers. comm.). Nests were constructed of thistle fibers, strands of dried willow bark, grasses, animal hair, and the fluffy "cotton" borne by willow seeds. The average nest height was 2.52 m (±1.39 standard deviation, range 1.0–6.4 m). The average distance from the nest to the top of the canopy above the nest was 4.82 m (±2.89 s.d., range 1.0–10.5 m). The average distance to the outer perimeter of the willow clump containing the nest was 7.03 m (±4.27 s.d., range 1.0–15 m).

Seventy-four percent (14 of 19) of the nests were over water or mud. The summer of 1987 was very dry; all nests would have been over water during the previous year. All nests but one were near beaver ponds; the exception was the only nest more than 4 meters from water. The percentage of each territory covered by standing water at the beginning of the summer ranged from 70 to 100%.

Cowbird Parasitism

Thirteen of the nineteen nests (68%) were parasitized on seven of eight (88%) territories (Table 3). Three nests (16%) were unparasitized. Three (16%) were abandoned for unknown causes. Of these three nests with unknown fates, one loss coincided with heavy winds that apparently knocked down the nest. Two of the nests could have been parasitized; one of these was dismantled to construct a new nest, a behavior frequently observed with parasitized nests. Thus up to 80% of nests may have been parasitized.

Parasitized nests suffered a variety of fates (Table 3). Seven of the 13 parasitized nests (53%) were abandoned, with abandonment occurring on four of eight territories. In at least five of these cases the female dismantled the abandoned nest, using the material to build the next nest. The extreme case was exemplified by a pair at Mariposa Marsh that constructed six successive nests, finally fledging three young from the sixth nest. Three parasitized nests each fledged one cowbird and no flycatchers. One parasitized nest had two cowbirds near fledging when it was destroyed by an owl. Two nests parasitized late in the season successfully fledged Willow Flycatchers and no cowbirds. In one of these cases, a single cowbird egg was laid in a nest with four healthy nestling flycatchers (about 1 week old); one Willow Flycatcher nestling disappeared at this time, but three were fledged on 8 July. This was probably the first nesting attempt by this pair of Willow Flycatchers. In the other case, a second nesting attempt, a single cowbird egg was laid at about the flycatcher's hatching date (30 June). In this nest, one flycatcher egg was apparently removed at the time of parasitism, one nestling flycatcher was unusually small and died, the third nestling fledged on 15 July, and the cowbird egg did not hatch.

The three unparasitized nests were all successful. All of these nests were renesting attempts (second, third, and sixth attempts), fledging one, two, and three young, respectively. The sixth nest of a pair at Mariposa Marsh

Table 3 Fates of Willow Flycatcher Nests in the Kern River Preserve, 1987

Territory	Nest Number[a]	Flycatcher Eggs	Cowbird Eggs	Nest Fate (Fledge Date)
Slough Channel B	1	1	2	Abandoned (14 July)[b]
	2	2	1	Abandoned
	3	3	0	Fledged two flycatchers (13 August)
Slough Channel D	1	2	2	Lost to predator 9 July
	2	2	1	Fledged one cowbird (8 August)
Mariposa Marsh A	1	3	1	Abandoned (5 July)[b]
	2	1	1	Abandoned
	3	4	1	Abandoned
	4	?	?	Abandoned
	5	?	1	Abandoned
	6	3	0	Fledged 3 flycatchers (9 August)
Mariposa Marsh C	1	3	?	Abandoned
	2	1	0	Fledged 1 flycatcher (22 July)
Mariposa Marsh E	1	?	1	Abandoned
	2	3	1	Fledged 1 flycatcher (15 July)
Mariposa Marsh G	1	4	1	Fledged 3 flycatchers (8 July)
	2	2	1	Fledged 1 cowbird (10 August)[b,c]
Mariposa Marsh F	1	4	0	Probably knocked down by wind
River Channel A	1	1	1	Fledged 1 cowbird (30 July)

[a]In sequence of construction.
[b]Estimated date when young would have fledged from initial nests had nest not been abandoned.
[c]As the adults were not banded, the two successful broods in this territory may have had different parents.

fledged three young on 9 August. The young from their first nest would have fledged on 3 or 4 July. The second nest of a pair at Mariposa Marsh never had more than one egg. The single young fledged on 22 July. The young from this pair's first nest would have fledged on 7 or 8 July. The third successful unparasitized nest was along the Slough Channel and was the pair's third nesting attempt. This nest had three eggs, one of which did not hatch. The two young fledged on 13 August. Young from the first nest would have fledged on 12 or 13 July.

Three young cowbirds fledged from the 13 parasitized nests, an egg success rate of 20% (3 of 15 eggs).

DISCUSSION

Nests

Willow Flycatcher nests in this study were similar in their mode of construction and supporting plant species to those previously described in the literature (Table 1). Throughout its range, the Willow Flycatcher uses a variety of riparian shrubs and trees, principally willows (*Salix* spp.) and dogwoods (*Cornus* spp.). Nests are open cups supported by slender branches.

Some nest characteristics measured on the Kern River Preserve differ from those in other habitats (Table 1). The nest heights I observed in this study were within the range for the species, but higher than those in California montane meadow habitats (Table 1). The differences in nest height between my results and those of Sanders and Flett (1989) ($t = 4.31$, $df = 37$, $p < 0.05$) and Valentine et al. (1988) ($t = 3.32$, $df = 39$, $p < 0.05$) are both significant, reflecting the difference in height between the short, shrubby willows of montane meadows and the larger willows characteristic of a mature riparian forest.

The distance from the nest to the top of the willow canopy above the nest also differed from that reported in the literature, apparently for similar reasons. In my study, this distance (4.82 m, range 1–10.5 m) was substantially larger than that reported in montane meadows of the Little Truckee River (0.96 m, range 0.5–1.5 m, Sanders and Flett 1989) or the Shaver Lake region (1.19 m, range 0.51–1.85 m, Valentine et al. 1988). These differences are significant for both the Little Truckee River ($t = 6.03$, $df = 37$, $p < 0.01$) and the Shaver Lake region ($t = 5.29$, $df = 35$, $p < 0.01$).

Another interesting contrast is provided by measurements of the distance from the nest to the outer perimeter of the willow clump. Willow Flycatchers construct their nests near the edge of willow clumps or near streams (King 1955, Kings River Conservation District 1985, Flett and Sanders 1987, Valentine et al. 1988). In my study, the distance to the nearest willow clump edge was greater (7.03 m, range 1–15 m), than that observed on the Little Truckee River (2.3 m, range 0.6–7.5 m, $t = 4.64$, $df = 37$, $p < 0.01$, Sanders and Flett 1989). This difference also reflects habitat differences; on the Kern River, Willow Flycatcher nests were in large openings under the willow canopy, thus they could be near an edge within the canopy but far from the outer edge of the willow clump. Therefore a different nest microhabitat results from similar behavior in structurally different habitats.

In montane meadows, the habit of constructing nests near the edges of willow clumps or near cattle trails (Sanders and Flett 1989) places Willow Flycatcher nests at risk from destruction by browsing livestock or by wind (Stafford and Valentine 1985, Taylor and Littlefield 1986, Valentine et al. 1988, Sanders and Flett 1989). On the Kern River and in similar riparian habitats, the placement of nests in spaces within the canopy may reduce the risk of knockdown, particularly if the depth of water beneath the nests discourages cattle use of the habitat.

Nest Success and Cowbird Parasitism

The Willow Flycatcher is subject to severe brood-parasitism by Brown-headed Cowbirds on the Kern River. The rate of nest parasitism, at least 68%, was higher than any previously reported (Table 2), but is similar in magnitude to rates observed along the Colorado River (Brown 1988) and in montane riparian habitat in Colorado (Sedgwick and Knopf 1988). These studies and my results refute the suggestion by Friedman et al. (1977) that western Willow Flycatchers are parasitized at rates lower than are eastern populations. High parasitism rates for Willow Flycatchers nesting in lowland southwestern riparian habitats are also supported by anecdotal historical data and egg collections (Hanna 1928, Rowley 1930, Friedman 1963), and by the coincidence of the species' decline with the spread of cowbirds in California (Gaines 1974, Laymon 1987).

Brood parasitism was the leading cause of nest failure during my study. Six young flycatchers fledged from three unparasitized nests, while four fledged from two of 13 parasitized nests. Thus ten Willow Flycatchers fledged on the eight territories with nests: a rate of 1.25 young per nesting pair or 0.83 per singing male detected in my study area. Forty-one Willow Flycatcher eggs were found in the study areas; thus the egg success rate was 24.4%. However, other eggs were probably removed, because unparasitized Willow Flycatcher clutches usually contain three or four eggs (King 1955, Walkinshaw 1966, Holcomb 1972, Kings River Conservation District 1985). I estimate that a minimum of eight additional eggs may have been removed, so the actual egg success rate was probably closer to 20%. This egg success rate is lower than that in midwestern populations parasitized at lower rates. Egg-to-fledging success rates of 81.4% (Berger 1967) and 65.6% (Walkinshaw 1966) have been reported from populations with parasitism rates of 10.1% and 5.3%, respectively. King (1955) reported a fledging success rate of 44.6% of hatched eggs from a population with a 4.5% parasitism rate. The percentage of nests fledging young from the heavily parasitized population (40.7%) in Colorado was a surprisingly high 40.7%. Successful renesting following abandonment of parasitized nests was responsible for this success rate (Sedgwick and Knopf 1988), but the overall egg success rate may have been lower, as renesting attempts usually result in smaller clutches (Holcomb 1974).

Successful Willow Flycatcher broods may have been negatively affected by the delays in fledging date caused by abandonment and renesting. Fledging dates ranged from 11 July to 13 August. Estimated or actual fledging dates of initial nesting attempts were from 1 to 15 July. Cowbird

parasitism resulted in fledging dates for renesting attempts of 1 to 15 August. Thus successful nesting of parasitized Willow Flycatchers was delayed by 2–4 weeks. Delay in fledging date could result in poor preparation for migration. Alternatively, late fledging may be an indication that Willow Flycatchers could produce two broods within a season if unparasitized (M. Whitfield, pers. comm.), although double broods have not been reported previously.

Other causes of nest failure may lower nest success rates to levels similar to that of this study. On the Little Truckee River, a mid-July snow storm was the primary cause of mortality during 1987, a year in which only 19% egg-to-fledging success was achieved (Flett and Sanders 1987, Sanders and Flett 1989). During the previous year, the success rate was 45%. Stafford and Valentine (1985), and Valentine et al. (1988) reported egg-to-fledging rates of 25% and 38% in two different years in the Shaver Lake area, Fresno County. Primary sources of egg failure were livestock knocking down nests and egg inviability. Clearly Willow Flycatcher populations may be limited by different factors depending on location and habitat. Brown-headed Cowbird brood parasitism may often be the most important limiting factor in low-elevation riparian habitats like the Kern River Preserve.

The most common response by Willow Flycatchers to brood parasitism in this study was abandonment of parasitized nests, followed by attempts to renest (7 of 13 parasitized nests). Nest abandonment in response to brood parasitism has also been reported in most other studies of cowbird-parasitized Willow Flycatchers (King 1955, Berger 1967, Holcomb 1972, 1974, Brown 1988, Sedgwick and Knopf 1988). Abandonment appears to be a beneficial strategy in that renesting attempts may eventually avoid parasitism (Sedgwick and Knopf 1988, this study), but the effects of the delay in fledging date are unknown. Some studies have reported burial of the cowbird eggs or construction of a new nest bottom over cowbird eggs (Walkinshaw 1966, Berger 1967, Holcomb 1972, Brown 1988, Sedgwick and Knopf 1988), although this response is never as frequent as nest abandonment or acceptance of cowbird eggs. Brown (1988) reported possible rejection of cowbird eggs based on discovery of cowbird egg fragments below a Willow Flycatcher nest. Comparison of reported acceptance rates is difficult because of differences between studies in the frequency of nest observation and because of small sample sizes in some studies (Table 2). Populations parasitized at a higher rate (>15%), however, accept cowbird eggs less often (8 of 28 nests, 28.6%) than those parasitized at a lower rate (31 of 48 nests, 64.6%). This difference is significant ($X^2 = 8.15$, $df = 1$, $p < .005$), suggesting that abandonment and other responses may become more likely as the parasitism rate in a population increases. Proximate mechanisms for such behavior remain unknown for this host species.

This study supports the hypothesis that parasitism in the Sierra Nevada may be indirectly related to elevation (Rothstein et al. 1980, Stafford and Valentine 1985). The parasitism rate observed on the Kern River Preserve differed sharply (Table 2) from that observed during two years of study in the Little Truckee River region (elevation 2010 m, Flett and Sanders 1987, Sanders and Flett 1989), and several years in the Shaver Lake region

(elevation 1731–2097 m, Kings River Conservation District 1985, Stafford and Valentine 1985, Valentine et al. 1988). Only a single parasitized nest was found during these two studies. This low parasitism rate has been hypothesized to result from the mid-July exodus of Brown-headed Cowbirds from high elevations combined with mid-summer breeding of the Willow Flycatcher in California (Rothstein et al. 1980, Verner and Ritter 1983, Stafford and Valentine 1985). The studies near Shaver Lake indicated that Brown-headed Cowbird egg-laying preceded the arrival and nesting of most Willow Flycatchers. Farther south and at lower elevations, cowbirds may be resident for longer periods and have more extended breeding seasons (Rothstein et al. 1980, Laymon 1987), and Willow Flycatchers arrive earlier in the spring (Garrett and Dunn 1981). Along the Kern River, Brown-headed Cowbirds decrease by the end of July (S. Laymon pers. comm.). Cowbird egg-laying took place from 9 to 20 July during my study, overlapping the flycatcher's initial nesting attempts.

Management Implications

The very high rate of Brown-headed Cowbird parasitism and low egg success rate of Willow Flycatchers at the Kern River Preserve during 1987 suggests that brood parasitism may affect the ability of Willow Flycatchers to recolonize or increase in lowland riparian habitat, even if efforts are made to restore suitable habitat. The population at the Kern River Preserve seems not to have fully occupied the suitable habitat present. Such a high parasitism rate is of great concern because of the endangered status of the species in California and of the subspecies *E. t. extimus* throughout its range (Unitt 1987).

Possible management strategies to reduce Brown-headed Cowbird parasitism include trapping of cowbirds and managing habitat to reduce cowbird feeding opportunities and success rate. Trapping of cowbirds may be an effective short-term strategy where cowbirds concentrate (Mayfield 1977b, Goldwasser et al. 1980, Laymon 1987). Willow Flycatchers increased from 5 to 17 singing males from 1981 to 1986 during a cowbird removal program designed to benefit the Least Bell's Vireo (*Vireo bellii pusillus*) on the Santa Margarita River, San Diego County (Unitt 1987). Because of the intensive effort and cost of such a program, this strategy should be applied where conditions contribute to success of trapping and where there are key populations of threatened species. At the Kern River Preserve the cowbird's feeding and nesting areas are adjacent, concentrating the cowbirds in a relatively small area and favoring trapping success. On the other hand, the surrounding habitat is arid and probably the density of hosts in it is much lower, so cowbirds may travel from a considerable distance (Rothstein et al. 1984) to search for hosts in the high-quality riparian habitat of the preserve. It might be difficult to remove enough cowbirds to reduce parasitism rates if the cowbirds are traveling to the preserve from great distances. In the short run, cowbird trapping and egg removal should be implemented to relieve Willow Flycatcher populations and evaluate the effect of Brown-headed Cowbirds on fledging success and population density.

Habitat management represents the best long-term strategy for cowbird control. Fragmentation and disturbance of habitat are associated with

higher parasitism rates (Rothstein et al. 1980, Brittingham and Temple 1983, Airola 1986). The linear nature of riparian habitat patches make the nests of riparian birds especially vulnerable to cowbirds (Bleitz 1956, Laymon 1987). Most willow thickets at the Kern River Preserve are close to very short grazed grassland or stubblefields. Increasing the width of riparian corridors by revegetation and reducing grazing in the vicinity of the riparian strip is an ongoing process at the preserve that will allow the usefulness of riparian habitat modification in reducing parasitism to be evaluated. Reduction of grazing intensity would allow grasses to grow to a height that inhibits the cowbird's foraging. Further benefits in areas where low willows provide nesting habitat (M. Whitfield pers. comm.) would include reduction of browsing and disturbance of foliage at the height of Willow Flycatcher's nests (Stafford and Valentine 1985, Flett and Sanders 1987, Valentine et al. 1988).

SUMMARY

This study shows that the Willow Flycatcher's nesting microhabitat and nest characteristics in lowland riparian forests differ from those in montane meadows. Nests on my study area were higher and tended to be located within the willow canopy, on the edge of within-canopy spaces. These differences are probably due to the difference between my study area and montane meadow sites in height and canopy structure of willows.

Willow Flycatchers on the Kern River are subject to a high rate of brood parasitism by Brown-headed Cowbird. Brood parasitism occurred in at least 68% of nests and was the leading cause of nest failure during my study. As a result, the overall egg success rate was low (at most 24.4%). The most common response of Willow Flycatchers to parasitism was abandonment of the nest followed by renesting attempts. This strategy was often successful, but fledging dates for some pairs were delayed two to four weeks.

My study supports the hypothesis that Brown-headed Cowbird brood parasitism rate is indirectly related to elevation. Overlap between the breeding seasons of Brown-headed Cowbirds and Willow Flycatchers is greater on the Kern River than at higher-elevation montane meadows, where cowbirds tend to depart near the beginning of flycatcher nesting.

The high rate of cowbird parasitism observed in my study is of concern because of the endangered status of the Willow Flycatcher. Possible management strategies to alleviate this situation include habitat restoration, reduction of grazing to reduce cowbird feeding habitat and nest destruction, and cowbird trapping. Habitat restoration and reduction of grazing are preferred long-term strategies, because they reduce the suitability of habitats for cowbird feeding near riparian areas and because they hinder the ability of cowbirds to locate hosts by reducing the amount of habitat edge relative to habitat area. Trapping of cowbirds or egg removal may be useful short-term strategies to provide immediate relief to critical populations of Willow Flycatchers.

Questions remaining for future study include the effect on parasitism rate of habitat differences within lowland riparian forests, differences in parasitism rates between natural and artificial revegetation sites, and the extent

of year-to-year variation in parasitism. These issues, which could influence management strategies for the species, may be clarified by ongoing studies at the Kern River Preserve (M. Whitfield, pers. comm.).

ACKNOWLEDGMENTS

This study was supported in part by a Mills College Faculty Development Grant. Susan Martinez and Minh Kelly assisted with field work. Advice, encouragement, and companionship in the field were kindly provided by Mary Halterman, Chuck Hunter, Steve Laymon, Ronald Schlorff, Reed Tollefson, and Mary Whitfield. Rick Hewett provided access and support at The Nature Conservancy Kern River Preserve. I am grateful to reviewers Bryan Brown, Steve Laymon, and Philip Unitt, and to the following persons who commented on earlier drafts of this manuscript: Dan Airola, Ted Beedy, Steve Laymon, Ron Schlorff, Susan Sanders, Jamie Uyehara, Mary Whitfield, and Brad Valentine.

LITERATURE CITED

Airola, D. A. 1986. Brown-headed Cowbird parasitism and habitat disturbance in the Sierra Nevada. J. Wildlife Mgmt. 50:571–575.

Arbib, R. 1979. The Blue List for 1980. Am. Birds 33:830–835.

Berger, A. J. 1967. Traill's Flycatcher in Washtenaw County, Michigan. Jack-Pine Warbler 45:117–123.

Bleitz, D. 1956. Heavy parasitism of Blue Grosbeaks by Cowbirds in California. Condor 58:236–238.

Brittingham, M. C., and Temple, S. A. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31–35.

Brown, B. T. 1988. Breeding ecology of a Willow Flycatcher population in Grand Canyon, Arizona. W. Birds 19:25–33.

Flett, M. A., and Sanders, S. D. 1987. Ecology of a Sierra Nevada population of Willow Flycatchers. W. Birds 18:37–42.

Friedmann, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

Friedmann, H., Kiff, L. F., and Rothstein, S. I. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. Smithsonian Contr. Zool. 235.

Gaines, D. 1974. A new look at the nesting riparian avifauna of the Sacramento Valley, California. W. Birds 5:61–80.

Gaines, D. 1977. Birds of the Yosemite Sierra. California Syllabus, Oakland.

Garrett, K., and Dunn, J. 1981. Birds of Southern California: Status and Distribution. Los Angeles Audubon Soc., Los Angeles.

Goldwasser, S., Gaines, D. A., and Wilbur, S. 1980. The Least Bell's Vireo in California: A de facto endangered race. Am. Birds 34:742–745.

Hanna, W. C. 1928. Notes on the Dwarf Cowbird in southern California. Condor 30:161–162.

Harris, J. H., Sanders, S. D., and Flett, M. A. 1987a. Willow Flycatcher surveys in the Sierra Nevada. W. Birds 18:27–36.

Harris, J. H., Sanders, S. D., and Flett, M. A. 1987b. The status and distribution of the Willow Flycatcher in the Sierra Nevada: Results of the 1986 survey. Wildlife Mgmt. Div., Admin. Rep. 87-2, Calif. Dept. Fish and Game.

Holcomb, L. C. 1972. Traill's Flycatcher breeding biology. Nebr. Bird Rev. 40:50–68.

Holcomb, L. C. 1974. The influence of nest building and egg laying behavior on clutch size in renests of the Willow Flycatcher. Bird-Banding 45:320–325.

King, J. R. 1955. Notes on the life history of Traill's Flycatcher (*Empidonax traillii*) in southeastern Washington. Auk 72:148–173.

Kings River Conservation District. 1985. Studies of the Willow Flycatcher in the central Sierra Nevada conducted during 1983 and 1984. Research Rep. 85-017, Kings River Conservation District.

Laymon, S. A. 1987. Brown-headed Cowbirds in California: Historical perspectives and management opportunities in riparian habitats. W. Birds 18:63–70.

Laymon, S. A., Beedy, E. C., Franzreb, K., and Gustafson, J., eds. 1987. Management and preservation of endangered birds in riparian ecosystems. Proceedings of a symposium, Cooper Ornithological Society. W. Birds 18:1–96.

Mayfield, H. F. 1965. The Brown-headed Cowbird, with old and new hosts. Living Bird 4:13–28.

Mayfield, H. F. 1977a. Brown-headed Cowbird: Agent of extermination? Am. Birds 31:107–113.

Mayfield, H. F. 1977b. Brood parasitism: Reducing interaction between Kirtland's Warbler and Brown-headed Cowbird, in Endangered Birds: Management Techniques for Preserving Threatened Species (S. A. Temple, ed.), pp. 85–91. Univ. of Wisc. Press, Madison.

Remsen, J. V., Jr. 1978. Bird species of special concern in California. Nongame Wildlife Investigations Rep. 78-1, Calif. Dept. Fish and Game.

Rothstein, S. I., Verner, J., and Stevens, E. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97:253–267.

Rothstein, S. I., Verner, J., and Stevens, E. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic Brown-headed Cowbird. Ecology 65:77–89.

Rowley, J. S. 1930. Observations on the Dwarf Cowbird. Condor 32:130.

Sanders, S. D., and Flett, M. A. 1989. Ecology of a Sierra Nevada population of Willow Flycatchers (*Empidonax traillii*), 1986–87. Wildlife Mgmt. Div., Admin. Rep. 88-3, Calif. Dept. Fish and Game.

Sedgwick, J. A., and Knopf, F. L. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90:253–256.

Serena, M. 1982. The status and distribution of the Willow Flycatcher (*Empidonax traillii*) in selected portions of the Sierra Nevada, 1982. Wildlife Mgmt. Branch Admin. Rep. 82-5, Calif. Dept. Fish and Game.

Stafford, M. D., and Valentine, B. E. 1985. A preliminary report on the biology of the Willow Flycatcher in the central Sierra Nevada. Cal-Neva Wildlife Trans.. pp. 66–77.

Stein, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatcher. Proc. Am. Philos. Soc. 107:21–50. Tate, J. 1981. The Blue List for 1981. Am. Birds 35:3–10.

Tate, J. 1986. The Blue List for 1986. Am. Birds 40:227–236.

Tate, J., and Tate, D. J. 1982. The Blue List for 1982. Am. Birds 36:126–135.

Taylor, D. M., and Littlefield, C. D. 1986. Willow Flycatcher and Yellow Warbler response to cattle grazing. Am. Birds 40:1169–1173.

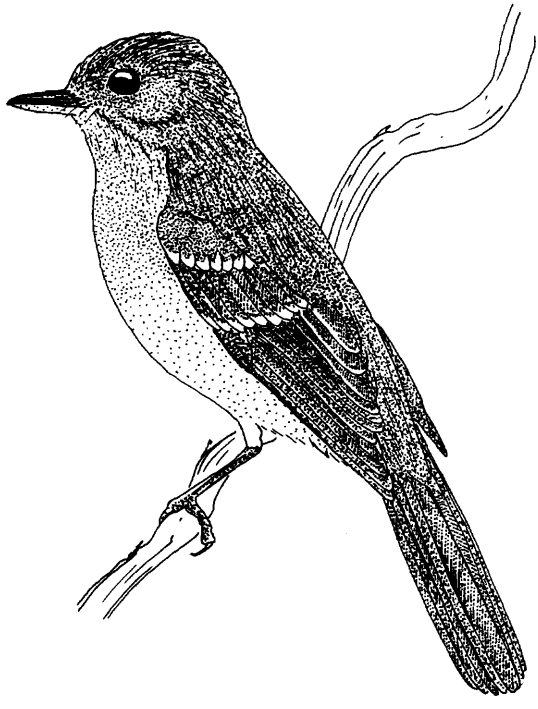
Unitt, P. 1987. *Empidonax traillii extimus*: An endangered subspecies. W. Birds 18:137–162.

Valentine, B. E., Roberts, T. A., Boland, S. P., and Woodman, A. P. 1988. Livestock management and productivity of Willow Flycatchers in the central Sierra Nevada. Trans. W. Section, Wildlife Soc. 24:105–114.

Verner, J., and Ritter, L. V. 1983. Current status of the Brown-headed Cowbird in the Sierra National Forest. Auk 100:355–368.

Walkinshaw, L. H. 1966. Summer biology of Traill's Flycatcher. Wilson Bull. 78:31–46.

Accepted 11 January 1991



Willow Flycatcher *Sketch by Eric Lichtwardt*