STATUS AND BREEDING ECOLOGY OF THE SOUTHWESTERN WILLOW FLYCATCHER IN THE GRAND CANYON

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Empidonax traillii extimus is one of several recognized subspecies of the Willow Flycatcher (Unitt 1987, Browning 1993), a neotropical migrant that breeds across much of North America. This southwestern race is a riparian obligate, nesting in dense patches of willow (*Salix* sp.), willow-cottonwood (*Populus* sp.), or other similarly structured habitats. In some areas of the Southwest, it nests in dense stands of tamarisk (*Tamarix* sp.). Willow Flycatchers were once widespread and locally common in the Southwest (Unitt 1987) but have declined to the point that *E. t. extimus* was listed as an endangered subspecies in 1995 (USFWS 1995).

Southwestern Willow Flycatchers have consistently nested along the Colorado River in the Grand Canyon in recent years. Reaching most portions of the Colorado River from Lee's Ferry downstream to Lake Mead was difficult and expensive prior to the construction and operation of Glen Canyon Dam in 1963, so information on the flycatcher's historical status and distribution in the Grand Canyon region is limited. The first record is of a single male collected at Lee's Ferry (where access was relatively easy) in 1909 (Woodbury and Russell 1945). The Lee's Ferry area also produced several other records, including a specimen collected on 7 June 1933 (Brown 1988), a used nest in the willows on 11 August 1935 (Woodbury and Russell 1945), and four adults (two male, one female, and one of unknown sex) collected by C. M. White on 29 June 1961 (University of Utah Museum specimen numbers 16718–16721). Historical records below Lee's Ferry are few: one was collected on 2 September 1931 by Vernon Bailey along the river corridor near Lava Canyon (McKee 1931), approximately 105 km downstream of Lee's Ferry, and another was taken at the confluence with the Little Colorado River on 17 June 1953 (Monson 1953). Willow Flycatchers were probably never common breeders in the Grand Canyon below Lee's Ferry because before Glen Canyon Dam was built this stretch of the river was subject to annual floods that scoured the river's edge and prevented the establishment of large patches of willow/cottonwood/tamarisk habitat (Turner and Karpiscak 1980). As recently as the 1970s, only one nesting pair was known in the Grand Canyon (Carothers and Sharber 1976).

In contrast, above Lee's Ferry where the Colorado River flowed through Glen Canyon and along the tributary San Juan River, Willow Flycatchers were relatively common summer residents (Woodbury and Russell 1945, Behle and Higgins 1959). Here, the river dropped less steeply and moved more slowly, allowing the development of extensive stands of dense riparian habitat well suited for breeding flycatchers (Woodbury and Russell 1945). During a single census conducted on 8 August 1938, in one willow patch 68 km above Lee's Ferry, Woodbury and Russell (1945)

Behle and Higgins 1959). Here, the river dropped less steeply and moved more slowly, allowing the development of extensive stands of dense riparian habitat well suited for breeding flycatchers (Woodbury and Russell 1945). During a single census conducted on 8 August 1938, in one willow patch 68 km above Lee's Ferry, Woodbury and Russell (1945) detected eight flycatchers, more than the cumulative total historically recorded in the 450 km of river corridor downstream of Lee's Ferry to Lake Mead. Unfortunately, this habitat was inundated and destroyed when Lake Powell filled between 1964 and 1980 (Stevens 1983).

Brown (1988, 1991) documented the distribution and abundance of the Willow Flycatcher in the upper Grand Canyon from 1982 to 1991 and described how post-dam increases in riparian vegetation may have provided habitat for increased numbers of breeding flycatchers. From 1982 to 1991, the number of singing flycatchers detected each year varied from 2 to 11, with a maximum of four nests found in any one year (Brown 1988, 1991). The flycatchers bred at only four sites scattered over 40 km of river, where relatively wide, slow-moving stretches with associated eddies or backwater sloughs supported a structurally varied canopy of tamarisk-dominated vegetation near the nest site (Brown and Trosset 1989). Brown (1994) found that flycatchers breeding in the canyon were subject to very high rates of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*).

Although the Willow Flycatcher population in the canyon is small, it is of scientific and management interest because it is one of the longest continuously monitored populations in the Southwest. It is also subject to potential human-related disturbances from recreational impacts and habitat changes brought about by the operation of Glen Canyon Dam. Here we report the results of an additional five years (1992–1996) of intensive flycatcher research and monitoring efforts in the Grand Canyon. We present new information on patterns of distribution, habitat characteristics, population trends, productivity and breeding ecology, and details of an observation of a female singing.

METHODS

From 1992 to 1996, we conducted 838 flycatcher surveys at 182 different habitat patches along the Colorado River in the Grand Canyon. At least four survey trips were conducted each year, and all patches were surveyed at least twice per year. Surveys were conducted from mid-May through July, and included riparian patches from just below Glen Canyon Dam downstream to the boundary between Grand Canyon National Park and Lake Mead National Recreation Area (Figure 1). Sites were named according to their location in river miles (RM) relative to Lee's Ferry, following Stevens' (1983) designations. We surveyed primarily from 05:00 to 10:00 daily, using the protocol of Tibbitts et al. (1994), which involves using a tape player to broadcast taped flycatcher songs to elicit a singing response from any nearby territorial flycatcher. Surveyors walked through, or adjacent to, surveyed habitats whenever possible. Where terrain or dense vegetation prohibited walking, we surveyed from boats drifting slowly past habitat patches.

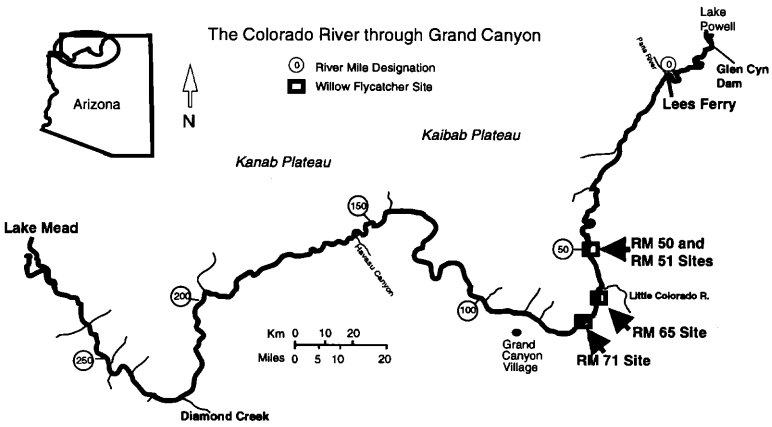

Figure 1. Distribution of Southwestern Willow Flycatcher breeding sites along the Colorado River in the Grand Canyon, Arizona, 1992–1996. RM refers to the river mile designation for that site.

We also monitored flycatcher nesting efforts at all four known breeding sites between 74 and 114 km downstream of Lee's Ferry. Extra time was spent at breeding sites to determine the flycatchers' number and sex, their approximate territories (by recording activity patterns on aerial photographs of each site), and to record their behavior. Nests were inspected by means of binoculars, mirror-poles, and micro-video cameras, and we noted clutch size, number and age of young, and presence of cowbird eggs or young. For each nest, we recorded the species of nest plant, height of nest plant and nest, distance to top of canopy over the nest, and horizontal distance from the nest to the closest surface water and the closest edge of the habitat patch. At all patches surveyed and territories monitored, we also recorded the presence of cowbirds, noted cowbird behavior, and recorded any flycatcher response. Statistical analyses were conducted using SPSS software, and unless otherwise noted values reported are the mean plus or minus one standard deviation.

RESULTS

Abundance

Resident Breeders. The breeding population of flycatchers in the Grand Canyon continues to be small (mean 2 ±1 pairs/yr) with no clear trend (Figure 2). The high count of four pairs (in 1994) followed a year in which no young were fledged from the study areas, suggesting that at least some of the new breeders in 1994 came from other populations. Depending on the year, one or two breeding pairs were found at one or more of the sites at RM 50, RM 51, and RM 71. In 1993, one patch contained a polygynous male with

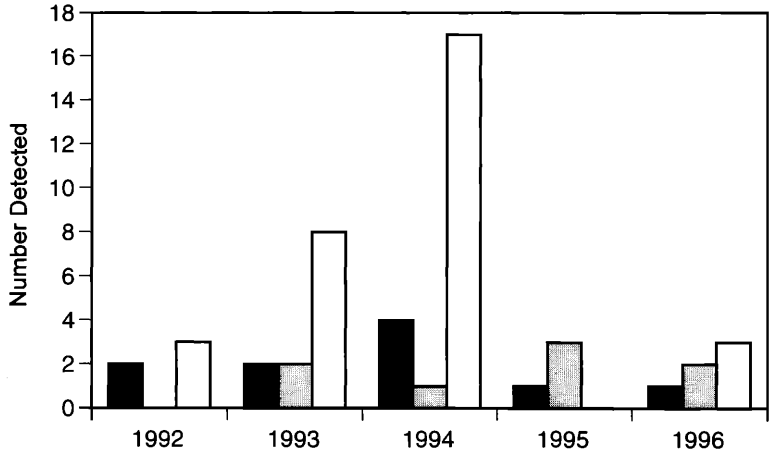

Figure 2. The number of Willow Flycatchers detected each year during surveys in the Grand Canyon, 1992–1996. Black bars, breeding pairs; gray bars, territorial unpaired males; white bars, migrants.

two concurrently nesting females (this polygynous trio is treated as one pair in all subsequent analyses).

Unpaired Territorial Males. In all years except 1992, we found one or more male flycatchers that established territories but did not secure a mate and breed (Figure 2). Each of these unpaired males was present on its territory during multiple surveys from mid-May and early June through at least early July. They were typically very vocal and responsive to the survey tape, at least through late June. Overall, the mean number of unpaired males each year (2 ± 0.8) was the same as the mean number of breeding pairs, although the two were not correlated. Unpaired males accounted for 0 to 75% of the territories in a given year, and 44% of all territories detected over the course of our study.

Migrants. We defined a migrant as any flycatcher that was detected on only one survey and absent on previous and subsequent surveys at the same site. In some cases, migrants responded strongly to the survey tape, in much the same manner as territorial birds. In other cases, migrants responded with only a few songs, and sometimes took several minutes to do so. The number of migrants varied greatly from year to year (Figure 2), with a maximum of 17 in 1994. The greatest number of migrants was detected in mid-May, with declining numbers present through mid-June (Figure 3).

Floaters. We detected three flycatchers that could not readily be classified as either territorial or migrants, which we designate as non-territorial floaters (Gill 1995). One floater was present for two days (18–19 June 1992) 308 km downstream of Lee's Ferry (RM 191) but not observed on subsequent surveys. Another was found singing spontaneously and continuously on the mornings of 17 and 18 June 1993 near the Lake Mead/Grand Canyon

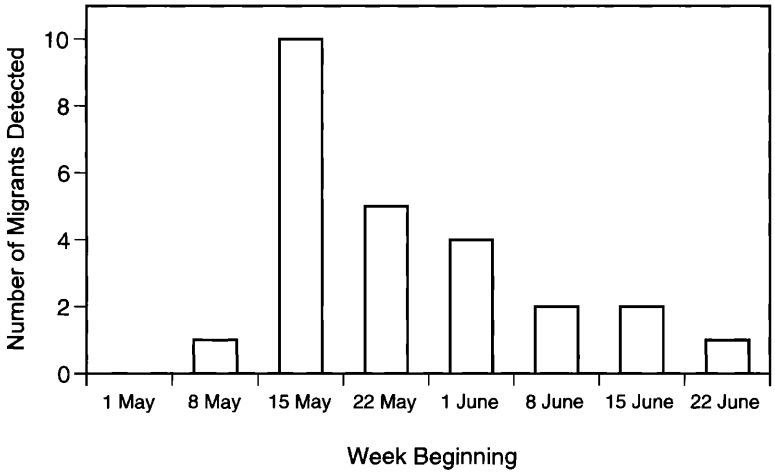

Figure 3. The total number of migrant Willow Flycatchers detected along the Colorado River in the Grand Canyon, 1992–1996.

boundary (RM 276) but was not seen during surveys three days before or two weeks after. It appeared that this flycatcher may have tried to establish a territory but did not remain long enough for us to classify it as a unpaired territorial male. The other floater was captured 76 km below Lee's Ferry (RM 47) on 9 July 1993, well past the time when migrants would be expected (Unitt 1987). However, intensive surveys before and after the capture found no resident flycatchers at this site.

Distribution and Habitat Use

Willow Flycatchers were detected at 21 sites along the river corridor from 18 km above (RM −11) to 114 km below Lee's Ferry (RM 71) and at four sites from 270 km (RM 168) to 477 km (RM 296) downstream of Lee's Ferry. None were detected in the middle reach of the river, where woody riparian vegetation is relatively uncommon (Turner and Karpiscak 1980). The flycatchers bred at only three sites (RM 50, RM 51, and RM 71; Figure 1); an unpaired male established a territory at RM 65 but did not breed during the time it was there (1994 and 1995). Only migrants and floaters were detected at the other sites.

We found flycatcher territories in the tamarisk-dominated riparian vegetation along the river corridor but not in the mesquite- (*Prosopis juliflora*), acacia- (*Acacia greggii*), and hackberry- (*Celtis reticulata*) dominated habitats higher on the slopes. The area of tamarisk-dominated habitat at breeding sites ranged from 0.6 to 0.9 ha (Table 1), but the flycatchers used only a portion of the habitat patch. Territory sizes were variable, and the largest territory was that of the unpaired male at RM 65 (Table 1).

Table 1 Area of Riparian Habitat and Associated Territories at Willow Flycatcher Breeding Sites along the Colorado River in the Grand Canyon, 1992–1996

Site	Size of riparian habitat patch (ha)	Territory size (ha)
RM 50	0.6	0.1
		0.06
		0.2
RM 51	0.6	0.1
		0.07
RM 65[a]	0.7	0.5
RM 71	0.9	0.12
		0.08
Mean ± SD	0.7±0.14	0.16±0.15
		0.10±0.05[b]

[a]Occupied by a non-mated territorial male. All other territories included breeding pairs.
[b]Value excludes the unpaired male's territory from RM 65.

Nests and Nest Placement

We found only a few nests each year (mean 3.4 ± 3.2, range 1–9; Table 2, Figure 4). Replacement nests (following failed earlier attempts) accounted for 7 of 17 nests. All nests were placed in tall (≥ 5 m) tamarisk, within 30 m of surface water and no more than 25 m from the nearest edge of the habitat patch (Table 3). Nest height was significantly correlated with nest plant height (Pearson's $R^2 = 0.79$, $p < 0.01$). Concurrent nests in adjoining territories were as close as 15 m apart. Replacement nests were built 5–24

Table 2 Nesting Effort and Nesting Success of Southwestern Willow Flycatchers Breeding along the Colorado River in the Grand Canyon, 1992–1995.

	1992	1993	1994	1995	1996	Total
Breeding pairs	2	2	4	1	1	na
Nest attempts	2	3	9	1	2	17
Successful nests	1 (50%)	0 (0%)	0 (0%)	1 (100%)	1 (50%)	3 (18%)
Parasitized nests	0 (0%)	3 (100%)	4 (44%)	1[a] (100%)	0 (0%)	8 (47%)
Nests failed, unknown cause	1 (50%)	0 (0%)	5 (56%)	0 (0%)	1 (50%)	7 (41%)
Young fledged	1–3	0	0	1–2	1–2	3–7

[a]When first checked, this nest contained only a single cowbird egg. Later checks revealed the cowbird egg gone or buried and three flycatcher eggs in its place.

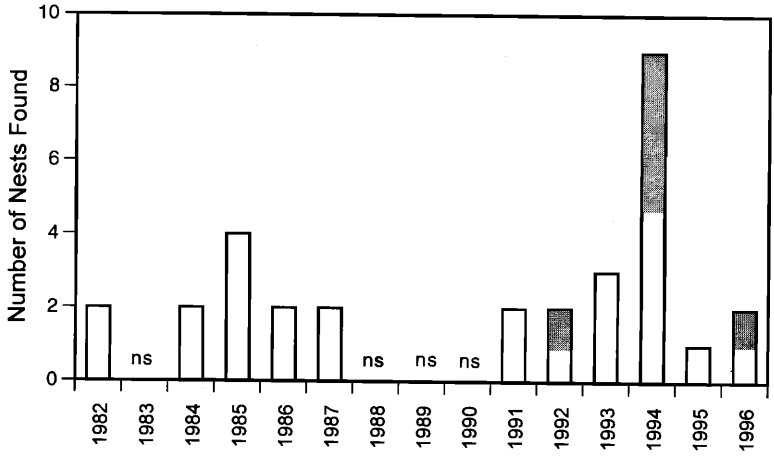

Figure 4. The number of Southwestern Willow Flycatcher nests found each year in the Grand Canyon, 1982–1996. Data for 1982–1991 are from Brown (1988, 1991); ns signifies that no searches were conducted that year. Shaded portions represent renesting attempts following failed first nests (unknown for 1982–1991 data).

m from the first nest (mean 11 ± 8 m, n = 5). Nests were constructed primarily or entirely of tamarisk leaves and supported by vertically angled forks of small branches and twigs.

Breeding Ecology

In most years, resident males were first detected in the third week of May, but this may be an artifact of the timing of our first survey trips, typically launched during this time. Our earliest record of a male on breeding territory is 8 May, suggesting that they may generally arrive earlier than our surveys suggest. Unpaired males were detected as early as 22 May and were usually present each year until at least 4 July (13 July is our latest record) but were absent during surveys later in July. Most nesting activity was noted from early June through mid-July. Our earliest recorded nest was under construction 22 May. The earliest date for flycatcher eggs was 30 May (2 eggs), although a Brown-headed Cowbird egg was found in a flycatcher nest on 23 May. Earliest and latest dates that we detected nestlings were 29 June (chicks approximately 8 days old) and 13 July (chicks approximately 10 days old), respectively. Dates of earliest and latest recorded fledging were 29 June and 13 July, respectively. Adult flycatchers were observed feeding fledged young on 2 and 21 July.

Because of the timing of survey trips and the high proportion of parasitized nests, we determined clutch size for only three unparasitized nests (each with three eggs). Of six parasitized nests found during the incubation period, five had two flycatcher eggs with one cowbird egg, while the sixth had three flycatcher and one cowbird egg. The reduced

Table 3 Characteristics of Southwestern Willow Flycatchers nests in the Grand Canyon, 1992–1996[a]

Variable	All nests (n=12)	Parasitized nests (n=8)	Nonparasitized nests (n=4)	Significance (t test)
Height of nest plant (m)	7.3±2.1 (5–13)	7.5±2.4 (5–13)	6.5±1.3 (5–8)	p=0.5
Height of nest (m)	4.8±0.8 (4–6)	4.8±0.8 (4–6)	4.5±0.7 (4–5)	p=0.6
Distance from nest to closest edge of habitat (m)	10.8±6.6 (5–25)	8.1±4.0 (5–16)	16.5±7.8 (7–25)	p=0.04[b]
Distance from nest to closest surface water (m)	14.5±6.7 (5–30)	13.0±5.6 (5–20)	17.8±9.7 (7–30)	p=0.3
Distance from nest to top of nest-plant canopy (m)	2.6±1.5 (1–7)	2.8±1.8 (1–7)	2.0±1.1 (1–4)	p=0.4

[a]Values given are mean ± one standard deviation, with range in parentheses.
[b]Significant at $p < 0.05$.

number of flycatcher eggs in most parasitized nests as compared to unparasitized nests suggests that female cowbirds may be removing a flycatcher egg when they parasitize the nest.

Annual nesting success varied greatly over the course of the study (Table 2). Overall, nesting success (the percentage of nests that fledged one or more flycatchers) was low, with 82% of nests failing because of cowbird parasitism or other unknown causes. Interestingly, the annual number and percentage of successful nests was not significantly correlated with either the number of nest attempts or the number of breeding pairs in a given year (Pearson's R^2= 0.55, $p > 0.05$). Young flycatchers fledged in only three of five years, and in each of these years all fledged young came from only one nest. Because of the timing of survey trips and concerns about visually checking the nest immediately prior to anticipated fledging, we were unable to verify the exact number of fledglings from each nest. Even if all nestlings in the successful nests fledged, only seven flycatchers fledged during the 5-year study (Table 2), with a mean number of young produced per pair per year of only 0.7 ± 1.2. We found no second nesting attempts following a successful first nest. In five of six cases, breeding flycatchers attempted a second nest after failure of first nests. We found only one case suggesting a third (and unsuccessful) nesting attempt after the first two failed.

Brown-headed Cowbird Abundance and Nest Parasitism

Cowbirds were found at virtually every site occupied by breeding or territorial flycatchers. Female cowbirds were often seen moving slowly through the habitat patches, characteristic behavior of searching for host nests (Lowther 1993). On several occasions resident flycatchers confronted cowbirds with aggressive actions such as tail fanning, erected crest, flying

directly at the cowbird, loud *whitting*, and bill-clacking. At least once, the flycatcher physically contacted the cowbird when it approached within 2 m of the flycatcher's nest.

Occurring at all three breeding sites, parasitism varied greatly from year to year with an overall rate of 47% (Table 2). The rate may actually have been higher, given that parasitism may have been responsible for the failure of at least some of the seven nests whose cause of failure we could not determine. Parasitized nests were located closer to the edge of the habitat than unparasitized nests (Table 3). The number of successful flycatcher nests each year was inversely correlated with the number of nests parasitized (Pearson's $R^2 = 0.90$, $p < 0.02$). The success rate of parasitized nests was lower (12%, $n = 8$) than that of unparasitized nests (33%, $n = 9$). In the only parasitized nest that succeeded in fledging flycatchers, a cowbird egg was laid prior to the first flycatcher egg but had disappeared or was buried within the floor of the nest by the time the nest was next checked (12 days later) and contained only three flycatcher eggs. Flycatchers fledged a cowbird from one nest but never fledged both cowbirds and flycatchers from the same nest.

Vocalizations

Many flycatchers vocalized spontaneously throughout the season and were detected without the use of survey tapes. Breeding males sang most persistently before pairing and early in the nesting cycle, then sang less frequently once nesting was underway. Before pairing, male flycatchers sang the characteristic *fitz-bew* song at virtually any hour of day, as early as 03:05 and as late as 20:00 hrs. Early morning (prior to 05:00) song remained common throughout the nesting period, even into July. However, late in the breeding season, mated males with active nests often failed to sing after dawn, even in response to broadcast songs and calls. The pattern for unpaired males was much the same, except that they continued high song rates throughout the day later into the season. Nine of 28 (33%) of the migrants found over the course of this study were heard singing prior to the use of a survey tape at the site. Migrants accounted for up to 64% (mean 22 ± 26) of the spontaneously singing flycatchers detected each year.

At 09:10 on 23 May 1995, we were observing a female flycatcher that was 5 m from her nest while the territorial male was approximately 30 m away countersinging with a neighboring male. While both males were singing, the female began to sing a series of strong, loud *fitz-bews*. The structure and pattern of the female's *fitz-bews* were indistinguishable by ear from those typical of singing males. The female sang periodically over the next 40 minutes, giving a total of 58 *fitz-bews*, in bouts of 2 to 15 songs each. She usually sang while her mate and/or the adjacent male were singing and always while she was at or near the nest. At one point, she sang five times while sitting on the nest. Although we had heard what was suspected to be female flycatcher song in the canyon during other years, this is the only instance in which we could conclusively verify that it was the female singing.

DISCUSSION

Abundance and Distribution

The breeding population of the Willow Flycatcher in Grand Canyon continues to be localized and small. From 1992 to 1996, the flycatcher bred at three historic nesting sites, but they no longer breed at Lee's Ferry and RM 46 (last recorded in 1961 and 1987, respectively). During the course of our study, flycatchers stopped breeding at RM 71 (1994) but reestablished breeding at RM 50 (1993) and 51 (1994) following 1- to 2-year absences. Because of the dynamic nature of the establishment and loss of breeding sites, only one or two were occupied in any given year.

It is difficult to determine if the Willow Flycatcher's abundance in the Grand Canyon has changed over the last 15 years. If all of the singing flycatchers detected by Brown (1988, 1991) from 1982 to 1991 were breeding, then the population has declined considerably from a high of 11 pairs in 1986. However, our observations suggest that some of the flycatchers detected in Brown's less intensive surveys could have been migrants, floaters, unpaired males, or females, rather than breeding males. Our mean total number of flycatchers (combining migrants, floaters, and females) detected without the use of tape playback each year (5.0 ± 3.5, range 2–11) is not significantly different from Brown's 1982–1991 totals (mean 5.4 ± 3.4, range 2–11; t test, $t = 0.21$, $p = 0.8$). Apparently there is high annual variation and no clear population trend (Figure 5).

The best available indicators of trends in flycatcher breeding activity within the canyon are the number of verified breeding pairs and active nests found

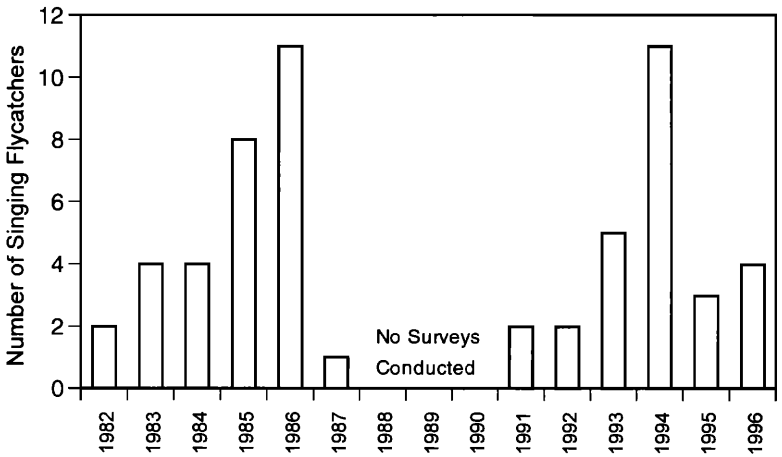

Figure 5. The number of singing Willow Flycatchers detected (without use of tape playback) in the Grand Canyon, 1982–1996. Data for 1982–1991 are from Brown (1988, 1991).

over time. C. M. White's specimens collected at Lee's Ferry provide evidence of only two breeding pairs at that site in 1961. In the 1970s, Carothers and Sharber (1976) noted only a single breeding pair per year. Even in the 1980s, when as many as 11 singing flycatchers were detected in one year (Brown 1988), the highest annual number of flycatcher nests found was only four (although this may be a function of Brown's less intensive survey effort). These historic numbers of breeding pairs and nests are similar to those found during our study.

Although *Empidonax* flycatchers are generally monogamous, polygyny occurs uncommonly among Willow Flycatchers in California (Whitfield 1990), Canada (Prescott 1986), Colorado, and Oregon (Sedgwick and Knopf 1989). Polygyny in the Grand Canyon appears to be similarly rare in that it was detected only once out of 18 established territories. In contrast, a large proportion (44%) of territorial males in the canyon were unpaired, approximately twice the estimated 20% of male *E. t. extimus* unpaired rangewide (Sferra et al. 1997, USFWS unpubl. data). The high proportion of unpaired males has contributed to the low productivity among flycatchers in the Grand Canyon since at least 1993.

The continued low population level makes the flycatchers susceptible to extirpation from the Grand Canyon by cowbird nest parasitism, natural attrition, or catastrophic events such as fire. Like most small migrant songbirds, Willow Flycatchers are relatively short-lived with an average adult lifespan of approximately 3 to 4 years (M. Whitfield, unpubl. data). Thus, if the flycatchers currently breeding in the canyon continue to produce few or no young for several breeding seasons, the older breeders that die are unlikely to be replaced. It is possible that Southwestern Willow Flycatchers from other areas could settle in the Grand Canyon area, given time and serendipitous dispersal. In fact, the canyon's population is probably not self-sustaining but composed (partially or primarily) of flycatchers immigrating from elsewhere. This hypothesis is supported by the increase in breeding pairs between 1993 (two pairs) and 1994 (four pairs), even though no young flycatchers were fledged in the canyon during 1993.

Breeding Ecology

Although Southwestern Willow Flycatchers were historically found primarily in willow–cottonwood and other native riparian tree and shrub associations (Phillips et al. 1964, Unitt 1987), the use of tamarisk as a nesting habitat is not unique to the Grand Canyon. Relatively large populations (approximately 20 pairs) currently inhabit tall, dense tamarisk-dominated habitats at two sites in central Arizona (Sferra et al. 1997). The tamarisk-dominated breeding sites in the Grand Canyon also include willow, cattail (*Typha latifolia),* and horsetail (*Equisetum*), which may be important habitat components. At other Arizona sites where willows and other native broadleaf vegetation dominate, flycatchers often place their nests in tamarisk even though other nest substrates are available (Sferra et al. 1997). This use of tamarisk contrasts sharply with documented loss of breeding flycatchers from areas such as the lower Colorado River and San Juan River, where tamarisk or other exotics have displaced the native broadleaf community (Unitt 1987, Rosenberg et al. 1991). One of the characteristics of occupied

tamarisk habitat in the Grand Canyon and elsewhere is that it is taller (usually >5 m) and denser (90% canopy closure; Sferra et al. 1997) than in areas where the flycatchers once bred but are no longer found.

Nest-placement characteristics at our sites are similar to those in other populations nesting in tamarisk, but nest height is greater than for flycatcher nests in native vegetation, particularly at higher elevations (Sferra et al. 1997). In tall, dense tamarisk stands the appropriately sized and oriented branches needed for nest placement are generally found in the upper portions of the plant, as reflected in the relationship that we found between nest plant height and nest height.

Vocalizations

Daily and seasonal song rate patterns followed those noted by Unitt (1987) and Brown (1991). During any part of the breeding season, males with active nests sometimes sang infrequently and did not respond to a tape-broadcast call, which has practical ramifications for survey design and timing. However, the persistence of very early morning (03:00–05:00) singing throughout the breeding season may provide surveyors with opportunities to detect resident flycatchers later in the season.

Song from females is not common among most passerines, although additional instances have been noted as attention to this phenomenon has increased (Catchpole and Slater 1995). Kroodsma (1984) first described female song in flycatchers injected with hormones. Seutin (1987) observed females singing in territorial defense in response to a broadcast tape of flycatcher song in their breeding territories. The nature and timing of the female song that we observed supports the interpretation that female Willow Flycatchers sing in a territorial aggression or defense context, as has been noted for several other *Empidonax* (MacQueen 1950, Kellner and Ritchison 1988). In fact, female song in Willow Flycatchers and other *Empidonax* may be much more common than currently recognized (Kellner and Ritchison 1988, Catchpole and Slater 1995). Females singing loudly and repeatedly (such as we observed) could easily be misinterpreted as territorial males, inflating estimates of the number of flycatcher territories at a site. Our intensive monitoring efforts minimized the potential for such misinterpretation in this study.

Brown-headed Cowbird Impacts

Cowbirds occur throughout Grand Canyon (Brown 1994, Johnson and Sogge 1995) and were seen at all flycatcher breeding sites. Approximately half of the flycatcher nests examined in the canyon during the 1980s were parasitized by cowbirds (Brown 1988, 1994), almost identical to our 47% parasitism rate for 1992 to 1996. This high rate of parasitism suggests that the flycatchers in the Grand Canyon are not effective in nest defense against cowbirds, despite our observations of aggressive interactions that could be interpreted as antiparasitic behaviors (Uyehara and Narins 1995). As demonstrated by Whitfield (1990) and Whitfield and Strong (1995) for flycatchers in southern California, cowbird parasitism in the Grand Canyon has clearly been a pervasive, long-term problem and may be the most

imminent direct threat to this breeding population of flycatchers (Sogge 1995).

Rothstein et al. (1984) and Cook et al. (1996) found that female cowbirds can travel up to 7 and 20 km, respectively, between areas where they parasitize nests in the morning then feed and/or roost later in the day. At the Grand Canyon, cowbirds concentrate at bird feeders and pack animal corrals along the south rim (Johnson and Sogge 1995, Drost 1996), within 4 to 6 km of the river and 10 km from the flycatchers' breeding site at RM 71. Drost (1996) recorded movements of color-banded cowbirds between feeding stations along the south rim averaging 19 km (range 5–8 km), suggesting that cowbirds foraging and roosting at the rim could readily reach flycatcher breeding sites along the river. In addition, livestock grazing (which attracts cowbirds) is common on adjacent Forest Service, Bureau of Land Management, and tribal lands, and cowbirds associate and forage with the Bison (*Bison bison*) herds at House Rock State Buffalo Ranch (Sogge, unpubl. data), approximately 16 km from the RM 50 site. Thus, many human-related activities provide cowbird concentration sites within commuting range of current (and potential) flycatcher breeding habitat in the canyon.

MANAGEMENT CONSIDERATIONS/IMPLICATIONS

The Southwestern Willow Flycatcher's endangered status, coupled with the small size, low productivity, and demographic instability of the population in the Grand Canyon, calls for continued monitoring and management along the Colorado River corridor. Human disturbance of the flycatcher's breeding areas in the Grand Canyon is likely because these areas are usually adjacent to sandy beaches, which are often popular camping sites. Flycatchers have bred for at least 10 years within approximately 100 m of popular camping areas such as the RM 71 site, suggesting that they are generally tolerant of low-level human activity that is not directly adjacent to or within the breeding territory. However, Taylor (1986) found a possible correlation between recreational activities and decreased riparian bird abundance, and Blakesley and Reese (1988) reported the Willow Flycatcher (probably *E. t. adastus*) as one of seven species negatively associated with campgrounds in riparian areas in northern Utah. Therefore, Grand Canyon National Park should continue to close public access to flycatcher sites during each breeding season to minimize disturbance and habitat degredation.

We also recommend that Grand Canyon National Park consider a cowbird control program. Such programs are effective at reducing cowbird parasitism at other flycatcher breeding sites (Whitfield and Strong 1995). Agencies and tribes that manage lands adjacent to the Grand Canyon should consider similar cowbird control efforts, especially around livestock grazing, horse and mule corrals, or bison ranches. Grand Canyon National Park should also take the lead in coordinating and developing an integrated Southwestern Willow Flycatcher management plan for the Colorado River corridor in the Grand Canyon. This plan would address near- and long-term flycatcher management and protection needs, and provide detailed recommendations, options, and tools to guide future flycatcher monitoring, research, and management.

The flycatcher surveyors and river guides worked incredibly hard under difficult field conditions—it was only through their excellent work that this project was a success. In particular, we thank Lawrence Abbott, Rob Marshall, Susan Sferra, and Brad Valentine for contributing their time, energy, and expertise to many years of surveys. Bryan Brown, Linda Sogge, Philip Unitt, and Mary Whitfield provided valuable reviews of an earlier draft of the manuscript.

LITERATURE CITED

Behle, W. H., and Higgins, H. G. 1959. The birds of Glen Canyon, in Ecological studies of the flora and fauna in Glen Canyon (A. M. Woodbury, ed.), pp. 107-133. Univ. Utah Anthropol. Paper 40.

Blakesley, J. A., and Reese, K.P. 1988. Avian use of campground and non-campground sites in riparian zones. J. Wildlife Mgmt. 52:399–402.

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

Brown, B. T. 1991. Status of nesting Willow Flycatchers along the Colorado River from Glen Canyon Dam to Cardenas Creek, Arizona. Endangered Species Report 20, U.S. Fish and Wildlife Service (order from U.S. Fish and Wildlife Service, 2321 Royal Palm Rd, Suite 103, Phoenix, AZ 85021).

Brown, B. T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. J. Field Ornithol. 65:160–168.

Brown, B. T. and Trosset, M.W. 1989. Nesting-habitat relationships of riparian birds along the Colorado River in Grand Canyon, Arizona. Southwest Nat. 34:260–270.

Browning, M. R. 1993. Comments on the taxonomy of *Empidonax traillii* (Willow Flycatcher). W. Birds 24:241–257.

Carothers, S. W., and Sharber, N. J. 1976. Birds of the Colorado River, in An ecological survey of the riparian zone of the Colorado River between Lee's Ferry and Grand Wash Cliffs (S. W. Carothers and N. J. Sharber, eds.), pp 109–122. Colorado River Tech. Rep. 10, Grand Canyon Natl. Park (order from Division of Resources Management, Grand Canyon Natl. Park, Grand Canyon, AZ 86023).

Catchpole, C. K., and Slater, P. J. B. 1995. Bird Song: Biological Themes and Variations. Cambridge University Press, Cambridge, England.

Cook, T. L., Koloszar, J. A., and Goering, M. D. 1996. Behavior and movement of the Brown-headed Cowbird (*Molothrus ater*) on Fort Hood, Texas—1995 annual report (order from The Nature Conservancy of Texas, P. O. Box 1440, San Antonio, TX 78295).

Drost, C. A. 1996. Monitoring of Brown-headed Cowbird impact on nesting neotropical migrant birds in Grand Canyon National Park—1996. Final report to the National Park Foundation (order from U.S.G.S. Colorado Plateau Research Station, Box 5614, Northern Arizona University, Flagstaff, AZ 86011).

Gill, F. B. 1995. Ornithology, 2nd ed. Freeman, New York.

Johnson, M. J., and Sogge, M. K. 1995. Cowbird concentrations at livestock corrals in Grand Canyon National Park, in Proceedings of the Second Biennial Conference on Research in Colorado Plateau National Parks, 25–28 October 1993 (C. van Riper, ed.), pp. 275–284. Natl. Park Service Trans. Proc. Ser. NPS/NRNAU/NRTP-95/11.

Kellner, C. J., and Ritchison, G. 1988. Possible functions of singing by female Acadian Flycatchers (*Empidonax virescens*). J. Field Ornithol. 59:55–59.

Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*), in The Birds of North

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

Brown, B. T. 1991. Status of nesting Willow Flycatchers along the Colorado River from Glen Canyon Dam to Cardenas Creek, Arizona. Endangered Species Report 20, U.S. Fish and Wildlife Service (order from U.S. Fish and Wildlife Service, 2321 Royal Palm Rd, Suite 103, Phoenix, AZ 85021).

Brown, B. T. 1994. Rates of brood parasitism by Brown-headed Cowbirds on riparian passerines in Arizona. J. Field Ornithol. 65:160–168.

Brown, B. T. and Trosset, M.W. 1989. Nesting-habitat relationships of riparian birds along the Colorado River in Grand Canyon, Arizona. Southwest Nat. 34:260–270.

Browning, M. R. 1993. Comments on the taxonomy of *Empidonax traillii* (Willow Flycatcher). W. Birds 24:241–257.

Carothers, S. W., and Sharber, N. J. 1976. Birds of the Colorado River, in An ecological survey of the riparian zone of the Colorado River between Lee's Ferry and Grand Wash Cliffs (S. W. Carothers and N. J. Sharber, eds.), pp 109–122. Colorado River Tech. Rep. 10, Grand Canyon Natl. Park (order from Division of Resources Management, Grand Canyon Natl. Park, Grand Canyon, AZ 86023).

Catchpole, C. K., and Slater, P. J. B. 1995. Bird Song: Biological Themes and Variations. Cambridge University Press, Cambridge, England.

Cook, T. L., Koloszar, J. A., and Goering, M. D. 1996. Behavior and movement of the Brown-headed Cowbird (*Molothrus ater*) on Fort Hood, Texas—1995 annual report (order from The Nature Conservancy of Texas, P. O. Box 1440, San Antonio, TX 78295).

Drost, C. A. 1996. Monitoring of Brown-headed Cowbird impact on nesting neotropical migrant birds in Grand Canyon National Park—1996. Final report to the National Park Foundation (order from U.S.G.S. Colorado Plateau Research Station, Box 5614, Northern Arizona University, Flagstaff, AZ 86011).

Gill, F. B. 1995. Ornithology, 2nd ed. Freeman, New York.

Johnson, M. J., and Sogge, M. K. 1995. Cowbird concentrations at livestock corrals in Grand Canyon National Park, in Proceedings of the Second Biennial Conference on Research in Colorado Plateau National Parks, 25–28 October 1993 (C. van Riper, ed.), pp. 275–284. Natl. Park Service Trans. Proc. Ser. NPS/NRNAU/NRTP-95/11.

Kellner, C. J., and Ritchison, G. 1988. Possible functions of singing by female Acadian Flycatchers (*Empidonax virescens*). J. Field Ornithol. 59:55–59.

Kroodsma, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.

Lowther, P. E. 1993. Brown-headed Cowbird (*Molothrus ater*), in The Birds of North America, No. 47 (A. Poole and F. Gill, eds.). Acad. Nat. Sci., Philadelphia.

MacQueen, P. M. 1950. Territory and song in the Least Flycatcher. Wilson Bull. 62:194–205.

McKee, E. D. 1931. Additional notes on the Tanner Trail trip. Grand Canyon Nature Notes 5:121–122 (order from Division of Resources Management, Grand Canyon Natl. Park, Grand Canyon, AZ 86023).

Monson, G. 1953. The spring migration. Southwest region. Audubon Field Notes 7:320–322.

Phillips, A. R., Marshall, J., and Monson, G. 1964. The Birds of Arizona. Univ. Ariz. Press, Tucson.

Prescott, D. R. C. 1986. Polygyny in the Willow Flycatcher. Condor 88:385–386.

Rosenberg, K. V., Ohmart, R. D., Hunter, W. C., and Anderson, B. W. 1991. Birds of the Lower Colorado River Valley. Univ. Ariz. Press, Tucson.

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 65:77–88.

Sedgwick, J. A., and Knopf, F. L. 1989. Regionwide polygyny in Willow Flycatchers. Condor 91:473–475.

Seutin, G. 1987. Female song in Willow Flycatchers (*Empidonax traillii*). Auk 104: 329–330.

Sogge, M. K. 1995. Southwestern Willow Flycatchers in the Grand Canyon, in Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems (E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, eds.), pp. 89–91. U.S. Dept. Interior, Nat. Biol. Service, Washington, D.C.

Sferra, S. J., Corman, T. E., Paradzick, C. E., Rourke, J. W., Spencer, J. A., and Sumner, M. W. 1997. Arizona Partners in Flight Southwestern Willow Flycatcher survey: 1993–1996 Summary Report. Ariz. Game and Fish Final Tech. Rep. 113 (order from Ariz. Game and Fish Dept., 2221 W. Greenway, Phoenix, AZ 85023).

Stevens, L. 1983. The Colorado River in Grand Canyon—A Guide. Red Lakes Books, Flagstaff, AZ.

Taylor, D. M. 1986. Effects of cattle grazing on passerine birds nesting in riparian habitats. J. Range Mgmt. 39:254–258.

Tibbitts, T. J., Sogge, M. K., and Sferra, S. J. 1994. A survey protocol for the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). Natl. Park Service Tech. Rep. NPS/NAUCPRS/NRTR-94/04 (order from U.S.G.S. Colorado Plateau Research Station, Box 5614, Northern Arizona University, Flagstaff, AZ 86011).

Turner, R. M., and Karpiscak, M. M. 1980. Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. U.S. Geol. Survey Prof. Paper 1132.

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

Uyehara, J. C., and Narins, P. M. 1995. Nest defense by Willow Flycatchers to brood-parasitic intruders. Condor 97:361–368.

U.S. Fish and Wildlife Service. 1995. Final Rule Determining Endangered Status for the Southwestern Willow Flycatcher. Fed. Register 60:10694 (27 Feb 1995).

Whitfield, M. J. 1990. Willow Flycatcher reproductive response to Brown-headed Cowbird parasitism. Masters Thesis, Calif. State Univ., Chico.

Whitfield, M. J., and Strong, C. M. 1995. A Brown-headed Cowbird control program and monitoring for the Southwestern Willow Flycatcher, South Fork Kern River, California, 1995. Calif. Dept. Fish and Game, Bird and Mammal Cons. Prog. Rep. 95-4 (order from Calif. Depy. Fish and Game, 1416 Ninth St., Sacramento, CA 94244).

Woodbury, A. M., and Russell, H.N. 1945. Birds of Navajo country. Bull. Univ. Utah 35:1–157.

Accepted 23 June 1997