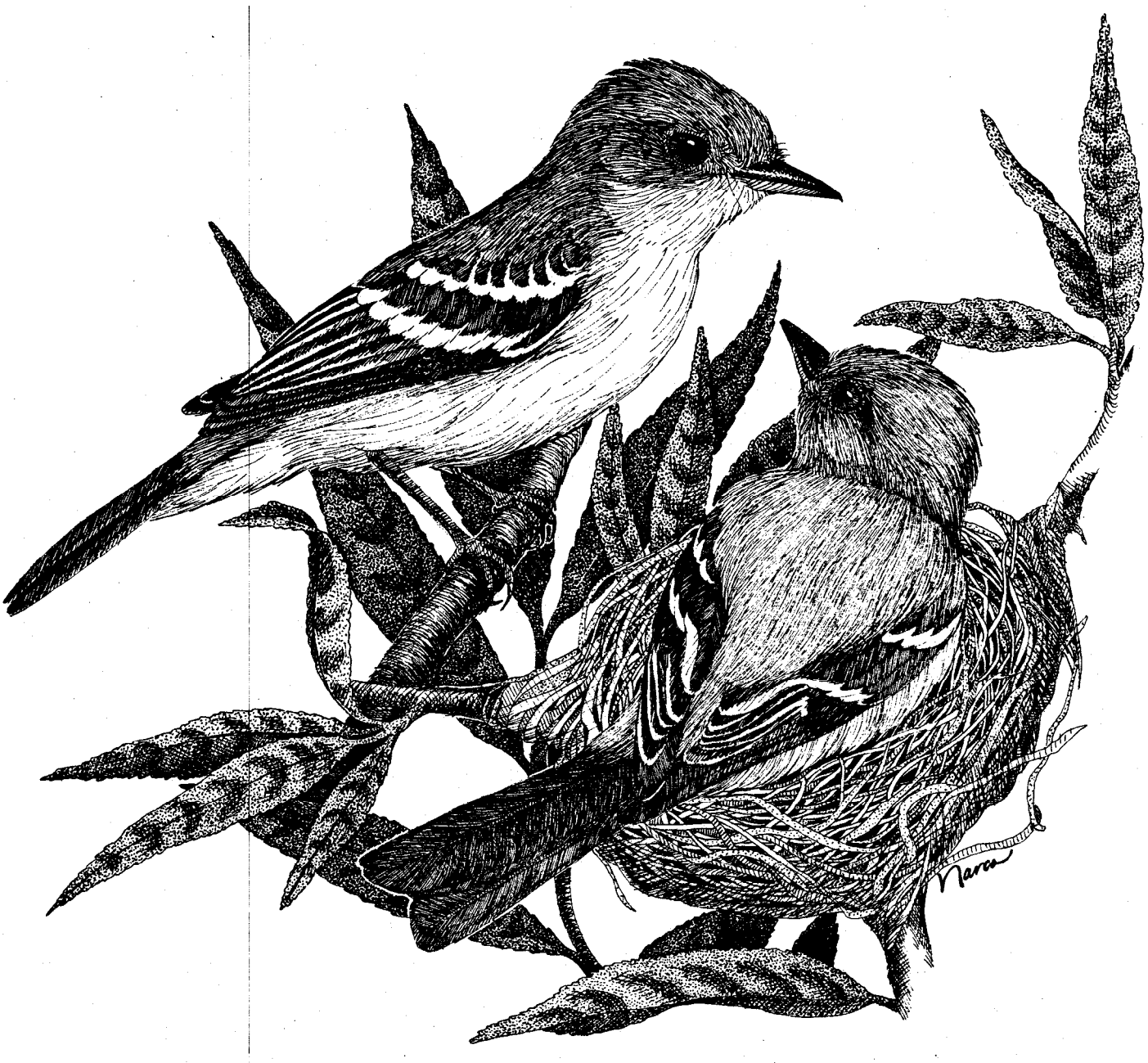
STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME
WILDLIFE MANAGEMENT DIVISION
NONGAME BIRD AND MAMMAL SECTION

ECOLOGY OF A SIERRA NEVADA POPULATION OF WILLOW FLYCATCHERS (Empidonax traillii), 1986-87

by

Susan D. Sanders and Mary Anne Flett

1989



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ABSTRACT

This report discusses the results of an ecological study of Willow Flycatchers along the Little Truckee River in Tahoe National Forest during the breeding seasons of 1986 and 1987. The chief objectives of this study were to gather information on Willow Flycatcher breeding biology, behavior, and habitat requirements, and to develop recommendations for the protection and management of this species.

We studied Willow Flycatchers inhabiting large mountain meadows at Perazzo Meadows and Lacey Valley, Sierra County, California. Willow Flycatcher territories at these sites always included willow clumps and standing or running water. The average territory size was 0.34 ha (0.84 acre) for 22 breeding pairs. Adult Willow Flycatchers used areas outside their territories for foraging, especially when feeding young. We estimated approximately one ha (2.5 acres) is typically needed for a family of Willow Flycatchers. This area includes average territory size plus a 20 m (66 ft) wide foraging zone around the territory.

Willow Flycatcher nests were always placed about one meter (3 ft) above the ground near the edge of a willow clump. In 1986, 14 or 15 Willow Flycatchers fledged from 11 nests, an egg-to-fledgling success rate of 29%. In 1987, 10 pairs of Willow Flycatchers produced 6 fledglings, a 19% success rate. A mid-July snowstorm was responsible for heavy mortalities of eggs and young in 1987. In 1986, severe weather was also responsible for two nest failures, and Brown-headed Cowbird parasitism caused the loss of another nest. Predation accounted for most of the remaining egg or nestling losses.

The net reproductive rate for Willow Flycatchers in the Sierra Nevada is less than that needed to maintain a stable population. If current reproductive trends continue, Willow Flycatchers could disappear as a breeding bird in California. We recommend several measures, including listing this species as endangered, to avert their extirpation in the state.

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2/ PAR & Associates, P.O. Box 160756, Sacramento, CA 95816-0756

3/ 1751 Delaware Street, Berkeley, CA 94703

SUMMARY OF RECOMMENDATIONS

1. List the Willow Flycatcher as endangered in California.
2. Protect Willow Flycatcher habitat on private and public lands.
3. Eliminate or delay grazing on meadows and riparian areas that support Willow Flycatchers.
4. Monitor existing Willow Flycatcher populations and survey for new ones.
5. Control Brown-headed Cowbird populations.
6. Avoid developments adjacent to montane meadows that support Willow Flycatchers.
7. Revegetate and restore Willow Flycatcher habitat.

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INTRODUCTION

The Willow Flycatcher (Empidonax traillii) was formerly a common summer resident throughout California, breeding wherever extensive willow (Salix spp.) thickets occurred (Grinnell and Miller 1944). It has now been extirpated as a breeding bird from most of its California range (Serena 1982). A few remaining populations inhabit isolated meadows of the Sierra Nevada. This species also occurs along the Kern, Santa Margarita, and San Luis Rey Rivers (Remsen 1978, Serena 1982, Unitt 1988) and the Santa Ana River (Laymon pers. comm.).

The loss of lowland riparian woodlands has been identified as the principal reason for the reduction of California's Willow Flycatcher population and contraction of its breeding range (Remsen 1978, Serena 1982). Nest parasitism by Brown-headed Cowbirds (Molothrus ater) and habitat modification by livestock grazing have also been suggested as contributing significantly to population reductions (Gaines 1977, Serena 1982, Beedy and Granholm 1985, Sharp 1986, Taylor 1986, Taylor and Littlefield 1986).

The California Department of Fish and Game (DFG) has designated the Willow Flycatcher a Bird Species of Special Concern (Priority 1) because of its greatly reduced population and range in the state (Remsen 1978). Region 1 of the U.S. Fish and Wildlife Service and Region 5 of the U.S. Forest Service consider the Willow Flycatcher a sensitive species in the western United States, and the National Audubon Society has placed this species on its "Blue List" of special concern species (Sharp 1986).

The objectives of this two-year study were to gather information on the life history and ecological relationships of Willow Flycatchers. The DFG requires information on the breeding, foraging, and habitat requirements of Willow Flycatchers in order to protect and manage this species in California.

STUDY AREAS AND METHODS

Study Areas - Overview

The Perazzo Meadows and Lacey Valley study areas are in the Little Truckee River drainage, Sierra County, California, approximately 32 km (20 miles) northwest of the town of Truckee (Figure 1). These meadows are at 2010 m (6,600 ft) on the east slope of the Sierra Nevada in the Tahoe National Forest. These large, wet meadows are dominated by grasses, rushes (Juncus spp.), and sedges (Carex spp.), with scattered patches of willow shrubs (Salix lemmonii and 5. jeosoni). No arborescent willows, cottonwoods (Populus trichocarpa) or alders (Alnus tenuifolia) occur in the meadows. The slopes above the meadow support scattered stands of aspen (Populus tremuloides) and lodgepole pine (Pinus contorta var. murrayana) forest surrounds the meadows.

Perazzo Meadows

Perazzo Meadows (Figure 2) is a series of large meadows adjacent to the Little Truckee River in Sierra County. These meadows comprise about 350 ha (865 acres). We confined our study to the western 60 ha (148 acres) because previous surveys showed that this area supported the densest concentration of Willow Flycatchers (Serena 1982). Perazzo Canyon Creek and the Little Truckee River are the two perennial streams that flow through the study site. In spring and early summer deep pools of water remain in remnant oxbows and secondary channels of these streams.

Shrubby willows range in height from 2-3 m (7-10 ft) and grow in clumps along the oxbows, and to a lesser extent along the streams. The streams and oxbows support beavers (Castor canadensis) and provide breeding habitat for wetland birds such as Mallard (Anas platvrhvnchos), Sora (Porzana carolina), Virginia Rail (Rallus limicola), Common Snipe (Gallinago gallingo), and Wilson's Phalarope (Phalaropus tricolor).

Two large knolls rising about 25 m (82 ft) above the meadow are prominent features in this site. The southern knoll occurs in a relatively dry portion of the meadow and is covered with sagebrush (Artemisia sp.) and lodgepole pine. The second knoll is a lodgepole pine-covered island surrounded by willows and by standing water in the early summer.

Lacey Valley

Lacey Valley (Figure 3) is approximately 3 km (1.9 mi) west of Perazzo Meadows, and covers about 90 ha (222 acres). Webber Lake, the origin of the Little Truckee River, occupies the northeastern part of the valley. We restricted our studies to the southwestern portion of Lacey Valley, an area of about 40 ha (99 acres). The vegetation and wildlife of Lacey Valley are similar to that of Perazzo Meadows. However, in contrast to Perazzo Meadows willows are not scattered over the meadow. Instead, they occur in noncontinuous clumps along the banks of the upper Little Truckee River. Old oxbows are not present here, and standing water occurs mainly in depressions during late spring and early summer.

Methods

We conducted field work from mid-June to late August in 1986 and 1987. To identify individual birds we captured a total of 25 Willow Flycatchers in mist nets and banded them with unique color combinations. Most behavioral observations were made from dawn to mid-morning, and consisted of recording the location and behavior of Willow Flycatcher individuals, pairs, or families. These observations were used to determine nest locations, habitat use, and territorial boundaries.

We checked nests regularly to monitor the fate of eggs and nestlings, and recorded nest characteristics, including height and location of nests in willow clumps, distance to edge of clump, distance to nearest livestock trail, and foliage density in the vicinity of nests. We assessed foliage density by placing a 1 m (3 ft) square board behind the nest, pacing back about 5 m (16 ft), and estimating the percentage of the board obscured by willow twigs and leaves.

To determine the territorial boundaries of mated males, we recorded the locations of perches at which males repeatedly sang, measuring the distances between these perches. We considered the area enclosed by the outermost song perches to be the male's territory. Because territorial boundaries shift during the breeding season, we mapped and measured territories only when eggs or young were present.

To assess habitat characteristics of Willow Flycatcher territories, we used aerial photos and on-the-ground surveys to estimate the percentage of each territory covered by willows, standing or running water, and trees. Using the technique described above, we measured foliage density at 0-1 m (0-3 ft) and 1-2 m (3-7 ft) above the ground at 10 sites throughout the territory. Since foliage on shrubby willows normally extends to the ground, measurements taken at 0-1 m (0-3 ft) were intended to document the effects of livestock browsing on the lower portions of the willows. Because Willow Flycatchers at our study sites place their nests approximately 1 m (3 ft) above the ground, measurements at 1-2 m (3-7 ft) were taken to assess the vigor and amount of foliage at heights appropriate for nesting. These measurements were taken every 5 m (16 ft) for 50 m (164 ft) along the outer edge of the longest willow clump in the territory. Length of willow clumps generally did not exceed 50 m (164 ft).

To document livestock use of willow clumps, we made regular observations of sheep and cattle at the study sites, noting the number of cattle grazing in willows and in the open. We also estimated the numbers of Brown-headed Cowbirds on a daily basis at the study sites, and noted associations of cowbirds and livestock.

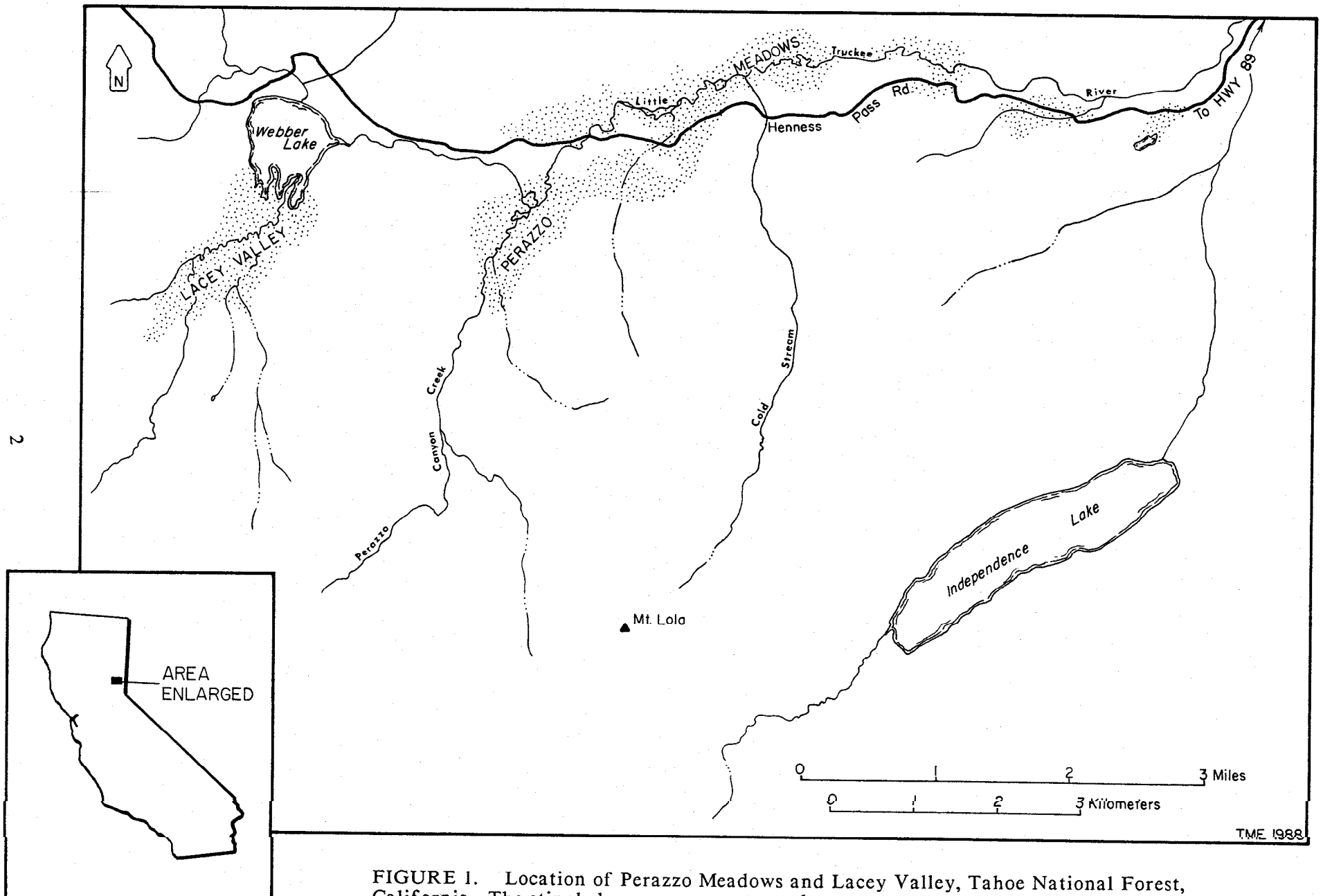

FIGURE 1. Location of Perazzo Meadows and Lacey Valley, Tahoe National Forest, California. The stippled areas represent meadows.

RESULTS AND DISCUSSION

Density

Breeding Pairs

In 1986 the Perazzo Meadows study site supported at least eight pairs of Willow Flycatchers. In 1987 the same area supported 11 pairs. The Lacey Valley study site supported five breeding pairs in 1986 and four in 1987.

The densities of breeding Willow Flycatchers at our two study sites were relatively low compared to other densities reported in the literature. Perazzo Meadows supported only 0.13 pairs per ha (about 5 pairs/100 acres) in 1986, and 0.18 pairs per ha (7 pairs /100 acres) in 1987. The Lacey Valley site supported about 0.09 pairs per ha (4 pairs/100 acres) in 1986, and 0.12 pairs per ha (5 pairs per 100 acres) in 1987. King (1955) reported densities of 0.25 - 0.35 pairs of Willow Flycatchers per ha (10 - 14 pairs/100 acres) in southeastern Washington. Wing (1949) found 0.22 pairs/hectare (9.2 pairs /100 acres) of Willow Flycatchers in his studies on the Palouse Prairie, Washington. Kings River Conservation District biologists (KRCD 1985) found an average of 0.24 Willow Flycatcher pairs per ha (9.7 pairs/100 acres) on meadows in the southern Sierra. For consistency with estimates from these authors, we included the entire study site in these calculations, not just the portion of the site occupied by willows.

Our estimates of breeding densities are probably low because we considered a singing male Willow Flycatcher to be mated only if we had definitive evidence that he was paired. Definite evidence included our finding a nest or observing nesting behavior (carrying food or nesting material) on the male's territory. We also considered a male mated if we repeatedly observed a non-singing, unchallenged Willow Flycatcher (i.e. a female) on the male's territory. Even if we assumed all the singing males at the study sites to be mated, the densities of breeding Willow Flycatchers at our sites are still lower than those reported elsewhere.

The low densities may reflect a relatively low carrying capacity at the meadows we studied. Alternatively, the meadows might be capable of supporting more Willow Flycatchers, but the population may be too small to fill the available habitat.

Unmated Singing Males

At both study sites and during both years we observed unmated singing males defending territories. In 1986 we observed one to two unpaired males at Lacey Valley, and at least three unpaired males at Perazzo Meadows. In 1987, Lacey Valley supported one or two unpaired males, and Perazzo Meadows contained three to five unmated singing males. We are uncertain as to the exact number of unpaired males because only a few of these individuals were banded.

Stafford and Valentine (1985) also noted unmated singing males at their study sites in the southern Sierra. They reported at least two unpaired male Willow Flycatchers out of 10 singing males. At the Nature Conservancy's Kern River Preserve, Harris (pers. comm.) confirmed paired status for only eight out of 12 singing male Willow Flycatchers.

Researchers attempting to estimate the number of breeding pairs based on the number of singing Willow Flycatchers should be aware that a significant percentage of the singers may be unmated males.

Behavior

Foraging

Willow Flycatchers are "sit-and-wait" predators that catch insects on the wing. Their two feeding behaviors are hawking (sallying forth from a perch to capture flying insects) and aerial gleaning (picking insects from vegetation) (Verbeek 1975). We observed far more hawking than gleaning at our study sites; Frakes and Johnson (1982) reported gleaning frequencies up to 45% and 35% at their two study sites in Washington. Males hawked mostly from perches greater than 3 m (10 ft) on their territories, particularly while singing. Females were less conspicuous, and perched and foraged in the lower willow branches.

Most foraging Willow Flycatchers flew less than one meter from a perch to hawk insects, although they occasionally pursued insects for up to 10 m (33 ft). Frakes and Johnson (1982) reported the average foraging flight distance from a perch to be about 4 m (13 ft). We noted that Willow Flycatchers shifted their foraging perches every few minutes, and sometimes foraged from perches outside their territories.

Both males and females fed the nestlings and fledglings. The average interval between feedings was 2.5 minutes (n = 29, s.d. = 1.7 minutes, range = 0.25 - 6.7 minutes).

Interspecific and Intraspecific Interactions

In 1986 we observed Willow Flycatchers engaged in 93 aggressive interactions (40 intraspecific, 36 interspecific, and 17 unknown) during 425 hours of observation. In 1987 we observed 27 aggressive interactions (10 intraspecific, 10 interspecific, and 7 unknown) in 385 hours of observation. Aggressive interactions typically consisted of a vocalization in response to an intruder, sometimes followed by a pursuit flight. Physical contact during interactions was rarely observed.

King (1955) observed that Willow Flycatchers were rarely involved in territorial fighting after laying began, but noted that territorial disputes among males were frequent and violent during the nesting season. Dawson (1923) described this species as "restless, energetic, and pugnacious to a fault." Bent (1963) also considered the Willow Flycatcher to be an aggressive bird, and quoted Wheelcock: "this Flycatcher is never so occupied as to miss a chance of driving another bird, great or small, away from the special clump of alders which the pugnacious mite has preempted for his own."

Nest Site Fidelity/Return Rates

We banded 16 birds in the two study sites in 1986. Five males, four females, and one fledgling were banded at Perazzo Meadows, and two males, three females, and one fledgling were banded at Lacey Valley. The only banded birds that returned in 1987 at either study site were four males banded at Perazzo Meadows. Of these four males, three (#l, #4A, and #12) returned to the same patch of willows and established similar territorial boundaries. The territory of male #4 in 1987 was approximately 1 km (0.6 mi) from his 1986 site.

The Kings River Conservation District (1985) studies recorded similar return rates for banded Willow Flycatchers in the southern Sierra. Of 12 adults and four nestlings banded in 1983, only four adults returned in 1984. One pair nested in the same territory in 1983 and 1984. In 1984 they placed their nest less than 15 m (50 ft) from the 1983 nest site. A female banded in 1983 successfully nested in 1984 at a site 14.5 km (9 mi) from her 1983 territory.

The return rates of adults and fledglings reported in this study and by the KRCD are similar to those observed in other migratory birds. Welty (1975) cited a study of Tree Swallows (Tachycineta bicolor) in which the return rate for adult swallows ranged from 7 - 55% and averaged 39.6%. The return rate for nestlings varied from 0 - 5% and averaged 2.4%. A similar study of House Wrens (Trogolodytes aedon) (Welty 1975) indicated adult return rates of 34%, and only 2.06% return for banded young. Franzreb (1988), however, reported remarkably high return rates for an endangered riparian bird, the Least Bell's Vireo (Vireo bellii pusillus). She reported 31 out of 50 banded birds returning after they had been banded.

Variation and Significance of Vocalizations

The songs and calls of the Willow Flycatcher have been well-described by King (1955), Stein (1963), and Weydemeyer (1973). We include some information here on Willow Flycatcher vocalizations at our study sites to compare and contrast our observations with those of other workers.

"Fitz-bew". This song sounds explosive, sneeze-like, and carries well. Its purpose is to defend territories and advertise for mates, and it is usually given from the highest, most exposed perch sites in the territory. King (1955) and others (Dawson 1923, Bent 1963) described a three-syllable vocalization given by Willow Flycatchers variously recorded as "fitz-be-o" or "zwee-bew, zzweet". We did not hear any three-syllable songs given by birds at our study sites. One-syllable songs that consisted of a single "fitz" were often given intermittently during "fitz-bew" song bouts.

It has generally been assumed that only the male gives the "fitz-bew" song, but Seutin (1987) reported female Willow Flycatchers singing in response to tapes. He believes they sing under natural conditions also. Among banded Willow Flycatchers at our study sites, the only birds we observed singing "fitz-bew" songs were ones we identified as males. Our identification of the birds as males was based on behavioral observations and in-hand inspection for cloacal protuberances and brood patches.

"Whit". The "whit" call is given by both males and females, and is probably a contact call between mates. It is often given when the birds are near the nest. The "whits" given by males and females differ slightly in quality. The female's call is quieter and softer, and the male's tends to be louder and more staccato.

"Whit" calls are given during aggressive interactions with other birds, and also when the birds are agitated. For example, a human observer approaching a nest will often elicit "whit" from the adults, although parents sometimes remained silent during nest inspections. Bill-snapping sometimes accompanies the "whits" during aggressive interactions or when humans are close to the nests, and seems to indicate extreme agitation.

"Churr". This low, slurred call is given by Willow Flycatchers when near the nest. The birds are usually out of sight in willow foliage when they give it. Its function is unknown.

"Da-dink". This metallic-sounding, two-part call is given only by fledglings. Fledglings utter this call almost continuously, and the vocalization accelerates into a twitter when the parents approach with food. It apparently functions as a location call for the fledglings, allowing them to remain in contact with each other and with the parents.

"Wheeo". Parent birds give this call near the end of the breeding season when fledglings are present and being fed. It probably serves as a contact call between parents and young.

Seasonal Song Frequency

Male Willow Flycatchers in Washington sang most frequently in the early stages of territory establishment, and that singing diminished throughout the incubation period (Ettinger and King, 1980). Singing had decreased to "essentially zero" by the time the young have fledged. In the southern Sierra Nevada males with females on the nest rarely sang (unless provoked by a tape recording) and even then at greatly decreased rates (KRCD 1985). The KRCD reported singing rates of 8-20 songs per minute in the pre-nesting season.

Our observations indicate that male Willow Flycatchers sing more often early in the season than during the later stages of breeding. However, we found that males sing at any time during the breeding season and sometimes sing intensely even with eggs, young, or fledglings on their territories. We recorded males singing at a rate of 2-18 songs per minute in the pre-nesting season. In the mid-to-late nesting season when nests contained eggs or young, a few males were singing at rates of 2-23 songs per minute. We even observed one male singing at the extraordinary rate of 33 songs per minute while he and his mate were feeding fledged young on his territory.

Although males sometimes sing spontaneously and intensely when they have active nests, they are much more likely to sing spontaneously early in the season. In late June or early July, before nesting is underway, most or all males sing in the morning. In the late nesting season, an observer might not hear a single Willow Flycatcher song from dawn to dusk.

No consistent patterns account for the variation in singing rates for individuals, or for the variation among individuals on different days. Windy or hot weather seemed to have a depressing effect on song (and most other activities) for all individuals. A singing male often provoked singing responses from neighbors, as would the intrusion of another Willow Flycatcher or other species on a male's territory. We did not detect any differences in singing rates between mated and unmated males, although the variation in singing rates for all males made discerning such differences difficult. The only generalization we can make is that males are less likely to sing spontaneously late in the breeding season than in the early part of the season. Our results have two implications for those studying or censusing Willow Flycatchers. First, caution should be exercised before inferring the breeding status of male Willow Flycatchers based on song rates. Second, breeding surveys conducted early (late June and early July in the mid-elevation Sierra Nevada) are likely to detect more singing male Willow Flycatchers than those conducted late in the breeding season.

Diurnal Variation in Song. Willow Flycatchers are usually the first birds to sing in the meadows at first light. The peak of Willow Flycatcher singing occurs from before dawn to a few hours after dawn. We compared singing activity of males from dawn to 0830, and from 0830 to noon. Singing activity was defined as the number of times per hour a male changed perches and sang from the new perch. The early morning singing activity rate ($n = 42$, mean $= 9.4$, s.d. $= 7.1$) was higher than the late morning singing rate ($n = 22$, mean $= 3.6$, s.d. $= 4$).

Although males were more likely to sing in the early morning, they spontaneously sang any time during the day. Wedemeyer (1973) also reported that Willow Flycatchers sang throughout the day. Other workers (Berger and Parmelee 1952, King 1955) have noted peaks of singing activity in the morning and the evening, and that few Willow Flycatchers "are heard in midday except in infrequent territorial disputes" (King 1955, p. 169).

Reproduction

Nesting Chronology

Willow Flycatchers arrive and breed late compared to other passerines nesting in Sierra meadows. Willow Flycatchers arrive at their breeding territories in early to mid-June, and form pairs and establish territories by late June. Incubation lasts 12 days and is performed only by the female (King 1955). Two to four eggs are laid, with three to four most common (Bent 1963). The nestling period lasts approximately 14 days (King 1955).

In 1986 Willow Flycatchers had paired and established territories by late June. The first Willow Flycatcher eggs were laid around 20 June, and the first fledglings appeared by mid-July (Figure 5). Eggs were still being laid by 22 July, and the last young fledged on 14 August. Territorial defense declined during the week of 28 July, and the last breeding Willow Flycatchers left the study areas by the final week of August.

The early part of the 1987 breeding season was similar to 1986 (Figure 6). The first eggs were laid around the third week of June. The first fledglings appeared on 15 July. Fledglings were last observed on 4 August, and territories had broken down by 10 August. Breakdown of territories was probably accelerated by a July 17 snowstorm which destroyed most of the eggs and young at our study sites.

Nesting Success

In 1986 ten pairs of Willow Flycatchers produced a minimum of 31 eggs from 11 nests (Figure 5). This figure probably underestimates the total number of nests because we found some nests late in the season after eggs and nestlings had already been lost. For example, by the time we found nest #6 it contained only two nestlings. The nest probably started with a clutch of three or four eggs. The total number of young fledged in 1986 was 14 or 15 (we are uncertain whether 3 or 4 young fledged from nest #5). For five of the 11 nests, we had complete egg-to-fledgling data. Fourteen eggs from these nests produced five fledglings.

In 1987 ten pairs of Willow Flycatchers produced at least 32 eggs (Figure 6). Only six survived to fledgling, an egg-to-fledgling ratio of about 19%.

Nice (1957) reported a 46% egg-to-fledgling success rate for open-cup nesting birds, a significantly higher value than reported in our study. KRCD (1985) reported egg-to-fledgling successes of 25% and 38% for Willow Flycatchers during the two years of its study, also substantially lower than reported by Nice (1957). Harris (pers. comm.) found a 24% nesting success for eight pairs of Willow Flycatchers nesting at the Kern River Preserve. The low success rate at the Kern Preserve was largely the result of nest parasitism by Brown-headed Cowbirds.

Sources of egg and nestling mortality

Unusually cold and wet weather was the primary known source of egg and nestling mortality in 1987. On 17 July, a snowstorm hit the northern Sierra, followed by four days of cold, rainy, and windy weather. According to local residents, a snowstorm of this duration and intensity was a rare event for that area. We found eighteen dead nestlings in six nests on 21 July. One nest containing nestlings was upset by heavy winds, but the other young probably died from exposure or starvation. The storm was also responsible for the loss of three of four eggs in two nests. One egg survived the storm and hatched twelve days later, but this nestling subsequently disappeared. Six young Willow Flycatchers from two nests at Perazzo Meadows fledged before the storm, and survived the bad weather. We observed no adult Willow Flycatcher mortality as a result of the storm.

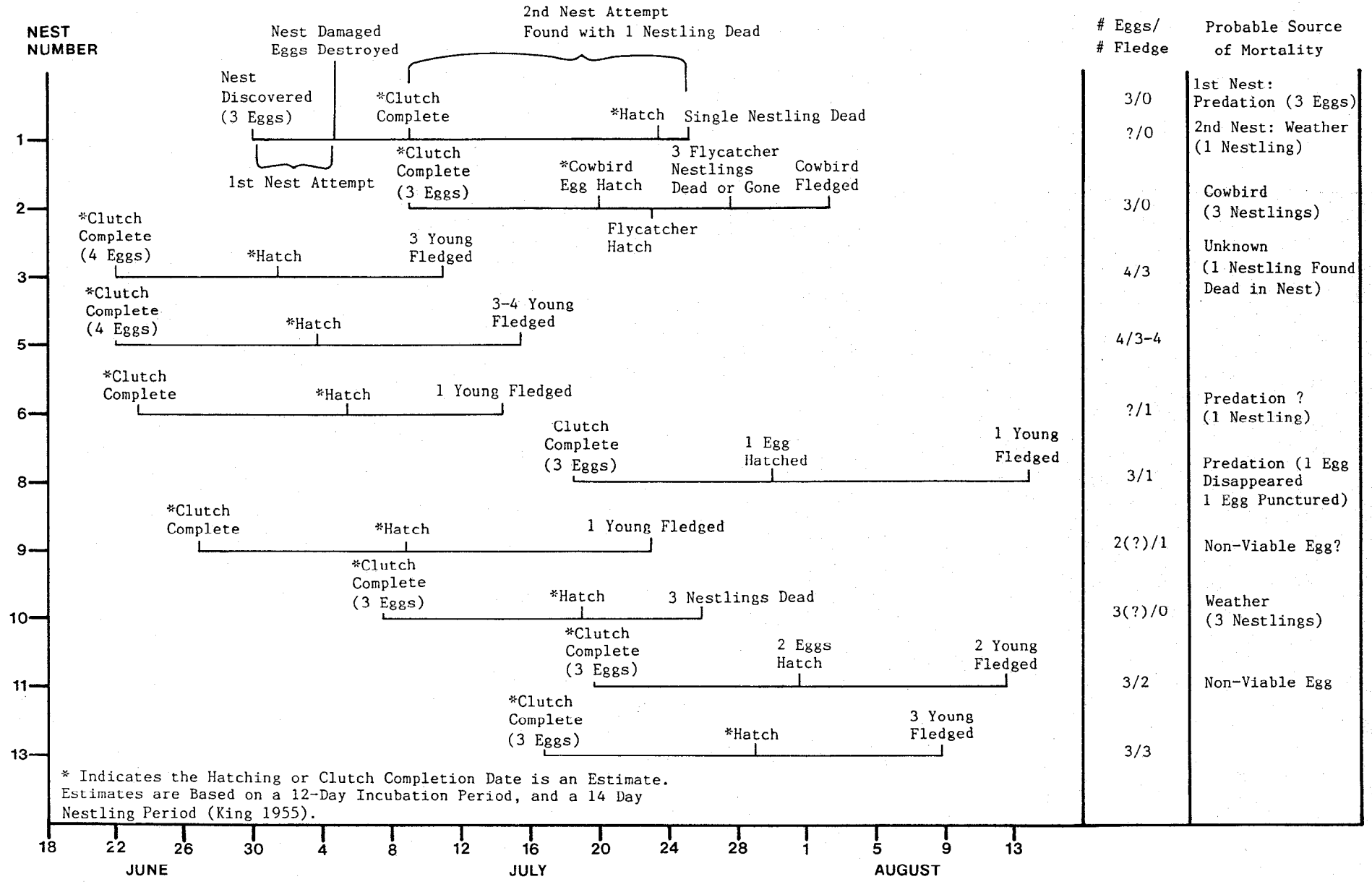

FIGURE 5. Reproductive chronology and nesting results from 11 Willow Flycatcher nests at Perazzo Meadows and Lacey Valley, California, 1986.

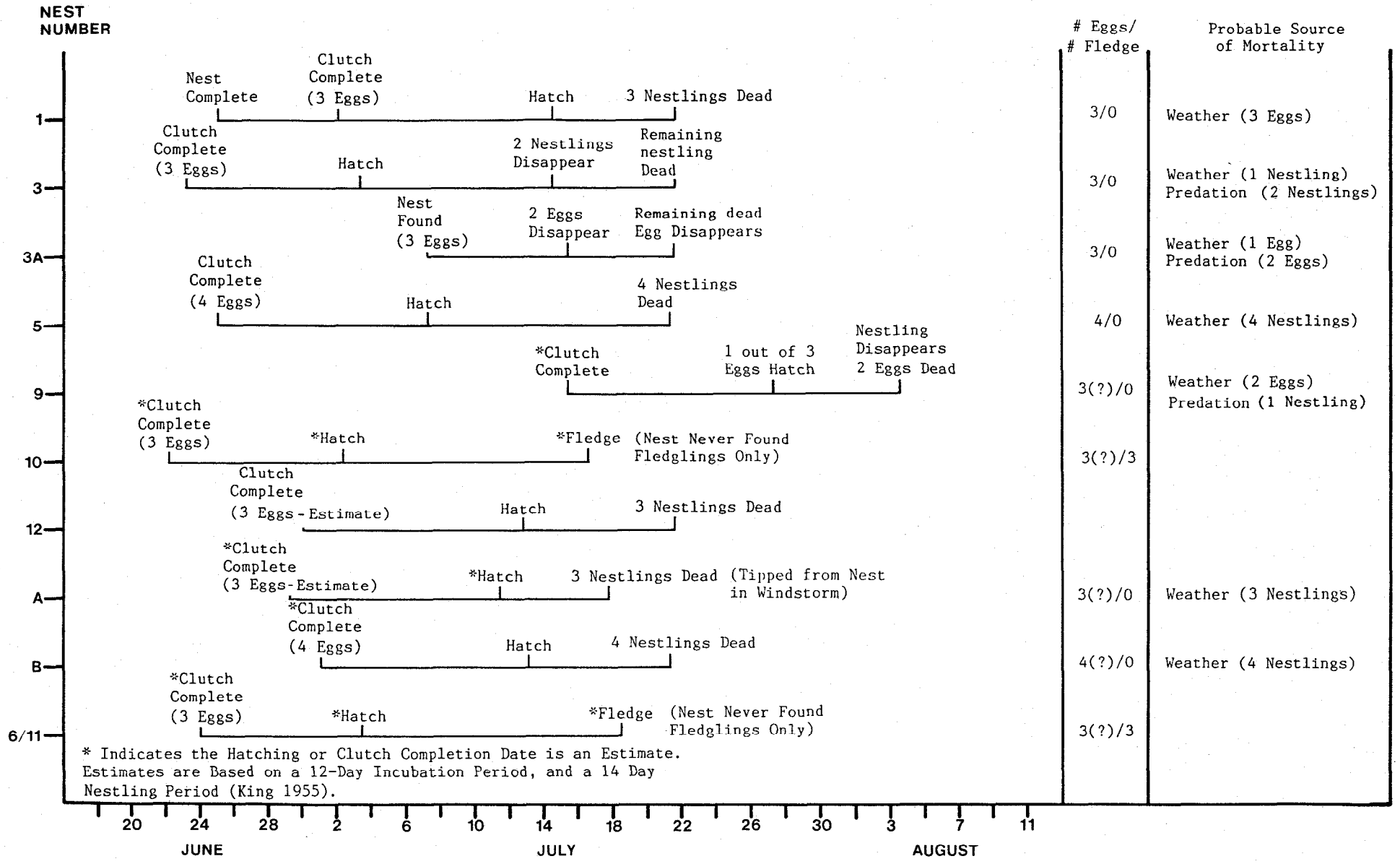

FIGURE 6. Reproductive chronology and nesting results from 10 Willow Flycatcher nests at Perazzo Meadows and Lacey Valley, California, 1987.

Inclement weather also caused nestling mortalities in 1986. The single nestling in nest 1A and all three nestlings in nest 10 died after a severe hailstorm on 25 July, 1986.

Predation may have been another important factor in egg and nestling loss. In 1986 an egg and a nestling from two different nests disappeared. In 1987, three eggs from two different nests and three nestlings from two other nests also disappeared. The nests were typically intact after the egg or young disappeared, and in no case did all the young or eggs disappear. This assessment of predation on eggs and nestlings may be an underestimate. We first discovered some nests after predation occurred and found only one or two remaining eggs or nestlings.

Nests were relatively accessible to predators because they were near the ground and close to the edge of willow clumps. However, there were few obvious potential predators in our study area. Steller's Jays (Cyanocitta stelleri) and other avian predators were uncommon in our study site. Long-tailed weasels (Mustela frenata) pine martens (Martes americana) and coyotes (Canis latrans) were also present, but these mammals would also be expected to damage the nests. As noted above, nests were not damaged after eggs disappeared.

Other known sources of egg and nestling loss included infertile or non-viable eggs (two eggs from two different nests). In addition, one egg did not hatch because it had been punctured. The number of non-viable eggs reported here is considerably lower than that reported from studies by the KRCD. Valentine et al. (1988) reported seven of 19 eggs as non-viable.

Net Reproductive Rate

The net reproductive or replacement rate for Willow Flycatchers in the Sierra Nevada can be calculated based on the two years of nesting results discussed above, and on studies by Harris (pers. comm.) and the KRCD (1985). The net reproductive rate is defined as the average number of female young produced by each female during her entire lifetime (Wilson and Bossert 1971).

Conservatively assuming a 50% annual mortality rate for young and adults, the net replacement rate for Willow Flycatchers in the Sierra Nevada is approximately 0.5 (Appendix I). A replacement rate less than one indicates a declining population (Wilson and Bossert 1971). This calculation does not include immigration and recruitment from populations outside California, and may be overly pessimistic because it incorporates the catastrophic 1987 season. Even without the 1987 nesting results from our study, however, the net replacement rate is still less than one. This calculation reflects the vulnerability of the state's remaining Willow Flycatcher populations to local extinction.

Habitat Requirements

Territory Size

Territories of mated male Willow Flycatchers ranged from 0.056 - 0.89 ha (0.145 - 2.19 acres) and averaged 0.34 ha (0.84 acres) (s.d. = 0.20 ha) (Table 1). Much of the willow habitat at Perazzo Meadows and Lacey Valley was undefended and unoccupied by Willow Flycatchers. Territories rarely overlapped or shared common borders.

The KRCD (1985) reported an average territory size of 0.20 ha (0.48 acre) and a range of 0.09 - 0.38 ha (0.22 - 0.94 acres) in the southern Sierra (n=15). Walkinshaw (1966) calculated an average territory size of 0.70 ha (1.74 acres) for 73 territories in Michigan.

Although Willow Flycatchers conduct most of their foraging and other activities within their territories, both males and females use areas adjacent to their territories, especially when feeding young. Throughout the breeding season, males and females regularly used perches outside their defended territory for foraging. These perches ranged from 4 - 30 m (13 - 98 ft)

beyond the boundaries of the territory. The average foraging perch distance from the territory was approximately 19 m (62 ft)(n = 30, s.d. = 8.4 m). When parents were feeding nestlings and fledglings, they sometimes foraged as far as 100 m (330 ft) from their territory.

These territory sizes do not necessarily reflect the amount of habitat required to sustain a family of Willow Flycatchers. A more conservative estimate would be an area amounting to the average territory size, with a 20 m (66 ft) foraging buffer surrounding it. Assuming a 0.34 ha (0.84 ac) Willow Flycatcher territory, with a 20 m (66 ft) buffer beyond the territorial boundary, the combined territory and adjacent area amounts to approximately 0.88 ha (2.2 acres).

The 0.88 ha (2.2 acres) area calculated here may also underestimate the area needed to support a pair of Willow Flycatchers and their young. Throughout the breeding season Willow Flycatchers feed on insects that are produced on their territories and in the surrounding wet meadow and pools (Harris et al. 1987). After surveying 125 meadows in the Sierra Nevada, Harris et al. (1987) found Willow Flycatchers only in meadows 4 ha (10 acres) or larger. Four ha (10 acres) may reflect the optimal area for Willow Flycatchers in the Sierra Nevada. It should be noted, however, that meadows as small as 0.25 ha have supported successfully breeding Willow Flycatchers (KRCD 1985a).

Territory Characteristics

Willows. All Willow Flycatcher territories included willow clumps interspersed with clearings. The willow cover on 22 territories ranged from 5 - 80% (mean = 44%, s.d.= 22%). Foliage density was 54% (range = 18 - 78%, s.d. = 17%) from 0 - 1 m (0-3 ft), and 69% (range = 45 - 96%, s.d. = 18%) from 1 - 2 m (3 - 7 ft).

Willow clumps on the 22 territories were patchily distributed, with thickets of willows interspersed with open meadow. The size and distribution of willow clumps varied widely among territories; some territories contained many small (less than 2 m (7 ft) at longest dimension) willow thickets, while others included one or several large (greater than 16 m (52 ft) at longest dimension) willow clumps. The consistent element in all of the territories was the interspersion of willow thickets with open space. Areas consisting of solid, contiguous masses of willows were available at both study sites, but did not support Willow Flycatchers.

Tree and Grass Cover. Eleven out of 22 territories included lodgepole pines or snags, but these trees typically covered less than one percent of the territory. Approximately 70% (range 10-90%, s.d. = 29%) of the territories were covered by sedges and grasses.

Water. Our results indicated that water is an essential component of Willow Flycatcher territories. Twenty of 22 territories encompassed the Little Truckee River, or less often old oxbows or small secondary channels. The other two territories were 10 meters (33 ft) or less from the river.

Willow Flycatcher territories dried out as the summer progressed; the deep pools and saturated soils characteristic of the entire meadow in late June and early July changed to empty channels and relatively dry soils by early August. Water was not necessarily present during the latter stages of the breeding cycle, but was always available during the early stages of breeding and pair formation for all 22 territories we measured.

Summary and Comparison with Other Studies. Our findings regarding Willow Flycatcher habitat affinities are supported by observations from other California ornithologists. KRCD (1985a) notes that free water is required for Willow Flycatcher breeding territories, and that 50 to 70 percent cover by patchy clumps of willow thickets is optimal. Dawson (1923, p.885) describes Willow Flycatcher habitat affinities as “a lover of the half-

open situations, brushy rather than timbered, of clearings, low thickets, and river-banks." Grinnell and Storer (1924 p.371) describe Traill's Flycatcher as: "restricted to willow thickets of broad bottomlands." Other workers have also commented on openings as a common element of Willow Flycatcher habitat (Meanley 1951, King 1955, Walkinshaw 1966, Gorski 1969, Serena 1982).

On the basis of our studies and those of other California researchers, water and willows emerge as the critical elements on Willow Flycatcher territories in the Sierra Nevada. This information should prove useful to land managers who want to enhance Sierra meadows for Willow Flycatchers. For example, where suitable conditions exist, meadows that lack willows could be enhanced by planting willows and by reducing grazing pressure to encourage their rapid growth. Meadows whose water tables have been lowered by erosion and deep incision of creek beds (usually brought about by livestock grazing [Ratliff, 1984]) could be restored to moister hydrological regimes by stream restoration techniques. Clay (1984) describes how installation of low cost rock grade-stabilization structures and revegetation along the rock sills encourages rapid willow growth and wetter meadows.

Characteristics of Nest and Nest Site

At Perazzo Meadows and Lacey Valley, Willow Flycatchers always built their nests in willows, the only shrubs available on their territories. Lodgepole pines were never used for nesting, although they occurred on half of the territories in Perazzo Meadows. Nests were consistently placed about one meter above the ground, and about one meter below the top of the willow foliage (Table 2). Willow Flycatcher nests were typically placed about two meters from the edge of the willow clump, and were invariably less than two meters from a livestock trail through or near the willows (Table 2). The density of willow foliage around the nest averaged about 70% (n = 11, s.d. = 25%, range = 10 - 95%).

Willow Flycatchers build open-cup nests. At our study sites the nests were constructed of sedges and grasses on the outside, and were lined with finer grasses. Nests at Lacey Valley, where sheep graze, were also lined with sheep wool. String, feathers, and tissue paper were occasionally used as lining. Grasses hung below the woven cups, giving the nest bottoms a beard-like appearance. The average outer diameter of the nest was 8.7 cm (3.4 inches) (n = 20, s.d. = 1.3 cm, range = 6 - 11 cm).

Nests were usually well-anchored on willow twigs, but sometimes were insecurely woven onto thin twigs, making them vulnerable to tipping. The cups of the nests were woven around and supported by 3 - 7 vertically slanting twigs (n = 9, mean = 4.7, s.d. = 1.3). The average diameter of the twigs supporting the nests was 0.62 cm (0.24 inches) (n = 36 twigs from 9 nests, range = 0.15 - 2.5 cm, s.d. = 0.54).

The nest characteristics of Willow Flycatchers at our study sites are similar to those reported by Valentine (1987), and Valentine et. al. (1988). They also reported Willow Flycatchers in the southern Sierra Nevada nesting about one meter off the ground in willows, with nest placement close to the edge of a willow clump.

TABLE 1. Size and characteristics of twenty-two Willow Flycatcher breeding territories at Perazzo Meadows and Lacey Valley in 1986 and 1987.

Terr #	Total Area (m^2)	Percent Willow	Percent Foliage Density 0-1m	Percent Foliage Density 1-2m	Proximity to water
1986					
3	2,397	40	62	77	on territory
5	1,159	80	78	82	10 m to river
8	3,575	30	76	77	on territory
9	6,977	50	44	96	5 m to river
10	594	20	58	78	on territory
11	4,332	66	72	74	on territory
13	1,746	16	76	76	on territory
15	2,925	70	47	81	on territory
1987					
1	1,804	40	24	63	on territory
3	1,950	80	52	46	on territory
3A	2,464	50	25	82	on territory
3B	3,991	25	18	50	on territory
3C	1,898	35	49	97	on territory
4A	1,789	60	44	59	on territory
5	2,700	40	57	45	on territory
8	8,944	30	45	45	on territory
9	5,907	80	--	--	on territory
10	2,161	45	--	--	on territory
12	5,181	20	55	48	on territory
A	5,400	30	74	75	on territory
B	3,611	60	64	66	on territory
C	3,164	5	60	47	on territory
mean =	3,94m^2	44%	54%	69%	
s.d. =	2,042 m^2	22%	17%	18%	

TABLE 2. Characteristics of 20 Willow Flycatcher nests at Perazzo Meadows and Lacey Valley in 1986 and 1987.

Nest #	Distance of nest from: Ground (m)	Top of Foliage (m)	Edge of Willow (m)	Livestock Trail (m)	Nest Diameter (cm)	Nest Depth (cm)	Foliage Density (%)
1986							
1	1.00	1.50	1.00	1.00	9.0	8.0	55
1A	1.98	1.00	2.40	2.40	9.0	7.5	65
2	0.90	1.30	1.50	1.50	6.0	11.0	10
3	1.30	1.10	1.40	1.40	9.0	7.0	85
5	1.75	0.50	2.30	2.30	11.0	--	--
6	1.10	1.00	0.60	0.60	8.0	11.0	--
8	1.57	1.00	2.00	2.00	8.0	10.0	--
9	1.46	1.25	2.00	2.00	10.0	14.0	--
10	1.28	1.00	6.00	1.50	10.0	8.0	90
11	1.10	1.25	7.50	2.50	9.0	8.0	--
12	1.56	0.80	2.00	0.60	8.0	10.0	75
1987							
1	1.15	0.75	1.00	1.00	9.0	10.0	--
3	0.80	0.70	1.80	1.80	8.0	12.0	90
3A	1.10	0.70	--	--	9.0	9.0	--
3B	1.23	0.84	1.66	1.66	6.0	12.0	95
5	0.90	1.25	2.50	2.50	8.0	10.0	--
9	1.25	0.60	1.30	1.30	7.5	8.0	90
12	0.80	0.60	2.00	2.00	9.0	8.0	80
A	0.80	1.00	1.00	1.00	9.0	9.0	60
B	0.70	1.00	3.50	3.50	11.0	11.0	--
mean	1.14	0.96	2.3	1.71	8.7	9.7	72%
s.d.	0.29	0.27	1.7	0.74	1.3	1.9	25

Effects of Cowbirds and Livestock

Brown-headed Cowbird Nest Parasitism

One out of 22 Willow Flycatcher nests at our study sites was parasitized by a Brown-headed Cowbird. A single cowbird fledged successfully, but its three Willow Flycatcher nestmates died. One of the newly hatched nestlings was pushed out of the nest, presumably by the 4-5 day old cowbird nestling. We found the ejected Willow Flycatcher nestling still alive beneath the nest and returned it to the nest, which contained two unhatched eggs. One Willow Flycatcher nestling died and two disappeared from the nest a few days after hatching.

We observed several other species feeding juvenile cowbirds at our study sites, including Song Sparrows (Melospiza melodia), Dark-eyed Juncos (Junco hyemalis), Dusky Flycatcher (Empidonax oberholseri), and Hermit Warblers (Dendroica occidentalis).

Low numbers of cowbirds were present at Lacey Valley and Perazzo Meadows throughout the study. We estimated a population of approximately 10 - 15 adult Brown-headed Cowbirds at Perazzo Meadows, and about the same number at Lacey Valley. By late July and early August this number rose to about 50 cowbirds at each site due to an influx of juveniles. Cowbirds were usually closely associated with cattle or sheep, foraging at their feet or on the sheep's backs. We observed cowbirds with the sheep flocks at Lacey Valley on nine of 20 visits to the site, with 5 -50 birds present.

Brown-headed Cowbird nest parasitism has been suggested as a cause of the Willow Flycatcher's decline in California (Remsen 1978). Their decline in central and coastal California coincides roughly with the spread of cowbirds in the 1920's and 1930's (Gaines 1977, Garrett and Dunn 1981). Friedmann (1963) reported 150 instances of Brown-headed Cowbird parasitism of Willow Flycatchers, 41 of which were reports from southern California.

Less evidence exists for cowbird parasitism in the higher elevations of the Sierra Nevada. Except for our observation of cowbird parasitism, the only other record of Willow Flycatcher nest parasitism in the mid-to high elevation Sierra Nevada was from the Lake Tahoe region in 1960 (Gaines 1977). Stafford and Valentine (1985) did not report any cowbird parasitism in their studies of Willow Flycatchers in the southern Sierra.

In contrast to our results, Harris (pers. comm.) found intense parasitism of Willow Flycatchers at the Kern River Preserve in 1987. The Kern River Preserve is a willow-cottonwood riparian woodland at 750 m (2400 ft) in the Sierra foothills. At least 13 and possibly 16 of 19 Willow Flycatcher nests were parasitized by cowbirds. The 19 nests were built by eight pairs, that typically abandoned parasitized nests and rebuilt new ones. Six fledglings were produced from three unparasitized nests, and four Willow Flycatcher young fledged from nests that were parasitized so late that the cowbirds did not hatch. Other parasitized nests did not produce any Willow Flycatcher fledglings. A total of ten fledglings were produced by eight pairs.

Stafford and Valentine (1985) suggested that peak Willow Flycatcher egg laying in the high-elevation Sierra Nevada often occurs after the peak of the cowbird breeding season. King (1955) also noted that the peak of egg deposition by Willow Flycatchers in Washington occurred considerably after the height of the cowbird egg-laying season. He found only two of 44 Willow Flycatcher nests parasitized. On the other hand, studies of a high elevation (2,500m) Willow Flycatcher population in north central Colorado documented cowbird parasitism in at least 11 of 27 nests (Sedgwick and Knopf, 1988). These 11 nests were built by 15 pairs of Willow Flycatchers, so at least 73 % of pairs were parasitized. Nest success was 18% for parasitized nests.

Cowbird parasitism of Willow Flycatcher nests is a potential threat at high elevations, and clearly is a serious problem at lower elevations in California. Actions can be taken to minimize this threat. Laymon (1987) suggested that reducing or eliminating livestock grazing in mountain meadows could increase the reproductive success of Willow Flycatchers. Elimination of grazing allows grass to grow too tall to be suitable cowbird foraging habitat, and it removes the large grazers with which cowbirds associate.

Results of another study of cowbird parasitism of songbirds may also have management implications for lower elevation Willow Flycatchers and cowbirds (Airola 1986). His studies in the northern Sierra Nevada indicate cowbirds frequently feed in disturbed areas where high-energy foods are concentrated, including residential areas with bird feeders, campgrounds, livestock concentration areas, and garbage dumps. Such developments should be located away from riparian areas to minimize the impacts of the cowbirds on host-rich areas (Airola 1986).

Effects of Livestock Grazing

Direct Effects. Cattle can directly impact Willow Flycatchers by knocking over their nests. Stafford and Valentine (1985) and Valentine (1987) reported 4 of 20 nests monitored over a four-year period were destroyed by cattle. Livestock also destroyed four nests shortly after the young had fledged.

Perazzo Meadows contained approximately 150 cattle in 1986, and up to 360 in 1987. Although cattle arrived during the Willow Flycatcher breeding season in late June and early July, we did not observe any nests upset by livestock. However, we found that Willow Flycatchers usually place their nests near the edge of willow clumps or along livestock trails (Table 2), making them vulnerable to disturbance by cattle. Our data also show that a small percentage of cattle graze within willow clumps in their search for shade and forage. An average of 6% of a cattle herd was found within a willow clump (n = 48, range = 0 - 76%, s.d. = 11.3%).

Lacey Valley supported about 1000 sheep in 1986, and 1500 in 1987. We did not observe any direct impacts of sheep on Willow Flycatcher nests, in part because the flock spent relatively little time in the riparian habitat at the meadow. Unlike cattle, sheep travel as a flock under the control of a shepherd. The few riparian areas that were grazed by sheep showed signs of localized but intense use. Streambanks were eroded at sheep crossings, soils were exposed where they grazed on preferred forage, and they created large tunnels through the willows.

Indirect effects. Livestock indirectly affect Willow Flycatchers by altering the vegetation and hydrology of montane meadows. Cattle and sheep consume the lower branches and shrub layers of streamside vegetation and consume or trample young riparian plants (Taylor 1986). Mosconi and Hutto (1982) found that obligate riparian species are more affected by grazing than other bird species. Duff (1979) reported a large increase in the number of passerine birds after excluding cattle from a riparian area. The increase was due to the reestablishment of the middle story of willows.

Livestock grazing can also reduce water quality, compact soils, and accelerate streambank erosion (Thomas et al. 1979, Platts 1984). Streambank erosion due to overgrazing can eventually result in incision and gullying of streambeds (Ratliff 1984). Gullying can lower the water table of moist meadows (Van Haveren and Jackson 1986), thus drying the soils and eliminating species that prefer saturated soils.

Taylor and Littlefield (1986) documented the adverse effects of cattle grazing on Willow Flycatcher populations at Malheur National Wildlife Refuge in Oregon. By censusing riparian transects with different grazing histories, they found that areas ungrazed for forty years supported significantly more Willow Flycatchers than grazed transects. Willow foliage volume and density was significantly lower in the grazed transects, and these areas had no Willow Flycatchers. Taylor and Littlefield (1986) also present 12 years of U.S. Fish and Wildlife Service Breeding Bird Survey data indicating a significant relationship between increased Willow Flycatcher numbers and decreased grazing intensity.

MANAGEMENT RECOMMENDATIONS

List the Willow Flycatcher as Endangered in California - Willow Flycatchers need the legal protection that Endangered status would provide. According to data presented in this and in other studies, Willow Flycatcher populations have dwindled to a small fraction of its former size, and very few are found in lowland California where it was once widespread and abundant. The remaining scattered populations are not replacing themselves (see Appendix I); if present trends continue, the Willow Flycatcher may be extirpated as a breeding bird in California.

Protect Habitat - Most of the Sierra Nevada meadows currently supporting breeding Willow Flycatchers are managed for livestock grazing and other consumptive uses rather than for wildlife resources. These meadows are vulnerable to inundation by hydroelectric projects, housing or recreational development, overgrazing by livestock and cowbird parasitism. Montane meadows and riparian areas that support Willow Flycatchers should be protected and managed as a primary resource on public lands. The U.S. Forest Service, which lists the Willow Flycatcher as a Sensitive Species, should abide by their own management guidelines in protecting habitat for this species. Occupied and potential sites on private lands should be protected by conservation easements with landowners or by land purchases or exchanges. In particular, efforts should be made to permanently protect the meadow system along the Little Truckee River. These meadows support the second largest known Willow Flycatcher population in the state, and our study indicates that this population may be declining.

Eliminate or Delay Grazing - To avoid the direct and indirect impacts associated with livestock, grazing should be reduced or eliminated on meadows and riparian areas that support Willow Flycatchers. One alternative to eliminating grazing is to delay putting cattle on high elevation meadows until mid-August, after Willow Flycatchers have fledged. Another option is to exclude cattle from the vicinity of streams and riparian vegetation by fencing, providing an alternate source of water by means of stocktanks.

Monitor Existing Populations and Survey for New Ones - Surveys are needed to determine the status of Willow Flycatchers in southern and north coastal California, the Klamath Mountains, the Warner Mountains, and the Cascade Range. Sites known to support this species should continue to be monitored on a regular basis to determine population trends.

Control Brown-headed Cowbird Populations - An active cowbird trapping program should be implemented to reduce cowbird parasitism at the Kern River Preserve and other low elevation areas that support Willow Flycatchers (e.g. San Luis Rey and Santa Margarita rivers). To minimize the chances of cowbird parasitism on Willow Flycatchers elsewhere in suitable montane meadows, livestock grazing and other developments that enhance cowbird habitat should be avoided.

Avoid Developments Adjacent to Montane Meadows - Cowbirds frequently feed in disturbed areas where high energy foods are concentrated, including residential housing with bird feeders, campgrounds, corrals, and garbage dumps (Airola 1986). Such developments should be kept away from riparian areas to minimize the impacts of cowbirds on Willow Flycatchers and other species nesting in willow thickets of mountain meadows.

Reveaetate and Restore Willow Flycatcher Habitat - The response of Willow Flycatchers to revegetation and meadow restoration should be explored as part of a comprehensive plan of habitat protection and enhancement. Restoration of Willow Creek in Modoc County provides a promising model of such efforts (Clay 1984). In addition, Valentine (1987) makes some specific suggestions for restoring Willow Flycatcher meadows.

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Willow Flycatcher ***(Empdionax traillii)***
Art Work by Keith Hansen

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APPENDIX I. Calculation of Replacement Rates for Willow Flycatcher Populations in the Sierra Nevada, California.

Definitions

l_x = The proportion of females surviving to age x.

m_x = The average number of female offspring produced per female at age x.

R_0 = The net reproductive rate or replacement rate of a population. If R_0 is 1, the population is stable and replacing itself. If R_0 is less than 1, the population is decreasing.

$R_0 = l_x m_x$

Assumptions

1. Mortality is 50% for young and adults. This assumption is probably an underestimate. Franzreb (1988) estimated that first year mortality among Least Bell's Vireos was 75%, and annual survival of adults 50%. Studies by Austin (1951) of mourning doves reported a mortality rate of 80% for the first year of life and 55% per year thereafter for the next ten years.

2. The average number of female young produced per female is 0.55 (i.e. $m_x = 0.55$). Calculation of m_x is based on the following information:

Source	Year	# of ♀	# fledged	# ♀ fledged/♀
This study	1986/7	20	20	0.5
Harris	1987	8	10	0.62
KRCD	1983/4	8	9	0.52
				mean = 0.55

Calculation of R_0

year	l_x	m_x	$l_x m_x$
0	1.0	0	0
1	0.50	0.55	0.275
2	0.25	0.55	0.138
3	0.12	0.55	0.069
4	0.06	0.55	0.003
5	0.03	0.55	0.002

$$R_0 = \sum_{x=0}^{\infty} l_x m_x = 0.48$$