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# THE STATUS OF THE WILLOW AND PACIFIC-SLOPE FLYCATCHERS IN NORTHWESTERN CALIFORNIA AND SOUTHERN OREGON

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*Abstract.* The Willow (*Empidonax traillii*) and Pacific-slope (*E. difficilis*) flycatchers are generally similar in their morphology and foraging, but differ in their habitat and population dynamics. Through a concentration of constant-effort mist-netting stations, we documented the movements and composition of populations over a relatively large geographical province of southern Oregon and northern California. Although the Pacific-slope Flycatcher is far more common as a breeding species in much of the province, it becomes much less common than the Willow Flycatcher during migration. After breeding, the Willow Flycatcher has a previously undocumented major influx of birds into the province from breeding sites to the north, including both young and adults. By contrast, the Pacific-slope Flycatcher appears to migrate differentially, with adults moving south before the young.

*Key Words:* California, demography, *Empidonax traillii*, *Empidonax difficilis*, Klamath Province, migration, mist-nets, Oregon, Pacific-slope Flycatcher, Siskiyou Province, Willow Flycatcher.

As a group, the *Empidonax* flycatchers of the Americas have always challenged ornithologists. With many sibling or superspecies that differ only slightly on the basis of morphology, identification is sometimes difficult, even in breeding individuals with species-specific songs. In the post-breeding season, identification becomes even more difficult as they fall silent and become another small, greenish bird among the foliage. Careful examination of birds captured at constant-effort mist-netting stations can give us new insight into the life history attributes during all seasons, especially outside of the breeding season.

Our objectives were to document, for the Willow Flycatcher (*Empidonax traillii*) and Pacific-slope Flycatcher (*E. difficilis*), the timing and magnitude of their use of various regions and the implications to land management. Little is known about dynamics of population and age structure at any time of the year for either species, and especially in the post-breeding and migration seasons when much of the selection takes place. The few previous studies during these seasons have been at a single station or in a small, restricted area (Ralph 1968, Otahal 1998, Yong and Finch 1997). Our data are based upon captures of birds in mist nets at stations in what we term the Klamath Physiographic Province of Oregon and California: a complex of the Siskiyou and Klamath mountains, drained by many rivers including the Rogue, Klamath, Trinity, northern Sacramento, and Eel (Fig. 1).

## The Willow Flycatcher

Gaining knowledge of the distribution and status of the Willow Flycatcher has been challenging to ornithologists, due in large part to the difficulty in separating forms of the genus. As Pyle (1997) pointed out, the majority of individuals of the Willow Flycatcher are not distinguishable from the very closely related Alder Flycatcher (*E. alnorum*). Based upon the geographic breeding ranges of the two flycatchers (AOU 1998), in our area we assume that all birds we captured are *E. traillii*.

In much of its range the Willow Flycatcher is rather habitat specific, occurring in "moist, brush thickets, open second growth, and riparian woodland" (AOU 1998). In Oregon it can be one of the most abundant birds in young, regenerating clear cut forests (Altman et al. *this volume*), in addition to the more typical riparian habitats. In California it was previously common in certain riparian woodlands (Grinnell and Miller 1944). However, it has been essentially extirpated from the Central Valley and remains in only a few sites along the western side of the Sierras and in the extreme northern part of the state. In 1990 all of the subspecies were listed by the state of California as endangered.

In the mountains of the Klamath Province, the Willow Flycatcher breeds very rarely in the upper Klamath River Valley (Harris 1996), and more commonly north and east of Mount Shasta, into the Upper Klamath Basin. Although known to occur as a migrant from its more northern breeding areas, its abundance was largely unknown in much of these mountains. Because of the paucity of breeding birds, forest and range management plans in the Province have not taken the species into account, except in the very few areas where an occasional bird has been recorded singing.

## The Pacific-slope Flycatcher

The former "Western" Flycatcher (*E. difficilis*) has been split into two morphologically very

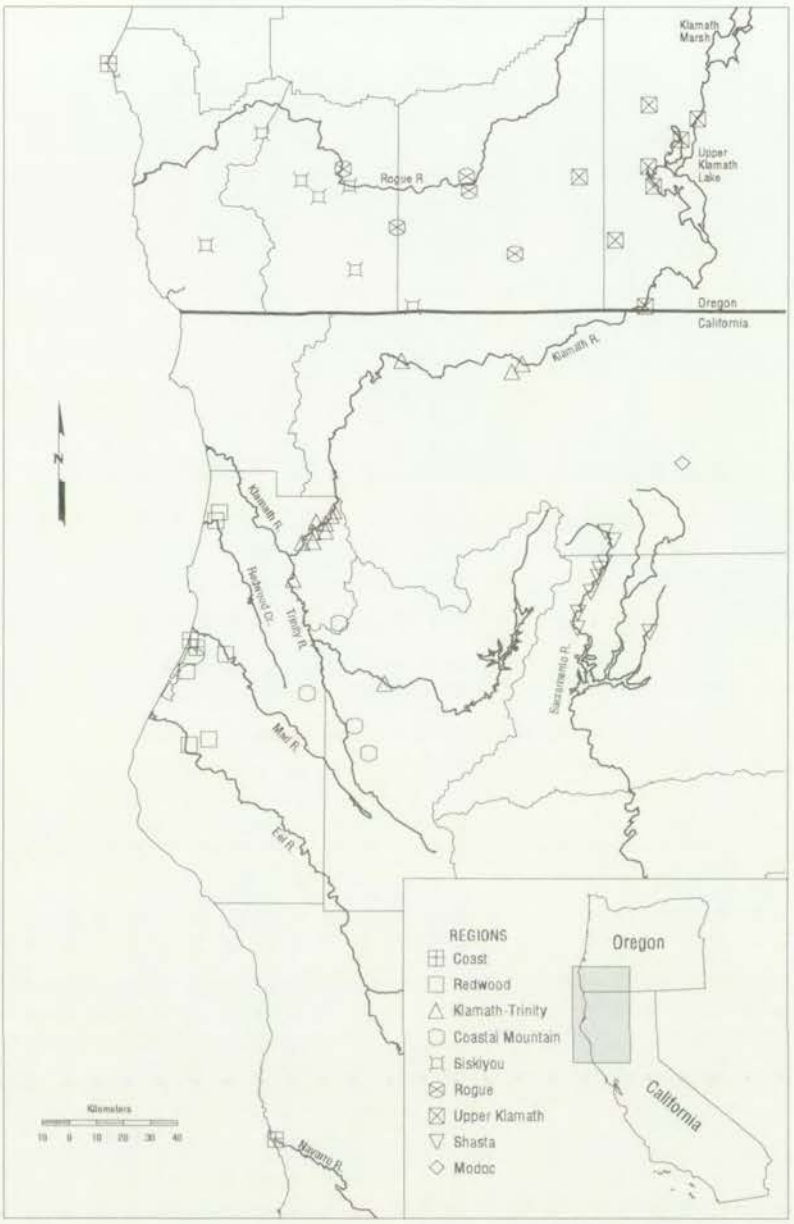


FIGURE 1. Study area with regions, mist-netting stations, and major rivers.

similar species (Johnson 1994, AOU 1998): (1) the Pacific-slope Flycatcher (which retained the former specific name), found in the Pacific coastal coniferous forests; and (2) the Cordilleran Flycatcher (*E. occidentalis*), which occurs in more inland coniferous habitats in the western mountains of North America. Johnson and Marten (1988) found the two taxa to be sympatric without interbreeding in north-central California, on the margin of our study area in Siskiyou County. Unfortunately, only about 60% of individuals can be identified as either Pacific-slope or Cordilleran Flycatcher even in the hand (Pyle 1997), making species separation imprecise. Although our easternmost stations are near or in the suggested range of the Cordilleran Flycatcher, we assume that the vast majority of birds breeding and moving through our study area can be safely referred to as the Pacific-slope form. We also assume that the migratory route of the

Cordilleran Flycatcher lies largely to the east of our stations, as that is the direct route to its wintering grounds. Additionally, we have noted no birds with the song type of the Cordilleran Flycatcher during our extensive censuses in the area.

The Pacific-slope Flycatcher is more of a habitat generalist than the Willow Flycatcher, inhabiting both deciduous and coniferous forests throughout its range (Bent 1942, Thomas 1979). In addition, it occupies many seral stages, from shrub-seedling to old-growth (Meslow and Wight 1975).

Most arrive in our study area by mid-April (Sakai 1987), and nesting is well underway by mid-May. Sakai (1987) found that peak incubation is during June, and fledging is from mid-July to the first week of August. The birds leave their territories beginning about the third week of July, peaking about the first of August, with the last departing in mid-August. Post-breeding up-slope movements have been suggested by Ziener et al. (1990) in California, and down-slope by Swarth (1904) in Arizona.

## METHODS

For all analyses except recapture rate, we used only the first capture of an individual in each year. This results in an assay of new birds moving into the area around a capture station.

### Constant-effort Mist-netting

These data were derived from birds captured in arrays of 12-m mist nets at 54 stations (Fig. 1), each operated from 1 to 18 years. Methods followed the protocol outlined in Ralph et al. (1993). Nets were operated during the breeding season from the beginning of May through the end of August, and on into the fall at many stations (Appendix). For analyses, we used 10-day periods, with the first period beginning 1 May and ending on 10 May (Table 1). We had a total of 2306 station ten-day periods (Appendix), all years and stations combined.

Each station consisted of 10 to 14 12-m long nets, opened within 15 min of dawn and closed after 5–6 hrs. Each station operated on a separate and regular schedule (every 1–10 days) during a season, with the same number of nets, in permanent net lanes, and for the same number of hours, weather permitting. For analyses, we grouped nearby stations with similar physiographic features into Regions (Fig. 1).

### Ageing and Sexing

Each captured bird was aged as young (hatched that year) or adult based on plumage or skull (Pyle 1997). Birds were considered males if they showed any sign of a cloacal protuberance. We have observed that these two species have relatively small protuberances as compared to other taxa, such as thrushes and sparrows, which may result in an underestimate of males. Females develop well-defined brood patches and are easily sexed by this trait that develops usually by June, indicating that incubation is underway. Birds maintain cloacal protuberances and brood patches for a period after the cessation of active breeding.

TABLE 1. Dates of 10-Day Periods Used for Analyses

| Period | "Month" | Dates |
|---|---|---|
| 1 | May | 1–10 May |
| 2 | May | 11–20 May |
| 3 | May | 21–30 May |
| 4 | June | 31 May–9 June |
| 5 | June | 10–19 June |
| 6 | June | 20–29 June |
| 7 | July | 30 June–9 July |
| 8 | July | 10–19 July |
| 9 | July | 20–29 July |
| 10 | August | 30 July–8 August |
| 11 | August | 9–18 August |
| 12 | August | 19–28 August |
| 14 | September | 29 August–7 September |
| 15 | September | 8–17 September |
| 16 | September | 18–27 September |
| 17 | October | 28 September–7 October |
| 18 | October | 8–27 October |

*Notes:* The "month" indicates the notation used in Figures 2 and 6 for convenience of viewing. Note that the last period is longer, and includes all late migrants.

### Age Ratio

We used the average proportion young in each Region as the age ratio metric. It was calculated separately for each station, for each year, and for each season the station was operated. Specifically, we divided the capture rate of young by the total capture rate of both adults and young for that season and year at the station. We averaged these proportions for all station-seasons in a Region, and tested the significance of differences between age ratios by a Duncan's Multiple Range test from the General Linear Models Procedure of SAS (1996). Age ratio is a unique metric that provides an estimate of the location of the route of the migrants, as hypothesized in Ralph (1981). An even age ratio (approximately 50% young) indicates the center of a species' migration route, while a high proportion of young suggests the edge of the route.

### Capture Rate As An Index Of Abundance

The capture rate per 10-day period at each station is our basic index of abundance. We calculated it by summing all the captures of a species at a station in a 10-day period and dividing by the number of net-hrs (one 12-m net operated for one hr is a net-hr), multiplied by 1000, giving the number of birds per 1000 net-hrs at the single station. This index is widely employed at single stations such as bird observatories, and has been expanded into multiple stations in various studies such as Ralph (1981), the Constant Efforts Sites Scheme of the British Trust for Ornithology (e.g., Baillie and Holden 1988, Peach et al. 1991), and the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante 1992).

For both abundance and age ratio, the Regional averages of these station-season data were used in vari-

ous comparisons. We considered this to be a relatively conservative approach, as we treated all the captures of a species in a season at a station as an independent datum.

### Seasons

For our seasonal analyses, we defined two seasons—breeding and the fall migration. The breeding season was centered on the two periods with the peak of abundance of birds in breeding condition. This resulted in the breeding season being the eight 10-day periods from 1 May to 19 July. The migration season was the seven 10-day periods centered on the peak of fall migration, which for both species was the 10-day period of 19–28 August; therefore, the migration season included the periods from 20 July to 27 September. With this convention, a small number of birds were captured after the main migration season and were included in the last migration period.

By contrast, for purposes of discussion (especially in Figures 2 and 3), we characterize birds as undergoing spring migration, breeding, post-breeding, or fall migration. These refer to the state of each individual bird, rather than the date of capture, and separate birds in breeding condition from others that were not. This was important because during spring, some individuals can be migrating north through an area while others there are breeding.

## RESULTS

The two species differ markedly in several aspects of their biology. We present the Pacific-slope Flycatcher first, as it provides a basis of comparison for the more variable Willow Flycatcher. Both species have substantial breeding populations to the north of the study area.

### Pacific-slope Flycatcher

#### *Timing of events*

Overall, this species breeds fairly commonly in most of the study area, is more abundant towards the coast, and the adults migrate south before the young (Fig. 2). The young appear to have two autumnal pulses of movement into the province, the post-breeding and then the fall migration.

We found substantial numbers of adult birds in non-breeding condition, and presumably spring migrants, moving through in May (Fig. 2). We captured breeding birds (those with a cloacal protuberance or brood patch) from late May through the end of June, when the first young appeared. In July and early August, we noted an increase in new adults (still in breeding condition) in most regions; this pulse of post-breeding adults was especially marked in the Klamath-Trinity, Redwood, and Coast regions. Adults then rapidly departed on their fall migration, leaving all regions by late August, with only a few captured in the Coast Region in very early September.

By July, young birds began to make up the majority of new captures. This post-breeding influx of young continued into early August in most areas, at times overshadowing the numbers in other seasons. In many regions the fall migration of young was signaled by an increase of captures in late August and September. In the inland and higher elevations of the Upper Klamath Region, the fall movements were largely concluded by mid-August. In the Coast, Redwood, and Siskiyou Regions, this influx of young was a separate pulse. In others, it apparently overlapped with the earlier post-breeding movements of adults and young.

#### *Comparison of abundance between regions*

In the breeding season (until 19 July), both adults and young were most commonly captured towards the coast, with higher capture rates at the Coast and Redwood Regions for adults (6 to 14 birds per 1000 net-hrs, respectively; Table 2). The highest abundance of young was at the Redwood and the nearby Coastal Mountain Regions (about 3 birds per 1000 net-hrs).

During the fall migration (after 19 July), relative abundance can give an indication of the route taken. Overall, adults were captured much less often than young (Table 3) and showed little propensity for any particular region. Young birds were abundant in all regions from the Coast to the inland river valleys (4 to 7 per 1000 net-hrs), and became less common far inland.

#### *Determination of routes through age ratio*

We found little difference among Regions in the percent young captured during the migration season (Table 4), except at the three stations at Shasta, which had only 33% young. The great majority of birds in all regions were young, suggesting a broad front of migration throughout most of the Province.

### Willow Flycatcher

#### *Timing of events*

The pattern of Willow Flycatcher captures (Fig. 3) differed markedly from that of the Pacific-slope Flycatcher, notably in the relative paucity of breeding populations, the greater post-breeding abundance in the inland regions, the synchronous migration of adults and young, and the prolonged passage in the fall.

We captured adults that were not in breeding condition moving through in late May and early June. These adults were in moderate numbers in most inland regions, in general avoiding the Coast and Redwood Regions. From late May through June, small to moderate numbers of birds in breeding condition were captured in the

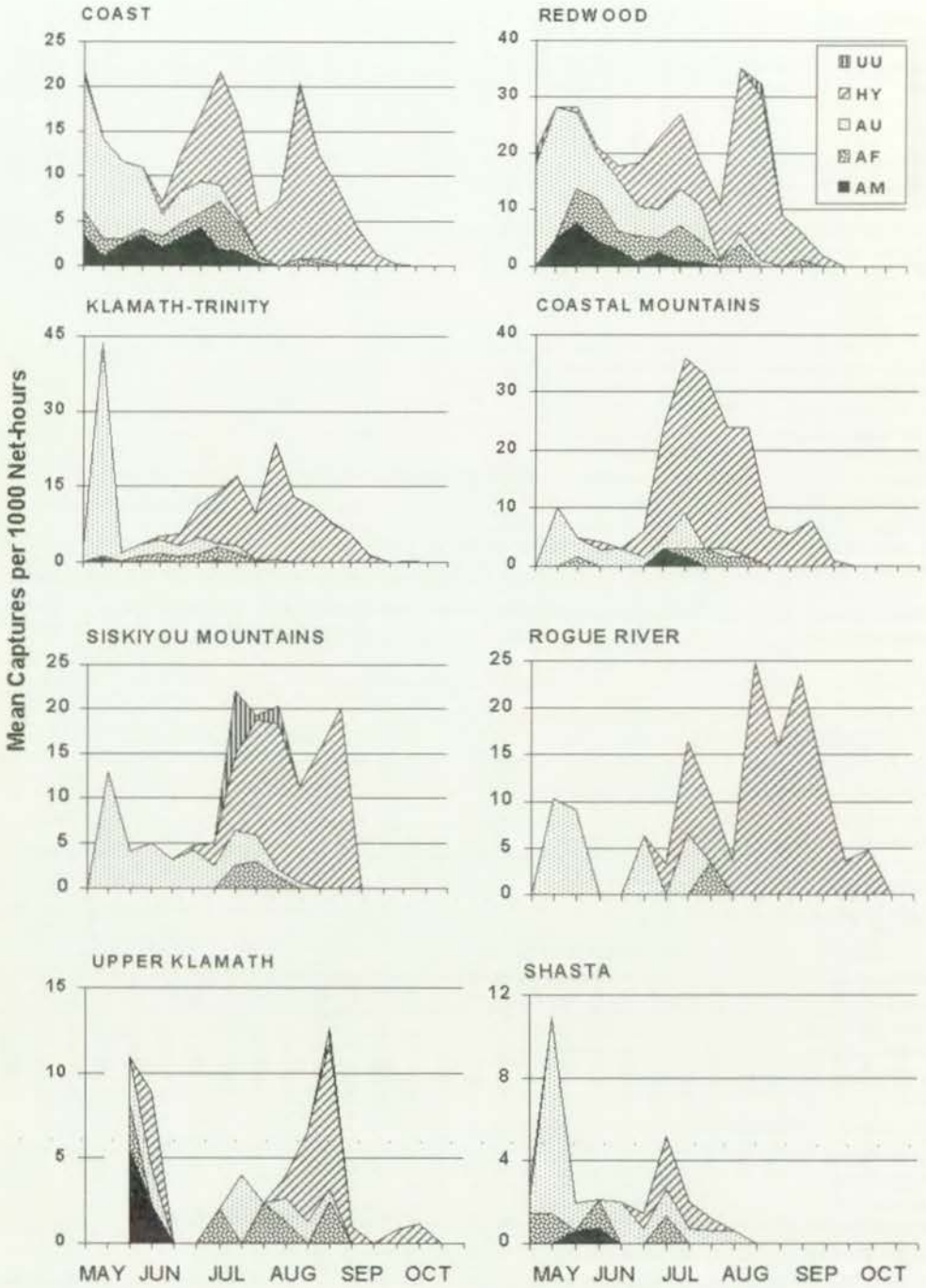


FIGURE 2. Average capture rate of adult, young, male, and female Pacific-slope Flycatchers per 1000 net-hours at stations in various regions of northern California and southern Oregon from May through October. Each station-season contributed a datum to the mean of a region. Age and sex classes are: UU = Unknown age and sex; HY = Hatching year, less than one year old; AU = Adult, unknown sex; AF = Adult female; and AM = Adult male. The "month" is as shown in Table 2.

TABLE 2. BREEDING SEASON AVERAGE CAPTURE RATES (NUMBER PER 1000 NET-HOURS) OF ADULT AND YOUNG PACIFIC-SLOPE FLYCATCHERS WITH EACH STATION-SEASON CONTRIBUTING A DATUM TO THE MEAN OF A REGION

| | Young | | | | Adult | | | |
|---|---|---|---|---|---|---|---|---|
| Region | Capture rate | SD | N | Duncan grouping[a] | Capture rate | SD | N | Duncan grouping[a] |
| Coast | 1.8 | 1.6 | 19 | A B C | 5.7 | 2.0 | 19 | A B |
| Redwood | 3.3 | 1.8 | 19 | A | 14.3 | 1.3 | 19 | A |
| Klamath-Trinity | 1.4 | 1.8 | 51 | A B C | 2.4 | 2.3 | 51 | B C |
| Coastal Mountains | 2.8 | 2.3 | 13 | A B | 2.7 | 1.8 | 13 | B C |
| Siskiyou | 0.6 | 1.3 | 40 | C D | 2.4 | 2.1 | 40 | B C |
| Rogue | 0.9 | 1.6 | 6 | B C D | 1.0 | 2.5 | 6 | C D |
| Upper Klamath | 0.2 | 0.9 | 9 | C D | 1.0 | 2.1 | 9 | C D |
| Shasta | 0.3 | 0.8 | 32 | C D | 1.1 | 1.8 | 32 | C D |
| Modoc | 0.0 | 0.0 | 4 | D | 0.0 | 0.0 | 4 | D |

[a] Regions not significantly different from others have the same letter.

farther inland and more northerly Klamath-Trinity, Rogue, Shasta, and Upper Klamath Basin Regions; elsewhere, few breeding birds were captured. During July, Willow Flycatchers were captured only in the Upper Klamath Basin Region, where they likely breed in small numbers. No post-breeding influx was noticeable in any other Region, in contrast to the Pacific-slope Flycatcher in which many adults still in breeding condition were moving through. In all regions except the Upper Klamath, a distinct and prolonged fall migration of Willow Flycatchers was evident. Beginning in mid-August and on into September, we captured large numbers of mostly young birds, far more than in other seasons. Capture rate was remarkably high in the Rogue, Klamath-Trinity, and Coastal Mountain Regions, with moderate numbers in all other regions except the Coast and Redwood, where the Willow Flycatcher was scarce. In contrast to the Pacific-slope Flycatcher, moderate numbers of Willow Flycatcher adults were still present through the migration at most regions.

The fall migration of Willow Flycatchers peaked in early September in the northern regions. Surprisingly, at the Farallon Islands (Point Reyes Bird Observatory, unpubl. data), some 500 km to the south and some 30 km offshore, the peak of fall migration was somewhat earlier, during August (Fig. 4). This indicates that their presence in the riparian habitats of most of our Regions was generally later than on this offshore island, though the movement of young through the Upper Klamath Region was similar in timing to the Farallones.

### *Comparison of abundance between regions*

Although few Willow Flycatchers bred in the Province, adults were significantly more abundant (based on average capture rate) during the breeding season only in the Rogue and Klamath-Trinity Regions (Table 5). In the fall migration, moderate numbers of adults were captured in some inland regions (i.e., the Shasta and Rogue Regions at 1.8 birds per 1000 net-hrs) as compared to the other inland and coastal regions (from 0 to 0.5 per 1000 net-hrs).

When the young Willow Flycatchers appeared

TABLE 3. FALL MIGRATION SEASON AVERAGE CAPTURE RATES (NUMBER PER 1000 NET-HOURS) OF ADULT AND YOUNG PACIFIC-SLOPE FLYCATCHERS WITH EACH STATION-SEASON CONTRIBUTING A DATUM TO THE MEAN OF A REGION

| | Young | | | | Adult | | | |
|---|---|---|---|---|---|---|---|---|
| Region | Capture rate | SD | N | Duncan grouping[a] | Capture rate | SD | N | Duncan grouping[a] |
| Coast | 4.0 | 1.2 | 27 | A B | 0.3 | 0.4 | 27 | B |
| Redwood | 6.6 | 1.3 | 19 | A | 1.5 | 1.3 | 19 | A |
| Klamath-Trinity | 6.5 | 1.7 | 50 | A | 0.3 | 0.7 | 50 | B |
| Coastal Mountains | 7.0 | 0.8 | 13 | A | 0.5 | 0.8 | 13 | A B |
| Siskiyou | 5.7 | 3.7 | 38 | A | 0.7 | 1.9 | 38 | A B |
| Rogue | 5.4 | 1.9 | 7 | A | 0.2 | 0.8 | 7 | B |
| Upper Klamath | 1.5 | 1.4 | 13 | B C | 0.7 | 1.2 | 13 | A B |
| Shasta | 0.1 | 0.4 | 31 | D | 0.1 | 0.7 | 31 | B |
| Modoc | 0.5 | 1.2 | 4 | C D | 0.0 | 0.0 | 4 | B |

[a] Regions not significantly different from others have the same letter.

TABLE 4. FALL MIGRATION PERCENT YOUNG OF PACIFIC-SLOPE FLYCATCHERS AND WILLOW FLYCATCHERS WITH EACH STATION-SEASON CONTRIBUTING TO THE MEAN OF A REGION

| Region | Pacific-slope Flycatcher | | | | Willow Flycatcher | | | |
|---|---|---|---|---|---|---|---|---|
| | Percent hatch year | SD | N | Duncan grouping[a] | Percent hatch year | SD | N | Duncan grouping[a] |
| Coast | 91.4 | 10.2 | 24 | A B | 94.9 | 10.2 | 17 | A |
| Redwood | 76.6 | 23.8 | 18 | A B | 100.0 | — | 1 | A |
| Klamath-Trinity | 95.1 | 11.1 | 44 | A B | 96.8 | 8.2 | 47 | A |
| Rogue | 91.7 | 20.4 | 6 | A B | 87.9 | 17.8 | 7 | A B |
| Coastal Mountains | 87.8 | 16.2 | 13 | A B | 99.3 | 2.3 | 10 | A |
| Siskiyou | 88.2 | 24.6 | 27 | A B | 80.2 | 32.6 | 12 | A B |
| Upper Klamath | 67.9 | 40.5 | 10 | B | 68.4 | 35.4 | 8 | B |
| Shasta | 33.3 | 57.7 | 3 | C | 29.3 | 31.2 | 12 | C |
| Modoc | 100.0 | — | 1 | A | 0.0 | — | 0 | |

[a] Regions not significantly different from others have the same letter.

after the breeding season, they were much more common overall than Pacific-slope Flycatchers (cf. Table 3). Abundance of young also differed markedly between regions (Table 6); they were significantly more common in the river valleys of the Rogue and the Klamath-Trinity regions, reaching high levels of 20–23 birds per 1000 net-hrs. In comparison, moderate numbers (1.0 to 3.6 per 1000 net hrs) were captured in most other regions, both inland and coastal. This pattern of abundance indicates the young migrate in the inland river valleys.

*Determination of routes through percent young*

While almost no young Willow Flycatchers were captured during the breeding season (before 19 July), almost all captured after that were young. In the fall, only the Shasta and Upper Klamath Regions had a significantly lower proportion young than the other regions, all of which had >80% young (Table 4). If higher proportions of adults occur in the center of the migration route, these age ratios indicate a more inland route than do the capture rates, with the main route generally to the east of the Province.

### RECAPTURE RATE

The recapture rate is a measure of the site persistence within a season (Table 7). Combining all regions, the Willow Flycatcher was recaptured much less often than the Pacific-slope Flycatcher, indicating that the Willow Flycatcher was more mobile in the study areas, with few birds apparently remaining for more than a day at a station. The return rate of birds captured in previous years (a measure of site fidelity between years) was 3.8% for the Pacific-slope Flycatchers during the breeding season; no Willow Flycatchers were recaptured (during breeding or migration periods), suggesting a largely transient population.

## DISCUSSION

### SCALE OF STUDY AND INDEPENDENCE OF DATA

*Utility of combining stations*

Our study combined data from many stations, because individual stations can have differing abundances and age ratios due to habitat and locality differences. However, an inspection of the data found no evidence that timing of age or sex classes capture rate peaks differed between stations within a region (C. J. Ralph, unpubl. data). Differences in habitat were related to abundance, but when three or more stations were combined in a Region, any such biases were minimal. In combining stations it is important that each station contributing to a regional mean was operated consistently through the season in question, on a constant-effort schedule (whether daily or weekly); the stations included in this study met this criterion.

*Independence of data*

The basic datum of our study was the abundance or age ratio at each station, in a unit of time (either a season or a 10-day period) and in a year. This station-season-year datum was not strictly independent. For instance, a station run multiple years contributes more data to a Regional mean than a station with only one year's data. At a given station, each year's datum would be expected to have a strong relationship with the datum from another year. In practice, we have found that the between-year differences were as marked as the between-station differences (C. J. Ralph, unpubl. data), and for purposes of this paper we considered them independent. Further, mist netting data may experience less site bias than some other methods, as a station will likely capture birds from over a large area, especially during the migration sea-

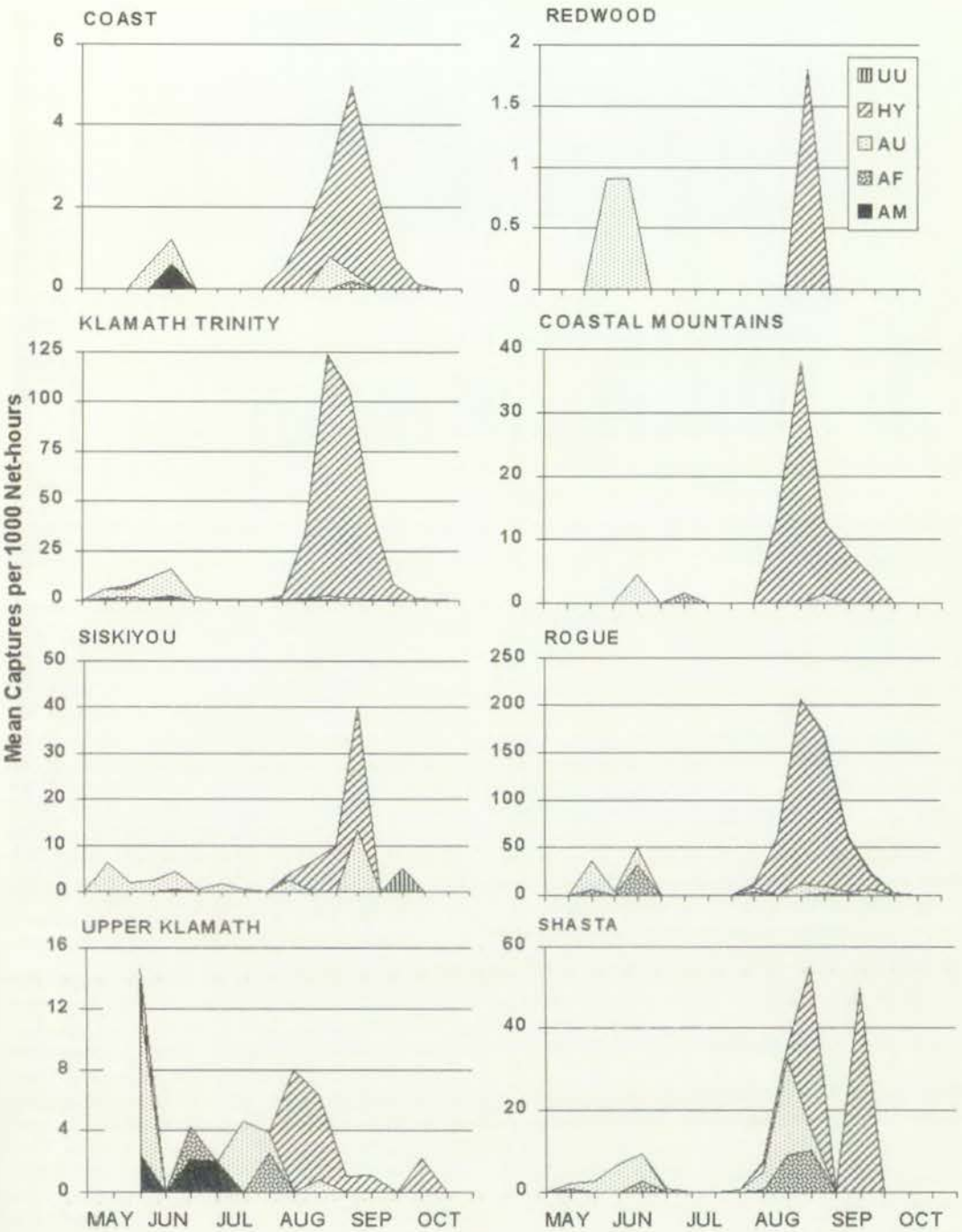


FIGURE 3. Average capture rate of adult, young, male, and female Willow Flycatchers per 1000 net-hours at stations in various regions of northern California and southern Oregon from May through October. Age and sex classes are: UU = Unknown age and sex; HY = Hatching year, less than one year old; AU = Adult, unknown sex; AF = Adult female; and AM = Adult male. The "month" is as shown in Table 2.

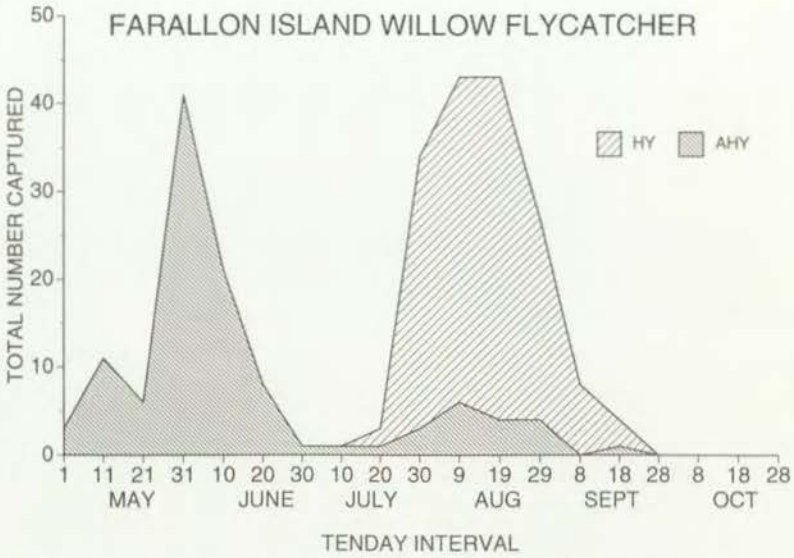


FIGURE 4. Total number of Willow Flycatchers caught on the Farallon Islands, 30 km west of San Francisco, California, by 10-day intervals. Each date is the beginning of a 10-day interval. Capture effort was constant throughout year.

son, when birds are moving in from their more northerly breeding areas.

*Importance of mist-netting data*

Mist netting is the preferred method of determining the local abundance of these birds, especially in the non-breeding season. In our study areas, censuses alone would not have provided the insight into the two species' abundances and migration. Most censuses are done during the breeding season, as this has been felt to be the time of critical habitat relationships. The breeding season is also the time when *Empidonax* can be identified by song, the most reliable field characteristic. However, the use of only one method in one season would not have identified the complexity of the species' differences nor the importance of the inland river valleys to the Willow Flycatcher. Although it is one of the most common birds netted in our region in the fall, the Willow Flycatcher has almost never been detected on censuses in the region, even by expert censusers (C. J. Ralph, unpubl. data). Additionally, the metrics of age composition cannot be gathered in any other fashion.

TABLE 5. Breeding Season Average Captures Rates (Number per 1000 Net-Hours) of Adult (No Young Were Captured) Willow Flycatchers with Each Station-Season in a Year Contributing a Datum to the Mean of a Region

| | Adult | | | |
|---|---|---|---|---|
| Region | Capture rate | SD | N | Duncan grouping[a] |
| Coast | 0.1 | 1.6 | 19 | A B C |
| Redwood | 0.1 | 0.4 | 19 | C |
| Klamath-Trinity | 2.5 | 2.2 | 51 | A B |
| Coastal Mountains | 0.4 | 1.0 | 13 | C |
| Siskiyou | 1.3 | 1.9 | 40 | B C |
| Rogue | 4.6 | 3.9 | 6 | A |
| Upper Klamath | 1.1 | 2.1 | 9 | B C |
| Shasta | 1.0 | 1.7 | 32 | B C |
| Modoc | 0.0 | 0.0 | 4 | C |

[a] Regions not significantly different from others have the same letter.

### Breeding Season Abundance

We have shown that the Pacific-slope Flycatcher is relatively common towards the coast. As Johnson (1980) noted, the Pacific-slope Flycatcher becomes much less common away from the coast, towards and into the suggested range of the very closely-related Cordilleran Flycatcher. Breeding Willow Flycatchers were, by contrast, most common in the far inland areas. They do breed in the far inland Upper Klamath Basin, the only region where adults in breeding condition were captured during the July post-breeding period, and censuses in the area had modest numbers of singing birds (C. J. Ralph, unpubl. data).

### Spring Migration

The two species migrated on quite different schedules. Pacific-slope Flycatchers migrate early (late March into April), as noted by Garrett

TABLE 6. FALL MIGRATION SEASON AVERAGE CAPTURES RATES (NUMBER PER 1000 NET-HOURS) OF YOUNG AND ADULT WILLOW FLYCATCHERS WITH EACH STATION-SEASON IN A YEAR CONTRIBUTING A DATUM TO THE MEAN OF A REGION

| Region | Young | | | | Adult | | | |
|---|---|---|---|---|---|---|---|---|
| | Capture rate | SD | N | Duncan grouping[a] | Capture rate | SD | N | Duncan grouping[a] |
| Coast | 1.0 | 1.0 | 27 | B C | 0.1 | 0.4 | 27 | B |
| Redwood | 0.1 | 0.3 | 19 | C | 0.0 | 0.0 | 19 | B |
| Klamath-Trinity | 20.5 | 2.2 | 50 | A | 0.4 | 0.8 | 50 | B |
| Coastal Mountains | 3.6 | 2.1 | 13 | B | 0.0 | 0.3 | 13 | B |
| Siskiyou | 1.3 | 3.0 | 38 | B C | 0.3 | 1.1 | 38 | B |
| Rogue | 22.6 | 1.1 | 7 | A | 1.8 | 1.4 | 7 | A |
| Upper Klamath | 1.0 | 1.0 | 13 | B C | 0.5 | 0.9 | 13 | A B |
| Shasta | 0.8 | 1.8 | 31 | C | 1.8 | 3.6 | 31 | A |
| Modoc | 0.0 | 0.0 | 4 | C | 0.0 | 0.0 | 4 | B |

[a] Regions not significantly different from others have the same letter.

and Dunn (1981), Davis et al. (1963), and Ralph (1968). Most have passed through or established in breeding areas in the region by mid-May and June, when most Willow Flycatchers move through. The highest spring capture rates for the Pacific-slope Flycatchers were in the Rogue, Siskiyou, and Coastal Mountain regions, where virtually no breeding birds were captured. This could indicate that the area functions largely for movements of birds to breeding areas to the north.

### POST-BREEDING/FALL MIGRATION

The contrast between the two species is marked in the post-breeding period. In July and early August, we found a pulse of post-breeding adult Pacific-slope Flycatchers, as had been documented by Ralph (1968). After this influx, the adults apparently rapidly left the area. The early departure of adult Pacific-slope Flycatchers is contrary to the assertion of Ralph (1968), based on a single station in coastal central California, where he assumed that adults moved on inland routes, but at the same time, as young. Our present results agree with Johnson (1973), who hypothesized that a preponderance of young in southern California and Arizona was in part due to the faster speed and earlier departure of the adults. Johnson (1973) also demonstrated that adult Pacific-slope Flycatchers are already on the wintering grounds in Mexico by early August, long before the first juveniles. The adult Willow Flycatchers, although being relatively scarce in our study areas, appeared to migrate later and at about the same time as the young. Similarly, Yong and Finch (1997) found adults with only a slight tendency to migrate earlier than young along the Rio Grande in New Mexico.

TABLE 7. THE NUMBER AND PERCENT OF FIRST CAPTURES AND RECAPTURES IN A YEAR, AND THE NUMBER RETURNED IN SUBSEQUENT YEARS BY SPECIES AND SEASON

| | Breeding | | Migration | |
|---|---|---|---|---|
| | N | Percent | N | Percent |
| Pacific-slope Flycatcher | | | | |
| First capture | 752 | | 853 | |
| Recapture | 78 | 9.0 | 38 | 4.2 |
| Return | 33 | 3.8 | 7 | 0.8 |
| Total | 863 | | 898 | |
| Willow Flycatcher | | | | |
| First capture | 220 | | 1270 | |
| Recapture | 0 | 0.0 | 23 | 1.8 |
| Return | 0 | 0.0 | 0 | 0.0 |
| Total | 220 | | 1293 | |

The adults and young of most species of landbirds appear to move southward together (Ralph 1981), including western populations of the Willow Flycatcher (from our data) and the Hammond's Flycatcher (*E. hammondii*; Johnson 1970). However, this is not the case for all populations of *Empidonax* flycatchers. Adults migrate earlier than young in the Pacific-slope Flycatcher (in our western regions), and in all four taxa of eastern *Empidonax* in Ontario (Hussell 1991b), including Least Flycatchers (*E. minimus*), Yellow-bellied Flycatchers (*E. flaviventris*), Alder Flycatchers, and (in contrast to our results) the Willow Flycatcher.

### ROUTES BASED ON AGE RATIOS AND ABUNDANCES

The route of migrants can be inferred by two metrics in this study, their relative abundance and age ratios. As hypothesized in Ralph (1981), a high proportion of young could indicate the edge of the route, as misoriented young would

be more common away from the center of a route.

Based on abundance, the route of the young Pacific-slope Flycatchers was throughout the study area, especially from the Coast inland to the Klamath-Trinity and Coastal Mountain regions. Since the adults had departed earlier and apparently rapidly, they provided no information on routes from age ratios.

Inferred from abundance, the fall migration route of young and adult Willow Flycatchers is likely through the inland river valleys and to the east, with the age classes together. However, based on age ratios, the main route would appear to be to the east of the study area, as the age ratios were most even in the Upper Klamath Region, and heavily skewed towards young in the inland river valleys and farther west. The great abundance of young in the inland valleys might suggest a difference in route, with the young preferring those valleys, while the adults migrated to the east. However, in the areas with large numbers of adults, we also found large numbers of young, largely precluding a difference in routes of the age classes. Perhaps habitat segregation may occur with adults preferring upland areas.

In both species, the proportion of young in migration was much larger than can be explained by normal reproduction. The preponderance of young, certainly in the case of the Pacific-slope Flycatcher, is likely due to the young delaying migration, perhaps lingering longer as their relative inexperience required longer to provision for their migration south.

### Timing of Migration

Our fall peak migration of Willow Flycatcher was about August 19 to 28, approximately a week earlier than the midpoint noted in the San Francisco Bay Area (Otahal 1998), as would be expected. However, on the offshore Farallon Islands, at the same latitude as Otahal's study site, the peak of birds was much earlier (in early August), similar to the far inland and farther north Upper Klamath Region. The birds on the Farallones were young birds orienting over the ocean that were forced to fly long distances without stopping, and so arrived farther south and sooner on the inhospitable Farallones. By contrast, birds in the more salubrious inland riparian valleys could linger, building energy stores for their southward migration.

The data from recaptures are difficult to reconcile with this overstaying scenario, as the recapture rate was lower for the Willow Flycatcher than the Pacific-Slope Flycatcher. If Willow Flycatchers were lingering at a site, their recapture rate should be higher than for Pacific-slope Flycatchers, unless (1) both species linger similarly, or (2) Willow Flycatchers move slowly and continuously through the regions. It should be added that these data were not standardized for effort; rather, all captures were pooled because relatively few birds were recaptured, which may obscure patterns. Yong and Finch (1997) also documented little stopover of Willow Flycatchers, with only seven recaptures of 84 migrants, and all within one day of initial capture.

In the Pacific-slope Flycatcher, our peak of migration was late in August or early September. At a coastal site at Point Reyes Bird Observatory, Ralph (1968) found a peak in mid-September of young migrants, indicating a relatively slow transit period of the young.

### Implications for Management

Young Willow Flycatchers appear to move into and possibly linger in our study area in large numbers during this previously undocumented pre-migration period. It is possible that the riparian systems, both at the lower elevation inland river valleys and the higher elevation meadows, become vital to the survival of the species. In the case of the Pacific-slope Flycatcher, we have also shown that while the adults appear to leave rapidly after breeding, the young also linger in the region prior to their fall migration to the tropics.

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APPENDIX. Constant-Effort Mist-Net Station Locations, Operator Organization, Number of Years Sampled, Number of Ten-Day Periods, and Number of Captures of Each Species by Region

| Region and location | Operator | Years sampled | Ten-day periods | Number of Captures: Pacific-slope Flycatcher | Number of Captures: Willow Flycatcher |
|---|---|---|---|---|---|
| Coast | | | | | |
| Cape Blanco, OR | Siskiyou NF (SNF) | 1994–1997 | 26 | 1 | 34 |
| Mad River Slough (HOME site), Arcata, CA | Humboldt Bay Bird Observatory | 1982–1997 | 208 | 347 | 787 |
| Mad River Slough (PARK site), Arcata, CA | Humboldt Bay Bird Observatory | 1992–1997 | 97 | 100 | 155 |
| Navarro River, Mendocino, CA | California State Parks, Mendocino | 1997 | 17 | 15 | 20 |
| | Total | | 348 | 463 | 996 |
| Redwood | | | | | |
| Lostman Creek, Orick, CA | Redwood National Park | 1993–1995 | 10 | 25 | 32 |
| Mad River, Korbel, CA | Simpson Timber Company | 1996–1997 | 19 | 24 | 39 |
| Redwood Creek, Orick, CA | Redwood Sciences Laboratory (RSL) | 1994–1997 | 34 | 102 | 73 |
| Wright Refuge, Eureka, CA | Humboldt State University | 1993–1997 | 65 | 89 | 0 |
| Van Duzen River, CA | LBJ Enterprises (LBJ) | 1997 | 9 | 5 | 9 |
| Yager Creek, Carlotta, CA | Pacific Lumber Company, RSL, LBJ | 1994–1997 | 58 | 45 | 64 |
| | Total | | 194 | 290 | 217 |
| Klamath-Trinity | | | | | |
| Seiad Valley, Klamath River, CA | Klamath NF (KNF) | 1993–1997 | 87 | 148 | 99 |
| Humbug Creek, Klamath River, CA | KNF | 1994 | 11 | 0 | 11 |
| West Humbug Creek, Klamath River, CA | KNF | 1995 | 17 | 1 | 20 |
| Whitmore Creek, Orleans, CA | RSL | 1992 | 11 | 4 | 11 |
| Ishi Pishi Road, Orleans, CA | RSL | 1992–1997 | 54 | 32 | 59 |
| Camp Creek, Orleans, CA | RSL | 1992–1997 | 103 | 56 | 118 |
| Red Cap Cr. 7.2 km SW Orleans, CA | RSL | 1992–1996 | 82 | 40 | 97 |
| Red Cap Cr. 7.6 km SW Orleans, CA | RSL | 1992–1997 | 101 | 48 | 120 |
| Red Cap Rd., 1.5 km SW Orleans, CA | RSL | 1992–1997 | 97 | 103 | 118 |
| Red Cap Rd., 2.2 km SW Orleans, CA | RSL | 1992–1996 | 53 | 27 | 54 |
| Weitchpec, CA | Six Rivers NF, RSL | 1991 | 7 | 24 | 55 |
| Aikens Creek, CA | RSL | 1992 | 11 | 0 | 11 |
| Trinity River, Big Bar, CA | Shasta-Trinity NF | 1991–1997 | 87 | 26 | 148 |
| | Total | | 721 | 509 | 921 |
| Coastal Mountains | | | | | |
| Grove's Prairie, Denny, CA | RSL | 1994–1997 | 52 | 33 | 79 |
| Grouse Creek, Hyampom, CA | RSL | 1994 | 10 | 4 | 0 |
| Quail Meadows, Hayfork, CA | RSL | 1994–1997 | 41 | 74 | 79 |
| Indian Valley Creek, Hayfork, CA | RSL | 1994–1997 | 41 | 33 | 78 |
| | Total | | 144 | 144 | 236 |

APPENDIX. CONTINUED

| Region and location | Operator | Years sampled | Ten-day periods | Number of Captures: Pacific-slope Flycatcher | Number of Captures: Willow Flycatcher |
|---|---|---|---|---|---|
| Siskiyou | | | | | |
| Bear Creek Botanical Area, OR | SNF | 1991–1997 | 57 | 26 | 63 |
| Carberry Creek, OR | Rogue River NF (RRNF) | 1993–1997 | 52 | 5 | 64 |
| Clear Creek, OR | SNF | 1985 | 6 | 1 | 8 |
| Gray Back Creek, OR | SNF | 1991–1997 | 39 | 25 | 11 |
| Horse Creek Meadows, OR | SNF | 1987–1997 | 104 | 97 | 107 |
| Long Ridge, OR | SNF | 1992–1997 | 40 | 13 | 60 |
| White Horse Prairie, OR | SNF | 1985 | 5 | 6 | 8 |
| | Total | | 303 | 173 | 321 |
| Rogue | | | | | |
| Applegate River, OR | RRNF | 1997 | 19 | 5 | 21 |
| Bear Creek, OR | RRNF | 1997 | 8 | 0 | 11 |
| Whetstone Savannah, OR | SNF | 1997 | 15 | 2 | 15 |
| Rogue River, Medford, OR | BLM, Medford District | 1994–1996 | 31 | 41 | 58 |
| | Total | | 73 | 48 | 105 |
| Upper Klamath | | | | | |
| Williamson River, OR | RSL | 1997 | 6 | 0 | 9 |
| Wood River, Upper OR | RSL, BLM, Lakeview District (LVB) | 1997 | 16 | 1 | 19 |
| Seven Mile Creek, OR | RSL | 1996–1997 | 25 | 2 | 30 |
| Recreation Creek, OR | RSL | 1996–1997 | 25 | 12 | 73 |
| Odessa Creek, OR | RSL | 1996–1997 | 25 | 3 | 31 |
| Johnson Creek, OR | RSL, LVB | 1997 | 16 | 2 | 19 |
| Skeeter Swamp, OR | RRNF | 1994–1997 | 33 | 19 | 41 |
| Topsy, Klamath River Canyon, OR | RSL, LVB | 1997 | 1 | 0 | 1 |
| | Total | | 147 | 39 | 223 |
| Shasta | | | | | |
| Mile 36, Sacto R.[a] Dunsmuir, CA | Point Reyes Bird Observatory (PRBO) | 1993–1996 | 44 | 1 | 44 |
| Prospect, Sacto R. Dunsmuir, CA | PRBO | 1993–1996 | 44 | 0 | 44 |
| Soda Creek, Sacto R. Dunsmuir, CA | PRBO | 1993–1996 | 44 | 10 | 46 |
| Castella, Sacto R. Dunsmuir, CA | PRBO | 1993, 1994, 1996 | 33 | 2 | 33 |
| Conant, Sacto R. Dunsmuir, CA | PRBO | 1993, 1994, 1996 | 40 | 3 | 45 |
| Sims Creek, Sacto R. Dunsmuir, CA | PRBO | 1993–1996 | 50 | 6 | 54 |
| Pollard Flat, Sacto R. Dunsmuir, CA | PRBO | 1993, 1994, 1996 | 25 | 1 | 25 |

APPENDIX. CONTINUED

| Region and location | Operator | Years sampled | Ten-day periods | Number of Captures | |
|---|---|---|---|---|---|
| | | | | Pacific-slope Flycatcher | Willow Flycatcher |
| Dog Creek, Sacto R. Dunsmuir, CA | PRBO | 1993, 1994, 1996 | 32 | 1 | 33 |
| Madrone Campground, Squaw Creek, CA | PRBO | 1993–1996 | 42 | 21 | 44 |
| | Total | | 354 | 45 | 368 |
| Modoc | | | | | |
| Antelope Creek, Tennant, CA | KNF, RSL | 1994–1997 | 22 | 2 | 49 |

*Notes:* Abbreviations are: BLM = Bureau of Land Management, NF = National Forest, CA = California, OR = Oregon.
[a] Sacto R. = Sacramento River.