

**CONSERVATION ASSESSMENT
OF THE
WILLOW FLYCATCHER
IN THE
SIERRA NEVADA**

Gregory A. Green

Foster Wheeler Environmental Corporation

Bothell, Washington

Helen L. Bombay

Pioneer, California

Michael L. Morrison

University of California, White Mountain Research Station

Bishop, California

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Chapter 1

Introduction

SCOPE

Populations of willow flycatchers (*Empidonax traillii*) have exhibited marked declines throughout the western United States (Sauer et al. 1997). The subspecies found in the southwestern United States (*E. t. extimus*) reached such critical levels that it was listed as federally endangered in 1995 (USFWS 1995), while another subspecies, *E. t. brewsteri*, has been extirpated from California's Central Valley (Grinnell and Miller 1944, Serena 1982). Populations of *brewsteri* and another subspecies, *E. t. adastus*, remain in the Sierra Nevada, but these, too, have undergone substantial declines (Harris et al. 1987, Bombay et al. 2001, Stefani et al. 2001). Recognizing these population declines, the USDA Forest Service has developed management strategies for conserving willow flycatcher populations in the Sierra Nevada under the Sierra Nevada Forest Plan Amendment.

The Regional Foresters for the Pacific Southwest and Intermountain Regions declared their intention in the Sierra Nevada Forest Plan Amendment (SNFPA) Record of Decision (ROD) to complete a conservation assessment for the willow flycatcher and to make recommendations for future actions (USDA Forest Service 2001). The conservation assessment will be used to support and further develop the willow flycatcher conservation strategy identified in the Record of Decision and specified in its Standard and Guidelines (Appendix A).

The Sierra Nevada Forest Plan Amendment includes the Sequoia, Sierra, Stanislaus, Eldorado, Inyo, Tahoe, Plumas, Lassen, and Modoc National Forests, as well as the Lake Tahoe Basin Management Unit of the USDA Forest Service Pacific Southwest Region. In addition, the plan includes the portion of the Humboldt-Toiyabe National Forest from the adjacent Intermountain Region that occurs in the Sierra Nevada. This assessment also

includes data pertaining to Yosemite, Sequoia, and Kings Canyon National Parks. Biogeographically, this administrative area exceeds the Sierra Nevada mountain range to encompass much of the Modoc Plateau, the southern Cascade Mountain Range, and the western edge of the Great Basin. Conservation assessments document all that is known or unknown about a species, including its ecology, habitat needs, population levels, and management risks. Conservation assessments also provide management recommendations based on the researched available knowledge. In turn, these management recommendations are incorporated into a single management strategy designed to benefit the species. Essentially, this conservation assessment was developed as a tool to guide future conservation strategy and recovery planning for the Sierra Nevada populations of the willow flycatcher (Blankenship et al. 2001).

A core team of willow flycatcher experts (representing the USDA Forest Service, U.S. Fish and Wildlife Service (USFWS), California Department of Fish and Game, and the Southern Sierra Research Station) and the authors met on 19 October 2001 to finalize the contents outline for the conservation assessment and to identify information not readily available in the literature. The members of this team are Rosemary Stefani, Mary Whitfield, Teresa Benson, Karen Hayden, Jesse Wild, Ron Schlorff, John Robinson, Mary Flores, Helen Bombay, and Greg Green.

Two subspecies of willow flycatcher predominate within the geographic area of the Sierra Nevada Forest Plan Amendment: *E. t. brewsteri* on the Pacific slope and *E. t. adastus* on the eastern slopes (Phillips 1948, Unitt 1987, Browning 1993). These subspecies are the focus of this conservation assessment. A third subspecies, the southwestern willow flycatcher

(*E. t. extimus*), is currently believed to be limited to the extreme southern range of the Sierra Nevada. Because it has already received intense conservation focus since its listing as federally endangered, including development of conservation assessments and recovery plans (Finch and Stoleson 2000, USFWS 2001), coverage of *E. t. extimus* in this assessment is limited to information relevant to the conservation and management of the other two subspecies.

CURRENT MANAGEMENT STATUS

All three subspecies of willow flycatcher occurring in California were listed as state endangered by the California Department of Fish and Game in 1990 (Steinhart 1990). The southwestern willow flycatcher (*E. t. extimus*), found in the southwestern United States including the Kern and Owens River regions of southern California, was listed as federally endangered by USFWS in 1995 (USFWS 1995). Both *brewsteri* and *adastus* are currently designated sensitive species by USDA Forest Service, Region 5, and are listed as species of concern by USFWS, Region 1 (Williams and Craig 1998). The willow flycatcher has been identified as a regional “species at risk” in the Sierra Nevada Forest Plan Amendment. Activity-related standards and guidelines for conserving willow flycatchers were developed under the Sierra Nevada Forest Plan Amendment ROD (USDA Forest Service 2001).

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Chapter 2 Distribution and Taxonomy

DISTRIBUTION

Breeding Range

The breeding distribution of *E. traillii* has been described as the conterminous United States, exclusive of the Southeast, and the southern margins of Canada (Browning 1993). At its northern limit, *E. traillii* gives way to its sibling species, the alder flycatcher (*E. alnorum*), the distribution of which extends on into northern Canada and Alaska (Browning 1993). The exact northern limit of the willow flycatcher is still unclear due to difficulty in identification of *E. traillii* and *E. alnorum* where the ranges of both species overlap.

The range of *E. t. extimus*, the southwestern willow flycatcher, extends into the southern reaches of the Sierra Nevada along the South Fork Kern River (near Weldon) and in the Owens Valley near Independence (Unitt 1987), although recent genetic investigations suggest that willow flycatcher populations in the Owens Valley immediately north of Bishop are *extimus* (Paxton 2000). All these sites occur within the Sierra Nevada Forest Plan Amendment area, but only the 1,200-acre South Fork Wildlife Area on the South Fork Kern River is managed by the USDA Forest Service. Willow flycatcher records in the Sequoia and Inyo National Forests' interior have not yet been classified to subspecies and may represent intergrades between *extimus* and *brewsteri*, although the inference is that west-slope Sequoia birds are *brewsteri*, and east-slope Sequoia and Inyo birds are *adastus* (Unitt 1987).

Following the range maps of Unitt (1987) and Browning (1993), *brewsteri* can be found in the drainages flowing westward (e.g., Warner Valley), while *adastus* occur in the drainages flowing east (e.g., Little Truckee River). In general, populations on the Lassen (including Lassen Volcanic National Park), Plumas, Eldorado, Stanislaus, and Sierra National Forests and the Yosemite, Sequoia, and Kings

Canyon National Parks fall within the presumed range of *brewsteri*, while populations on the Modoc, Toiyabe, and Inyo National Forests and the Lake Tahoe Basin Management Unit are considered *adastus*. The Tahoe and Sequoia National Forests straddle the Sierra Nevada crestline and, therefore, may support both subspecies.

However, the close proximity and similar habitat of these potentially separate populations suggest that interbreeding may occur (Phillips 1948, Williams and Craig 1998). For example, Middle Fork Feather River *brewsteri* and Little Truckee *adastus* are separated by only about 25 km. Because *brewsteri* and *adastus* have been separated based largely on subtle differences in coloration, and coloration can vary greatly within populations, several authors have suggested that the two subspecies are synonymous (Miller 1941, Behle 1948). Further, Paxton (2000) could not find genetic separation between *brewsteri* and *adastus* and attributed this to a large number of his samplings coming from a possible intergradation zone (e.g., Sierra Nevada). Finally, Bombay et al. (2001) did observe a willow flycatcher disperse approximately 13 km (8 miles) between the Little Truckee River headwaters (east side) and the Yuba River headwaters (west side), suggesting that the Sierra Nevada crestline is not a definitive boundary between the two subspecies. From a conservation standpoint, it probably matters little whether or not the Sierra Nevada represents an intergradation zone, unless behavioral differences (e.g., dispersal patterns, habitat selection) between the purported subspecies call for different management strategies.

Table 2-1 shows the number and distribution of willow flycatcher breeding sites (i.e., point locations) by forests and national parks within

Table 2-1. Number and distribution of known willow flycatcher point locations in the Sierra Nevada Forest Plan Amendment area by ownership (USDA Forest Service, unpubl. data).

Forest or Park*	Ownership						Total	Percent
	National Forest	National Park	BLM	State	City/County	Private		
Modoc	6	0	1	0	0	0	7	5%
Lassen	10	0	0	1	0	8	19	14%
Plumas	12	0	0	1	0	5	18	13%
Tahoe	12	0	0	1	0	5	18	13%
LTBMU	4	0	0	2	0	1	7	5%
Eldorado	1	0	0	0	0	0	1	1%
Toiyabe	5	0	0	2	0	0	7	5%
Stanislaus	7	0	0	0	0	1	8	6%
Inyo	8	0	1	0	4	4	17	13%
Yosemite NP*	0	5	0	0	0	0	5	4%
Sierra	9	0	0	0	0	4	13	10%
Sequoia	8	0	0	1	0	1	10	7%
Sequoia/Kings Canyon NP*	0	5	0	0	0	0	5	4%
Total	82	10	2	8	4	29	135	100%
Percent	61%	7%	1%	6%	3%	21%	100%	

Table 2-2. Number and distribution of known willow flycatcher territories (site average) in the Sierra Nevada Forest Plan Amendment area by ownership (USDA Forest Service, unpubl. data).

Forest or Park*	Ownership						Total	Percent
	National Forest	National Park	BLM	State	City/County	Private		
Modoc	10	0	1	0	0	0	11	3%
Lassen	17	0	0	32	0	14	63	20%
Plumas	15	0	0	2	0	8	25	8%
Tahoe	35	0	0	3	0	23	61	19%
LTBMU	6	0	0	2	0	4	12	4%
Eldorado	1	0	0	0	0	0	1	0%
Toiyabe	8	0	0	4	0	0	12	4%
Stanislaus	14	0	0	0	0	1	15	5%
Inyo	12	0	2	0	13	8	35	11%
Yosemite NP*	0	12	0	0	0	0	12	4%
Sierra	12	0	0	0	0	9	21	7%
Sequoia	9	0	0	2	0	30	41	13%
Sequoia/Kings Canyon NP*	0	6	0	0	0	0	6	2%
Total	139	18	3	45	13	97	315	100%
Percent	44%	6%	1%	14%	4%	31%	100%	

the Sierra Nevada Forest Plan Amendment area by ownership. Most (61 percent) of the point locations are found on National Forest System lands, but a substantial percentage (21 percent) is found in private lands.

Many of the USDA Forest Service sites support few willow flycatcher territories. Only 44 percent of the territories (based on site averages) have been found on 82 National Forest sites, while 31 percent have been found on only 29 private sites (Table 2-2). Exact locations of all territories are not recorded, and some meadows overlap multiple ownerships (National Forest, private, etc.); therefore, there may be a few instances where some territories assigned to one ownership may actually occur across boundaries on another ownership. Similarly, survey efforts may not have occurred equally across all ownerships. Nonetheless, this dataset represents the best available information at this time. Although reported values may vary somewhat from actual values, the overall relative patterns of occupancy and ownership are assumed to be representative.

The number of territories is also skewed towards just a few meadows. Only 6 of the 135 known sites have ever been recorded to support 10 or more territories (USDA Forest Service, unpubl. data). Collectively, these six sites support a third of all territories and half of the currently active territories. Of these six sites, two support *extimus* populations (South Fork Kern River and Owens Valley) that are outside the scope of this Conservation Assessment. Only two (Perazzo Meadow and Little Truckee) of the remaining four occur on National Forest System lands. Lacey Valley is private, and Warner Valley Wildlife Area is owned by the California Department of Fish and Game.

Wintering Range

The winter range delineation for the willow flycatcher has been problematic, again due to the confusion between willow flycatchers and alder flycatchers. However, recent investigations, some quite detailed, have shown willow flycatchers to winter in tropical

and subtropical areas from southern Mexico to northern South America (Gorski 1969, Meyer de Schauensee and Phelps 1978, Ridgely and Gwynn 1989, Stiles and Skutch 1989, Ridgely and Tudor 1994, Howell et al. 1995, Unitt 1997); the flycatcher is thus termed a neotropical migrant. Significant wintering areas have recently been found in Costa Rica, Panama, and El Salvador where they occupy seasonal wetland habitats (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999, Lynn and Whitfield 2000, Koronkiewicz and Sogge 2000).

TAXONOMY

The willow flycatcher and its sibling species, the alder flycatcher, were once recognized as a single species: Traill's flycatcher (Grinnell and Miller 1944). As similar as both species are in appearance, studies by Stein (1963) revealed that they build different nests, sing different songs, and do not interbreed where their ranges overlap. Consequently, in 1973, the American Ornithologists' Union reclassified the southern *fitz-bew* song type into the willow flycatcher and the northern *fee-bee-o* type (Aldrich's [1951] nominate *E. t. traillii*) into the alder flycatcher. Aldrich's (1951) nominate *E. t. campestris* then became *E. t. traillii* (Stein 1963, Unitt 1987). Browning (1993) has since argued that *E. t. campestris* is a valid subspecies separate from *E. t. traillii*. *E. t. campestris* has been described as a Midwest subspecies that has extended its range eastward to western New York, while *E. t. traillii* occurs along the eastern seaboard from Maine south to North Carolina, then westward across the Appalachia to eastern Arkansas and Missouri (Browning 1993).

Three subspecies occur in California: *E. t. brewsteri*, *adastus*, and *extimus*. They have been distinguished from each other based on distribution and color (Unitt 1987, Browning 1993). Unitt (1987) concluded that willow flycatcher subspecies could not be defined based on measurements of size and proportions. In California, *brewsteri* ranges along the west slopes of Cascade/Sierra and

Nevada ranges, while the *adastus* inhabits the east slopes (Unitt 1987, Browning 1993). The southwestern willow flycatcher, *extimus*, extends into the southern extreme of the Sierra Nevada province, with known locations in the South Fork Kern River and Owens Valley (Stefani et al. 2001), though the definitive range of the three subspecies in the area remains to be confirmed by further analysis.

The subspecies *brewsteri* is darker above than other subspecies of willow flycatcher and has been described by Unitt (1987) as dark brownish olive. Unitt further described *adastus* as dark grayish green and *extimus* as pale grayish green. Miller (1941) and Behle (1948) found enough color variation in eastern Oregon willow flycatchers to conclude that *adastus* and *brewsteri* were synonymous. However, Browning (1993) reexamined the eastern Oregon specimens and concluded that the darker individuals from the western edge range of *adastus* were actually migrant *brewsteri*.

Intergrades between *adastus* and *brewsteri* are known from Oregon and northern California, but Browning (1993) believed that interbreeding between the two subspecies is rather limited. However, Paxton (2000) collected genetic samples from 232 adult *extimus*, *traillii*, *adastus*, and *brewsteri* at 49 breeding sites and could not find significant genetic variation between *adastus* and *brewsteri*. He attributed his results to possible biased sampling of *brewsteri* along an intergradation zone with *adastus* (e.g., Sierra Nevada). Further, Paxton's (2000) *cytochrome-b* sequencing data showed that Little Truckee River (Perazzo Meadows) "*adastus*" were closely grouped with "*brewsteri*" populations, including the Warner Valley population on the Lassen National Forest. Further research is necessary before genetic distinctions can be made between Sierra Nevada populations of *brewsteri* and *adastus*.

Although intergrades between *adastus* and *extimus* have also been reported regularly (Behle 1985, Unitt 1987), Browning (1993)

concluded that there was not a gradual cline and that many of the earlier reports suggesting intergradation were incorrect. Regardless, although recent genetic research by Paxton (2000) concluded that *extimus* is genetically distinct from other subspecies and its northern range (based on *cytochrome-b* pattern analysis) follows closely the taxonomic distributions of Unitt (1987) and Browning (1993), his data suggest an intergradation zone in southwestern Colorado.

Interbreeding between *brewsteri* and *extimus* in California is also unclear. In his examination of museum collections, Unitt (1987) found possible *brewsteri/extimus* intergrades from Los Angeles and San Bernardino Counties. Curiously, his results also show a single breeding *brewsteri* and a single breeding *extimus* collected from the same location on the same date in 1917, confounding conclusions.

POPULATION INSULARITY

Willow flycatcher breeding habitat in the Sierra Nevada can be described as "islands" of meadows in a "sea" of forest conifers. Inasmuch as these meadows (or clusters of meadows) are geographically isolated from other meadows, some level of population insularity can be inferred. However, genetic isolation, or lack of movement between populations, is much more difficult to determine. Buskirk and Ruggiero (1994) pointed out that lack of movement between populations is difficult, if not impossible, to prove. Further, habitat isolation is less significant a factor for migratory birds than for any other vertebrate group for the obvious reason they can circumvent long distances between isolated areas (Harris 1984). This would be especially true for the willow flycatcher, a neotropical migrant.

Nevertheless, a significant number of breeding sites in the Sierra Nevada appear no longer to support viable breeding populations of willow flycatchers (USDA Forest Service, unpubl. data). The remaining meadows, often occurring in loose clusters, are now further separated from the closest active populations.

Implications of isolation of these patches depend on site fidelity and dispersal capabilities and are further confounded by the presence of three subspecies, which may or may not interbreed. To qualify as a habitat isolate (Morrison et al. 1998), the distance between a breeding location and its closest neighbor should exceed either the maximum known willow flycatcher dispersal distance

(190 km; using *extimus* data from Nettor et al. 1998), or should be twice the average dispersal distance (63.5 km; Nettor et al. 1998). Because the maximum of the closest neighbor distances in the Sierra Nevada, for breeding locations active since 1982, is only 44 km, or well below qualifying as an isolated population, none of the breeding locations is a habitat isolate.

Chapter 3

Reproductive Biology

PHENOLOGY

As with other regions of the species' range, male willow flycatchers in the Sierra Nevada generally arrive at breeding areas first, with females typically arriving approximately 1 week later (Stafford and Valentine 1985, Sogge 2000, H. Bombay, pers. obs.). When comparing 2-year-old southwestern willow flycatchers in Arizona with older birds, Kenwood and Paxton (2001) reported that the capture/resighting date (which approximates the arrival date) was significantly later for 2-year-old birds. Earliest arrival dates range from late May to early June in the southern Sierra Nevada (Grinnell and Storer 1924, Linsdale 1932, Stafford and Valentine 1985), while willow flycatchers in the northern Sierra Nevada typically begin arriving around the first of June (Serena 1982, Sanders and Flett 1989, Bombay and Morrison, unpubl. data).

Nest building usually begins within a week or two of pair formation, depending on the arrival date and site/vegetation phenology (Stafford and Valentine 1985, Harris 1996). Egg laying for first nest attempts sometimes begins as early as the second week in June, but more often begins between 25 June and 5 July (Stafford and Valentine 1985, Valentine et al. 1988, Flett and Sanders 1987, Sanders and Flett 1989, Bombay and Morrison, unpubl. data) (Figure 3-1). Renesting attempts result in laying dates through the first week of August (Bombay and Morrison, unpubl. data). Based on an overlay of the incubation onset dates for known renesting attempts compared to presumed first nest attempts, it appears that renesting attempts surge in numbers after about 7 July (Figure 3-2). Nestlings are present in nests from early July through late August (Sanders and Flett 1989).

Incubation lasts 12 to 14 days from the date the last egg is laid, and all eggs typically

hatch within 24 to 48 hours of each other (Bent 1942, King 1955, Walkinshaw 1966, Stafford and Valentine 1985, Flett and Sanders 1987, Valentine et al. 1988, Sanders and Flett 1989, Sogge 2000, Bombay et al. 2001). In the Sierra Nevada, as elsewhere, young willow flycatchers typically fledge at 12 to 16 days of age and stay close to the nest and each other for 3 to 5 days (Valentine et al. 1988, Sanders and Flett 1989, Sedgwick 2000, Bombay et al. 2001). Recently fledged birds may repeatedly return to and leave the nest during this period (McCabe 1991, Sedgwick 2000). Fledglings stay in the natal area a minimum of 14 to 15 days after fledging, possibly much longer (Walkinshaw 1966, Stafford and Valentine 1985, Bombay and Morrison, unpubl. data). Young typically fledge from nests from mid-July through the end of August; later fledging dates are the product of renesting attempts (Stafford and Valentine 1985, Sanders and Flett 1989, Bombay and Morrison, unpubl. data). Adults depart from breeding territories as early as mid-August, but may stay until mid-September if they fledged young late in the season (Stafford and Valentine 1985, Bombay 1999, Bombay and Morrison, unpubl. data). Males that fail to attract or retain mates, and males or pairs that are subject to significant disturbance (such as repeated nest predation, etc.), may leave territories earlier (mid-July) (Bombay et al. 2001).

Timing of fledgling departure is largely unknown for the Sierra Nevada, but fledglings have been documented foraging independently 2 to 3 weeks after leaving the nest. All willow flycatchers appear to be gone from their territories by mid-September (Stafford and Valentine 1985, H. Bombay, pers. obs.). On 24 August 1997, a willow flycatcher banded as a nestling was recaptured 29 days after fledging at a constant effort mist net station 350 meters from its natal territory on the Tahoe National Forest (Bombay and

Morrison, unpubl. data; J. Steele, unpubl. data). This suggests that fledglings may leave their natal territories, but not begin long-distance migration for some time (although sample sizes of one should be viewed cautiously). This observation is supported by the fact that juvenile willow flycatchers undergo their first prebasic molt before leaving the breeding grounds, while adults delay their molt until reaching the wintering grounds (Unitt 1987, Pyle 1997). Yong and Finch (1997) also reported that hatching year willow flycatchers tended to migrate through the Rio Grande valley later than adults.

Figure 3-1 presents a generalized breeding chronology for willow flycatchers in central and northern California. Assessment of data and literature available for the Sierra Nevada suggests that, for most breeding locations north of Alpine County (in the vicinity of Lake Tahoe), nest phenology is fairly uniform with nest initiation and fledging dates falling within the middle of the time periods shown in Figure 3-1 (Ingersoll 1913, Ray 1913, Sanders and Flett 1989, Bombay et al. 2001, King and King *in press*, T. Ratliff, pers. comm.). Fewer data are available for the portion of the Sierra occurring south of Alpine County. However, willow flycatcher nests monitored in the 1980s in the Sierra National Forest (South of Kings Canyon National Park), as well as some historic records (Bennett 1934), suggest that nest initiation occurs in the earlier portions of the nest stages displayed in Figure 3-1 as one moves further south (Stafford and Valentine 1985, Valentine et al. 1988). Extreme or record dates for any stage of the breeding cycle may vary as much as a week from the dates presented. At higher elevations, for example, seasonal differences in snow pack and timing of snowmelt may delay starting dates for each stage by up to 2 weeks (Valentine et al. 1988, Bombay and Morrison, unpubl. data).

MATING SYSTEMS

Males are usually monogamous, but polygyny has been recorded in the Sierra Nevada. Valentine et al. (1988) reported two

incidences of polygyny in a small population between 1983 and 1987 (4 of 20 nest attempts). Bombay and Morrison (unpubl. data) found a minimum of nine polygynous males between 1997 and 2001, accounting for at least 9 percent of matings (18/204). In other parts of the species' range, polygyny is not uncommon, and polygyny rates as high as 15 percent have been reported in Oregon and as high as 59 percent for southwestern willow flycatchers in California and Arizona (Prescott 1986, Sedgwick and Knopf 1989, Sedgwick 2000, Sogge 2000, Davidson and Allen *in press*). Polygynous males usually, but not always, divide time and care between females and nests (Sedgwick 2000).

MATE FIDELITY

Little information is available regarding mate fidelity in the Sierra Nevada. On the Sierra National Forest one female deserted her territory after nest failure and was replaced by another female who used the remains of the first nest to construct her own. The next year, the first female was back on her original territory with the same male (Stafford and Valentine 1985). Sogge (2000) reported that preliminary data for southwestern willow flycatchers suggest that mate fidelity may be low and that even within-year mate shuffling may be common. Alternately, Sedgwick (2000) reported that 29.5 percent (n = 325 returns) of males and 36.0 percent (n = 267 returns) of females remated with a previous mate over a 10-year period in Oregon, and one pair remained together for 5 consecutive years.

NEST SITE SELECTION AND BUILDING

Females select the nest site, collect the nest material, and construct the nest while the male follows her or perches nearby (McCabe 1991, Sedgwick 2000, Sogge 2000). Exact duration of the nest building stage is unknown for the Sierra Nevada, but McCabe (1991) and Bent (1942) reported nest-building periods of 5 to 10 days. Holcomb (1974) reported 3.9 days for nest building in Nebraska and an

additional 1 to 6 days before the first egg was laid. In the Sierra Nevada, more than 10 days have been documented between nest completion and the laying of the first egg (Bombay and Morrison, unpubl. data).

In the Sierra Nevada, willow flycatchers build open-cup nests approximately 9.5 cm tall and 8.5 cm in diameter (outside dimensions), exclusive of any dangling material at the bottom (Sanders and Flett 1989, Bombay 1999). These dimensions suggest that willow flycatchers in the Sierra Nevada build nests that are somewhat larger than those built in other parts of the species range (Sedgwick 2000, Sogge 2000). Frequently nests have a bearded appearance due to additional dried vegetation hanging up to 10 cm below the base of the nest (Sanders and Flett 1989, Sedgwick 2000, Sogge 2000).

As elsewhere in their range, Sierra Nevada willow flycatcher nests are typically constructed using a primary base of dried grasses, sedges, forbs, and willow (*Salix* spp.) bark (Sanders and Flett 1989, Valentine 1987, Sedgwick 2000). Nests are lined with finer stems, willow down, and the down or feathers from other bird species, especially waterfowl (Sanders and Flett 1989, Sedgwick 2000, Bombay pers. obs.) When available, deer hair, horsehair, and feathers can make up a considerable portion of both the lining and outer portion of nests (Bombay pers. obs.). Manmade materials such as string, paper, and plastic bags are also included in some nests (Sanders and Flett 1989, McCabe 1991, H. Bombay, pers. obs.)

Nests are typically placed in the fork of a branch with the nest cup supported by several small stems (Stein 1963, Flett and Sanders 1987, Valentine et al. 1988, Sanders and Flett 1989, Harris 1991, McCabe 1991). The main forked branch may be oriented vertically, horizontally, or at an angle (McCabe 1991). Bombay (1999) reported that the mean number of supporting stems at 70 nests was 5.77 (SD = 1.60), and Sanders and Flett (1989) reported the mean number at 9 nests was 4.7 (SD = 1.3). Stems supporting the nest cup are typically small with diameters of

only 0.3 to 0.75 cm. Valentine et al. (1988) reported that 68 percent of stems at 22 nests were less than 0.5 cm in diameter, and 96 percent were less than 1.0 cm. In the north-central Sierra Nevada, Sanders and Flett (1989) and Bombay (1999) reported mean supporting branch diameters of 0.62 cm (SD = 0.54) and 0.71 cm (SD = 0.21), respectively.

Nest height varies considerably and may be correlated with height of nest plant, overall canopy height, and/or height of the vegetation strata that contain small twigs and live growth suitable for nest support and concealment (Stein 1963, Flett and Sanders 1987, Valentine et al. 1988, Sanders and Flett 1989, Harris 1991, McCabe 1991). There are 42 nests, dated between 1898 and 1950, from the Sierra Nevada in the collection at the Western Foundation of Vertebrate Zoology. Of these, 29 document the nest height: the closest to the ground is from Bijou Marsh at Lake Tahoe and is recorded at 0.38 m, and the highest is from Bear Valley in Mariposa County in the western foothills and is recorded at 5.5 m above the ground (mean = 2.0 m, median = 1.8 m, SD = 1.2 m). Valentine et al. (1988) reported a range of 0.77 m to 2.18 m in the south-central Sierra Nevada (n = 22, mean = 1.49 m, SE = 0.78 m). On the Tahoe National Forest, Sanders and Flett (1989) reported a range in nest heights of 0.70 m to 1.98 m (n = 20, mean = 1.14 m, SD = 0.29 m). Bombay (1999) reported nest heights from 0.40 m to 2.50 m for the north-central Sierra Nevada (n = 77, mean = 1.11 m, SD = 0.34 m). In the extreme northern Sierra Nevada, King and King (*in press*) reported nest heights from 0.9 m to 1.9 m (n = 10, mean = 1.3 m, SD = 0.31 m).

RENESTING

Although occasionally reported for the southwestern willow flycatcher (Whitfield 1990, Sogge 2000, M. Whitfield, unpubl. data), second clutches after a successful first nest are unknown for willow flycatchers in the Sierra Nevada (Stafford and Valentine 1985, Sanders and Flett 1989, Valentine et al. 1988,

Flett and Sanders 1987, Bombay and Morrison, unpubl. data). Sierra Nevada willow flycatchers frequently attempt a second and even a third nest after earlier nest failures (Stafford and Valentine 1985, Bombay 1999, Morrison et al. 1999). Bombay et al. (2001) reported that renesting attempts between 1997 and 2001 accounted for 12 to 35 percent of all nests annually ($n = 264$ nests, mean = 27 percent, SE = 9). Nine of these were known to be third nesting attempts. Harris (1991) reported as many as six nest attempts in a single season for southwestern willow flycatchers in the extreme southern Sierra Nevada. Substantial declines in clutch size with subsequent nesting attempts are reported for many regions (Holcomb 1974, McCabe 1991, Sedgwick 2000, Stoleson et al. 2000).

Replacement nests, or new nests built for renesting attempts, are built in the same territory, typically within 50 m of the previous nest (McCabe 1991, Bombay and Morrison, unpubl. data). In the Sierra Nevada, the distances of renests from previous nests range from within the same shrub to as far as 100 m (Bombay and Morrison, unpubl. data). Although not documented in the Sierra Nevada, renesting southwestern willow flycatchers have been known to reuse the same nest in a single year on a few occasions (Whitfield 1990, Yard and Brown 1999). Frequently, willow flycatchers disassemble failed nests in order to use the nesting material to build new nests (Stafford and Valentine 1985, McCabe 1991, H. Bombay, pers. obs.).

Many researchers report that second and third nests are built much more quickly than first attempts (McCabe 1991, Sedgwick 2000, Sogge 2000). Alternately, Holcomb (1974) reported no difference in the time involved in building first nests versus renests; rather, the mean time between nest completion and egg laying decreased from 3.1 days to 1.4 days. In the Sierra Nevada, replacement nest building and egg laying can occur (uncommonly) as late as early August (Stafford and Valentine 1985, Sanders and Flett 1989, Bombay et al. 2001, Bombay and Morrison, unpubl. data).

EGG LAYING AND INCUBATION

Willow flycatcher eggs are buffy or creamy white, approximately 18 mm long and 13 mm wide, with brown markings in a loose wreath at the blunt end (Bent 1942, Walkinshaw 1966, Sedgwick 2000). Unspotted eggs (or those that are nearly so) have been reported (Sedgwick 2000, H. Bombay, pers. obs.). Across the species range, clutch size is usually three or four eggs for first nests (Bent 1942, King 1955, Sanders and Flett 1989, Whitfield and Enos 1996, Sedgwick and Iko 1999, Sedgwick 2000, Sogge 2000), although occasional five-egg clutches are reported in some bioregions (Holcomb 1974, Sedgwick 2000). Sedgwick (2000) reported mean first clutch sizes ranging from 2.92 to 3.69 in five different study areas. In the Sierra Nevada (1997 to 2001), presumed first nest attempts with data adequate to determine actual number of eggs laid had a mean clutch size of 3.52 eggs ($n = 126$ nests, SD = 0.68). Known renests had a mean clutch size of 2.96 eggs ($n = 49$ nests, SD = 0.61 (Bombay and Morrison, unpubl. data). Flett and Sanders (1987) reported 2.8 eggs per nest based on five nests with complete data. One egg is laid each day until the clutch is complete, with an occasional day skipped (Sedgwick 2000). Laying most frequently occurs in the morning (Sedgwick 2000). Most authors report that females perform all incubation activities (King 1955, McCabe 1991, Sedgwick 2000), but Gorski (1969 *in* Sedgwick 2000), and Yard and Brown (unpubl. data *in* Sogge 2000) reported occasional incubation by males.

Exact timing of the onset of incubation relative to egg laying is uncertain, with some authors reporting incubation to begin during laying, while others report onset to occur after the last egg is laid (Sedgwick 2000, Sogge 2000). Incubation lasts from 12 to 15 days after the last egg is laid (McCabe 1991). In the Sierra Nevada, Sanders and Flett (1989) reported a 12-day incubation period. Bombay and Morrison (unpubl. data) recorded similar incubation periods of 12 to 14 days.

Based on limited observations of two females in Ohio, Holcomb (1972) reported that

females were at the nest 64 percent of the time, with attentiveness increasing later in the incubation cycle. Mean attentive and inattentive bouts lasted 10.1 and 5.7 minutes, respectively. Sogge (2000) reported similar unpublished results of 50 percent attentiveness during the day and constant incubating during nighttime hours for southwestern willow flycatchers.

HATCHING

McCabe (1991) reported that in Wisconsin all eggs hatch over 1 to 3 days, with 90 percent of 160 clutches hatching in 2 days or less. Females are known to remove and discard eggshells away from the nests (McCabe 1991, Sedgwick 2000).

NESTLING STAGE

In the Sierra Nevada, the mean nestling period appears to be slightly longer than that reported in other regions. At their Sierra Nevada study sites, Sanders and Flett (1989) used an estimate of 14 days, and Bombay et al. (2001) found that most nests observed over 6 years of study required 15 days before fledging occurred. Extreme nestling periods of 19 to 20 days have been observed during extended periods of cool wet weather or very dry conditions (Bombay and Morrison, unpubl. data). In Nebraska and Ohio, Holcomb (1972) reported a mean nestling stage of 12.5 days and a range of 11 to 14 days. In the Great Lakes region, McCabe (1991) and Walkinshaw (1966) reported 14 to 15 days and 13.8 days, respectively. For southwestern willow flycatchers, Sogge (2000) reported a nestling stage that ranges from 12 to 15 days; however, the nestling period used for Mayfield calculations in Arizona is 12 days (Rourke et al. 1999).

Brooding behavior in the form of sitting low over the young to protect them from cool wet weather, or standing on the nest edge and shading them with outstretched wings, occurs most frequently during the first 5 days after hatching (McCabe 1991, Sedgwick 2000). This behavior is important because these

altricial nestlings cannot fully thermoregulate during this early stage of life (Welty 1962).

The female provides most, if not all, of the initial care of the young, although the role of the male in providing food increases with the age and size of nestlings (Holcomb 1972, Ettinger and King 1980, Prescott 1986). In Washington, Ettinger and King (1980) reported that males visited the nest only 0.75 times as often as females. In Oregon, Sedgwick (2000) found that the female parents and male parents fed nestlings at three nests 59.3 percent and 3.7 percent of the time, respectively. A presumably unrelated adult of unknown gender provided the remaining 37 percent of feedings. Similarly, Sedgwick and Knopf (1989) reported that a polygynous male made 17.9 percent of all feedings at both of his mates' nests. Both sexes remove fecal sacs generated by nestlings, especially early in the nestling phase (McCabe 1991, Sedgwick 2000).

Bird blow flies (*Protocalliphora*) that parasitize nestlings are common in the nests of flycatchers, and willow flycatchers are known hosts of *Protocalliphora cuprina*. Heavy blow fly infestations (e.g., 10 or more larvae per nestling) can make nestlings anemic and more susceptible to starvation, hypothermia, and other parasites like mites, fleas, and lice. Severe blow fly infestations may be lethal (T. Whitworth, www.birdblowfly.com), although studies of natural populations of *Protocalliphora* in 48 species of birds indicate that the larval populations are usually too small to kill or seriously injure most nestlings (Whitworth and Bennett 1992). In most areas, approximately 5 to 10 percent of infested nests are likely to have sufficient larval populations to make nestlings sick (T. Whitworth, www.birdblowfly.com). Though blow fly parasite loads in willow flycatcher nests in the Sierra Nevada have not been investigated, nestling parasites are not believed to be a significant threat to the willow flycatcher population.

FLEDGLING STAGE

Willow flycatcher nestlings are capable of flight 2 to 3 days prior to natural fledging and, therefore, may be prompted to prematurely fledge if disturbed by predators or researchers (Rourke et al. 1999, Sogge 2000). Once fledging occurs, young stay near the nest and each other for 3 to 5 days (Walkinshaw 1966, McCabe 1991, Sedgwick 2000, Sogge 2000). During this time, fledglings often huddle together and may make repeated visits back to the nest (McCabe 1991).

Both adults feed the fledged young, which beg loudly and may mob or chase the adults in pursuit of food (Ettinger and King 1980, Prescott 1986, Sanders and Flett 1989, H. Bombay, pers. obs.). In the south-central Sierra Nevada, Stafford (1986) reported three banded adult willow flycatchers and one banded dusky flycatcher feeding a single brood of willow flycatcher fledglings. Two of the adult willow flycatchers were not related to the young, suggesting that floaters, migrants, or unsuccessful breeders may be stimulated to feed begging fledglings that are not their own. As described above, Sedgwick (2000) witnessed similar behavior when observing an unidentified adult (both parents were banded) providing 37 percent of the feedings to a brood of nestlings.

Fledglings typically remain in their natal territory for approximately 14 to 25 days (Walkinshaw 1966, Sedgwick 2000, Bombay and Morrison, unpubl. data). During this time, they become increasingly independent and begin foraging for themselves between feedings by adults (Bombay and Morrison, unpubl. data).

BEHAVIORAL FACTORS INFLUENCING PRODUCTIVITY

Early vs. Late Nesting

In a study of more than a thousand nests in Oregon, Sedgwick and Iko (1999) found that willow flycatchers that fledged on or before 15 July ($n = 127$) were nearly six times more likely to return the following year (survive the

winter) than young that fledged after 15 July ($n = 1,144$). Likewise, Whitfield and Sogge (1999) found, over an 8-year-period, that southwestern willow flycatchers that fledged early were almost twice as likely to return the following year. Similar results have been reported for white-crowned sparrows (*Zonotrichia leucophrys*) (Morton 1992) and house wrens (*Troglodytes aedon*) (Drilling and Thompson 1988). Therefore, management that results in decreased predation and parasitism and protects nests from direct impact should also improve juvenile return rates, since late fledging dates are typically the result of renesting due to earlier nest failure.

Polygyny

Polygyny has been reported for several populations of willow flycatcher and may be a response to demographic stochasticity (uneven sex ratios in small populations) (Burgman et al. 1993, Sedgwick and Knopf 1989, M. Whitfield, unpubl. data) or skewed nestling sex ratios at a site and insufficient dispersal (Paxton et al. 2002). When sex ratios on the breeding ground are skewed towards males (Sogge et al. 1997, Johnson et al. 1999 in Paxton et al. 2002, Walkinshaw 1966, Sedgwick and Knopf 1989), perhaps as a result of lower survivorship for females (Walkinshaw 1966, Sedgwick and Knopf 1989), a significant number of males go unmated. However, unmated females have not been reported, probably because polygyny ensures that all females are mated where female numbers exceed males (Paxton et al. 2002, Sedgwick and Knopf 1989, M. Whitfield, unpubl. data). Energetic demands of simultaneous nesting within a single territory are not known, but appear to be wholly viable, especially when timing between the nests is offset (Prescott 1986). Consequently, polygyny may be an important reproductive strategy to ensure maximum productivity from females. However, this premise still has to be viewed with some caution as unmated and polygynous males have been observed simultaneously in the

same breeding population (M. Whitfield, unpubl. data). Yet even this phenomenon may indicate a strategy on the part of willow flycatchers to maximize production. Female great reed warblers (*Acrocephalus arundinaceus*) in northern Europe frequently shared territories with other females, even when unmated territorial males were

available. Hansson et al. (2000) attributed this to varying habitat quality, especially in respect to predation risks. Using artificial nests, they found predation rates were much higher in unmated male territories than polygynous male territories, compensating for costs associated with sharing a male with another female.

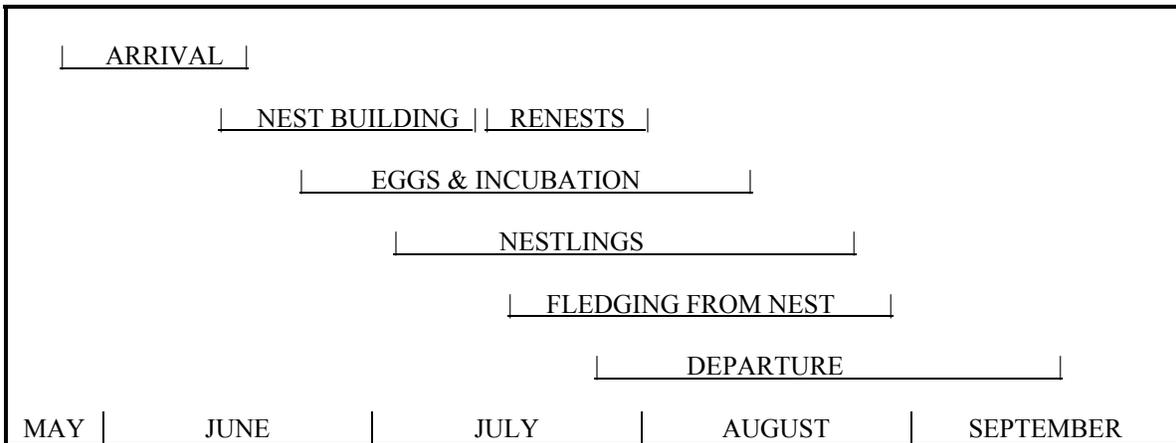


Figure 3-1. Generalized willow flycatcher breeding chronology for the Sierra Nevada, California. (Sources: Stafford and Valentine 1985, Flett and Sanders 1987, Valentine 1987, Sanders and Flett 1989, Bombay and Morrison, unpubl. data.)

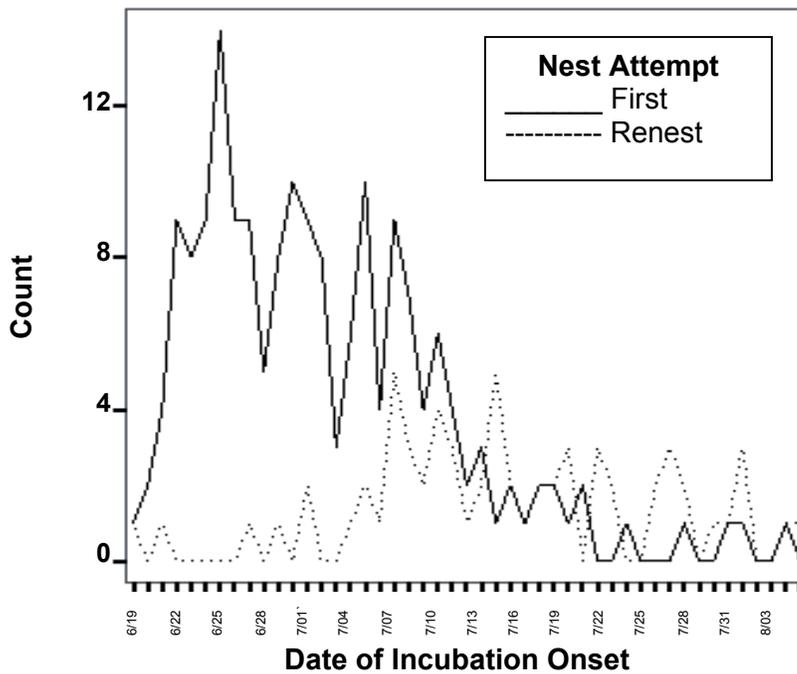


Figure 3-2. Willow flycatcher incubation onset dates for the central Sierra Nevada, California. (Sources: Stafford and Valentine 1985, Sanders and Flett 1989, Bombay and Morrison, unpubl. data.)

Chapter 4

Food Habits and Prey Relationships

GENERAL FORAGING ECOLOGY

The general foraging strategy of willow flycatchers is to sit and wait from a perch providing good visibility, then pursue and capture flying arthropod prey that have ventured near (hawking) (McCabe 1991). Pursuit flights are short, usually less than 5 m (15 ft) (McCabe 1991). Via (*in* Dickson et al. 1979) recorded average flight distance of only 0.9 m (3 ft) for 50 pursuit flights observed. In the Sierra Nevada, Sanders and Flett (1989) reported that most foraging willow flycatchers flew less than 1 m (3.3 ft) in pursuit of insects, although flight distances of up to 10 m (33 ft) were observed. Willow flycatchers will also glean insects from vegetation (Peters and Burleigh 1951, Via *in* Dickson et al. 1979, McCabe 1991), but probably more frequently when weather is less conducive to insect flight (Phillips et al. 1964). However, Koronkiewicz and Sogge (2000) found willow flycatchers wintering in Costa Rica to primarily “sally glean” or pull insects from vegetation surfaces while maintaining flight.

GEOGRAPHIC VARIATION IN DIETS

Beal (1912 *in* Bent 1942) reported on the stomach contents of 135 willow flycatchers collected in 17 states and found that 41 percent of the captured prey were bees, wasps, and ants (Hymenoptera), followed by beetles (Coleoptera; 18 percent), flies (Diptera; 14 percent), moth and butterfly caterpillars (Lepidoptera; 8 percent), and true bugs (Hemiptera; 7 percent). McCabe (1991) recorded 214 food samples delivered to willow flycatcher nestlings in Wisconsin. Over half the captures were from just five groups of insects: deer flies (Tabanidae), bee flies (Syrphidae), common skipper (Hesperiidae), spittlebug (Cercopidae), and scarab beetles (Scarabidae). Deer flies alone comprised 20 percent of the deliveries. Diets

of *E. t. extimus* in Colorado and Arizona were apparently similar to those reported by Beal (1912), although dragonflies (Odonata) are also of importance (see Williams and Craig 1998).

In the Sierra Nevada, bees, wasps, and flies are apparently as important to the willow flycatcher as elsewhere in its breeding range. Sumner and Dixon (1953) reported that willow flycatchers in the Kings Canyon and Sequoia National Parks consumed “wasps, bees, beetles, flies, caterpillars, moths, grasshoppers, and occasionally berries.” In the central Sierra Nevada, H. Bombay (pers. obs.) observed adult willow flycatchers capturing wasps and willow sawflies (*Euura*), deer flies (Tabanidae), moths and caterpillars (Lepidoptera), mayflies (Ephemeroptera), and damselflies (Odonata).

The most important prey consumed by *extimus* at the South Fork Kern River were true bugs, flies, and small beetles, followed by dragonflies and damselflies, bees and wasps, leafhoppers (Cicadellidae), and spiders (Araneae) (Drost et al. 2001). Nestlings ate significantly higher numbers of true bugs, flies, and leafhoppers than adults, for reasons that remain unclear.

PRINCIPAL PREY

The collective studies of willow flycatcher diet indicate that this bird feeds on a wide variety of insect and other arthropod prey and, on rare occasions, fruit (berries). There are, however, some prey groups that are universally common to all studies. Willow flycatchers have a predilection for hymenopterids such as bees, wasps, and sawflies; dipterids such as deer flies and bee flies; moths and butterflies (and their caterpillars); and small flying beetles. Hymenopterids and deer flies are especially

important in the Sierra Nevada (Sumner and Dixon 1953, H. Bombay, pers. obs.). H. Bombay (pers. obs.) observed that fledging willow flycatchers capture grasshoppers by hopping from lower branches of shrubs onto the ground. Thus, grasshoppers might be very important to willow flycatchers during a brief, but critical, life stage.

HABITAT ASSOCIATIONS OF PREY

Erman (1984) examined the associations between 10 insect orders and riparian systems specific to the montane meadows in the Sierra Nevada. Most members of Ephemeroptera (mayflies), Odonata (damselflies and dragonflies), Hemiptera (true bugs), Coleoptera (beetles), and Diptera (flies) found here have aquatic egg or larval stages and, therefore, are abundant in areas with extensive water. Deer flies, mayflies, and damselflies, insects commonly found Sierra Nevada willow flycatcher diets (H. Bombay, pers. obs.), are prime examples. Even the terrestrial adults of the above insect orders depend on

the vegetation found immediately adjacent to stream channels (Erman 1984).

Wasps and sawflies, also very important to willow flycatcher diets, may not have aquatic life stages, but many depend directly on riparian vegetation. The willow sawflies (*Euura* spp.), for instance, produce galls on willow leaves to protect their larvae (Borror et al. 1976). Other sawflies and wasps have similar relationships with riparian plants.

Several studies have linked insect abundance with hydrologic conditions (Gosselink and Turner 1978) and riparian vegetational changes (Voigts 1976, Weller 1978). In turn, increased insect abundance has been linked with increased bird abundance. Kelly and Wood (1996) found foraging by common yellowthroats (*Geothlypis trichas*) to increase where insect abundance was greatest, and this correlated with diurnal temperature patterns and seasonal vegetation and hydrology patterns. Gray (1993) found increasing abundance of birds in the flycatching guild at times and locations of increasing insect abundance.

Chapter 5

Breeding Habitat Relationships

GENERAL

Habitat has been defined by Morrison et al. (1998) as an area with a combination of resources (food, cover, water) and environmental conditions (temperature, precipitation, presence or absence of predators or competitors, etc.) that promotes occupancy and allows for survival and reproduction. Appropriate breeding habitat provides the necessary requisites of nesting cover and insect food resources. As its name implies, the willow flycatcher inhabits riparian deciduous shrub and small tree riparian zones, generally dominated by willow (*Salix* spp.). Across its range however, there is considerable variability in habitat characteristics (Harris 1996), including use of upland thickets not close to water (King 1955).

In California, Grinnell and Miller (1944) described the breeding habitat of *E. t. brewsteri* as "...strikingly restricted to thickets of willows...", generally in a riparian situation. Habitat typical of willow flycatchers in the central and northern Sierra Nevada includes moist meadows lined with willows and alders (*Alnus* spp.) (Serena 1982, Gaines 1988, Harris et al. 1988). Sawyer and Keeler-Wolf (1995) classified this meadow type as "montane wetland shrub habitat." However, dense thickets are generally avoided in favor of more patchy willow sites providing considerable edge (Valentine 1987, Sanders and Flett 1989, Harris et al. 1988). In the southern Sierra Nevada, willow flycatchers are more often associated with dense thickets of willows and other trees along stream courses (Harris 1991). Because these thickets are more linear in nature and have greater stand structure (taller trees), they inherently provide considerable edge.

HISTORY OF MEADOW HABITAT MANAGEMENT AND USE

California's riparian ecosystems, including meadows, have been profoundly impacted by human use for the last 150 years. The extent of this impact is illustrated in the loss of riparian forest in the Central Valley alone. The Central Valley riparian forest in 1848 was estimated at greater than 373,000 ha (Katibah et al. 1983, Katibah 1984), with 324,000 ha in the Sacramento Valley alone (Smith 1977, Roberts et al. 1977). By 1979, this acreage had been reduced to approximately 41,300 ha, of which 75 percent was in a degraded or human-impacted state (Katibah et al. 1983).

Reasons for streamside riparian loss in the Central Valley include the gold rush; agricultural needs for fencing, lumber, fuel, and irrigation; Sacramento River steamships, farming of natural levees; construction of flood control levees; water diversions; and grazing (Katibah et al. 1983, Katibah 1984). They may also account for the extirpation of the willow flycatcher from the Central Valley (Gaines 1977, Serena 1982).

These impacts also spread into the Sierra Nevada. For instance, the Los Angeles aqueduct project has greatly reduced or nearly eliminated riparian vegetation along the lower reaches of Lee Vining and Rush Creeks (Stine et al. 1984) and the Owens River downstream of the intake (Brothers 1984). Willows are virtually absent from the Owens River riparian zone from the intake to approximately 45 km downstream due to reduced flows (Brothers 1984).

Like the stream riparian zones, the meadow ecosystems were also impacted. Grazing began in the 1860s (Gomez-Ibanez 1967, McKelvey and Johnston 1992, Kinney 1996, Kondolf et al. 1996, Menke et al. 1996, Allen-Diaz et al. 1999). Early grazing included not only sheep and beef cattle, but

dairy cattle confined to meadows as well (Sudworth 1900). Overstocking of livestock in the Sierra Nevada apparently began almost immediately (Burcham 1982), with competition between established cattle and nomadic sheep ensuing. By the 1890s, laws were being passed to exclude sheep from forest lands as trespassing and overcrowding increased tensions between cattlemen and sheepherders. The USDA Forest Service ended the nomadic sheep herding way of life by requiring all grazers to own base properties, a tenet eventually adopted by the Taylor Grazing Act of 1934.

The number of livestock using the Sierra Nevada in the nineteenth century is unknown, but it apparently peaked in the 1880s at the height of the “open-access” (uncontrolled) period (Allen-Diaz et al. 1999). Dudley (1898) spoke disparagingly about the trampled state of the meadows of the Sierra Forest Reserve in the late 1890s compared to the U.S. Army-protected meadows of the Sequoia National Park. By 1900, Sudworth (1900) noted sheep bands forced to subsist on pine needles, indicating that range conditions had severely declined.

In the early twentieth century, the federal government began to gain control of the rangelands under the Forest Reserve system. However, World War I sparked increased demands for livestock products, and the ranges were again overstocked (Rowley 1985). From the 1920s to the 1970s, livestock grazing in the Sierra Nevada decreased significantly (Menke et al. 1996), with a more gradual decrease occurring since then (Forero et al. 1998). The 1900s also saw varied levels of pack stock use, which also declined substantially in the latter half of the century (McClaran 1989).

Numerous other human-induced activities were co-occurring with grazing that apparently had negative impacts on meadow conditions. Roads were constructed to allow access to the forest for mining, timber harvesting, building construction, recreational activities, and other uses. Roads were often placed along or through meadows, and ditches

and culverts were constructed to reduce or eliminate flooding of roadways. Such activities changed meadow hydrology and likely led to meadow desiccation. Opening of the forest canopy through road construction and logging also likely allowed cowbirds to gain access to meadows.

There is (some) evidence that the hydrology of Sierra Nevada meadows has changed since the introduction of livestock. Although hydrological regimes of meadows are complex, and include influences from fire (DeBenedetti and Parsons 1979), drought, and other stochastic events, meadow desiccation as a result of gully erosion appears to be a geologically recent phenomenon coeval with the introduction of livestock (Hagberg 1995, Dull 1999). Dull (1999), in his pollen analysis of Sierra Nevada meadows (dating back to 3140 BP), also observed a marked decline in willows since 1850 that he attributed to livestock presence. Mining, water diversions, and streamside timber harvest are contemporaneous with intensive livestock grazing during the second half of the nineteenth century in the Sierra and could also have contributed to meadow desiccation (McKelvey and Johnston 1992, Kattelman and Embury 1996). Others suggest climate variation is also pertinent for determining influences on changes in meadow conditions. Other pollen studies of Sierra Nevada montane meadows show willow declines from several hundred to thousands of years ago, which predate livestock grazing effects and indicate that willow has responded to other conditions in the past such as climatically induced changes in the water table (W. Woolfenden, pers. comm.). This review indicates that, while natural processes (e.g., drought, climate change) certainly determine long-term patterns in meadow condition, the evidence is also strong that human activities (e.g., road building, water diversion, over-grazing) have more recently accelerated changes in meadow condition in the context of flycatcher needs.

As such, there are several interacting factors that have led to a general decline in the condition of meadows. As reviewed elsewhere

in this document, these human activities have led to both direct and indirect effects on flycatcher habitat and population parameters.

SUITABLE HABITAT

Understanding habitat requirements of willow flycatchers is paramount not only in understanding causes for population decline, but in developing management strategies towards protection and restoration of Sierra Nevada populations. The concept of habitat use is, however, not straightforward. Occupancy, for instance, does not necessarily equate to suitability or preference, and potentially optimal habitat may not be occupied if availability of such habitat exceeds the available nesting pairs in a depressed population. Consequently, when assessing habitat associations, a number of concepts must first be defined.

Habitat use, or occupancy, defines the range of tolerance a species has among the habitat choices (or habitat gradient). It reveals nothing about suitability or preference, only that the habitat is tolerable enough to occupy. Suitable breeding habitat can, however, be defined as locations in which reproduction and survival result in a stable or growing population (Sogge and Marshall 2000, McCallum 1994). It is habitat where the rate of population change (termed Lambda [λ]) is either stable or growing. In contrast, unsuitable habitat is defined as occupied habitat where the rate of population change is decreasing or is maintained by immigration (sink populations) from stable or growing populations (source populations) (McCallum 1994). The concept of preferred habitat suggests that a species with a range of habitat choices will seek specific habitats based on internalized standards (desirability) (McCallum 1994).

Each definition has its separate purpose in developing management strategies. Understanding the *range of occupancy* and what constitutes *unsuitable habitat* is important in identifying sink habitat or sites that might be good candidates for future restoration. Determining *suitable habitat*

reveals the characteristics important to breeding success and becomes the measuring stick against which change is monitored. It helps identify those sites in need of protection while implementing Forest Plan management activities. *Preferred habitat* is important for restoration. It is the subset of suitable habitat, defining the “best” conditions (an analog for preference), and is the goal responsible restoration activities are designed to reach.

Determining suitable habitat is one of the first goals of willow flycatcher habitat conservation efforts. If a requirement of suitable habitat is that the population of its occupants be stable or growing, however, then long-term studies may be required to accurately measure the rate of population change. Rate of population change or fitness (termed Lambda [λ]) is measured using a number of functions such as fecundity, over-winter mortality, and dispersal. Each is difficult to accurately measure, and inaccuracy of any one results in an inaccurate λ , leading to an inaccurate measure of suitable habitat. Sogge and Marshall (2000) have stated that for the southwestern willow flycatcher, at least, there are not enough long-term data to accurately determine population stability and, therefore, suitable habitat.

While recognizing the problems mentioned above, attempts have been made to develop discrete definitions of suitable habitat (Stefani et al. 2001) using existing data (Serena 1982, Harris et al. 1988, Flett and Sanders 1987, Sanders and Flett 1989, Bombay 1999). These become working definitions with recognition that future refinement is needed as new data become available. Further, Habitat Suitability Index (HSI) Models have been developed (KRCD 1985a, PG&E 1986, Fowler et al. 1991) and tested (Scully 1995) that also attempt to define the suitable habitat range. Collectively, these studies and definition building exercises have resulted in developing five components that may best define Sierra Nevada willow flycatcher habitat requirements.

- **Elevation:** Most (88 percent or 119/135 known sites) Sierra Nevada meadows

used by breeding willow flycatchers occur between 1,200 and 2,500 m (4,000 to 8,000 ft) elevation, although meadows as low as 365 m (1,200 ft) and as high as 2,900 m (9,500 ft) have been used (Stefani et al. 2001).

- **Wetness:** Successful nesting territories are strongly associated with standing or flowing water or heavily saturated soils.
- **Meadow Size:** Although use of meadows less than 0.5 ha (1 ac) has been documented, more than 95 percent of the breeding meadows are greater than 4 ha (10 ac), and the most successful (i.e., ≥ 1 territory fledged young) meadows are greater than 6 ha (15 ac).
- **Shrub Coverage:** Riparian deciduous shrub coverage has generally been measured or modeled as a percentage of meadow area; 20 to 30 percent has been suggested as a minimum for suitable habitat. Scully (1995), however, measured absolute area and found sites for male willow flycatchers to average 525 m². In her HSI model, Scully awarded an optimal coefficient value of 1.0 for shrub patches greater than 400 m².
- **Foliar Density:** Foliar density is a measure of the riparian deciduous shrub at the 2-m shrub height level, or the level of the shrub layer where actual nesting generally occurs. Based on her research, Scully (1995) awarded a coefficient value of 1.0 for foliar densities of greater than 76 percent in her HSI model.

Although research has been conducted to characterize willow flycatcher habitat, none of these studies was specifically designed to determine discrete definitions for suitable habitat. Doing so requires further research correlating habitat use with nesting success over a long enough time to determine accurate trends in nesting success. The HSI approach is a valuable tool in grading habitat suitability, but it does not incorporate, except by inference, fitness measures (λ). Continued research on habitat use, coupled with demographic studies designed to measure

fitness, should ultimately lead to a reliable definition for suitable habitat.

SPATIAL SCALES

Habitat use by willow flycatchers can be viewed at hierarchical scales. There is no single set of spatial scales ecologically meaningful for all wildlife species. Rather, scale should be based on the questions being asked. For the Sierra Nevada willow flycatchers, it is important to understand habitat use at the microhabitat scale to assess site-specific conditions and at the broad scale to establish regional strategies for conservation.

The smallest scale at which habitat use by Sierra Nevada flycatchers has been investigated is the nest site. Habitat use at the breeding patch level has also been investigated and is generally synonymous with willow stands. However, because several flycatcher pairs will establish territories within the same willow stand, territory is also a useful scale on which to examine habitat use. Because of their structural similarities, willow stands and territory are discussed together. Meadow, the next hierarchy, is the level where management activities are most likely to be targeted and is, therefore, the level of greatest conservation importance. For purposes of this assessment, breeding habitat is examined at four hierarchical scales: nest site, territory/willow stand, meadow, and broad scale.

Nest Site

The nest site scale is important because it allows us to understand the plant species that are most important to willow flycatchers for nesting substrate.

Historically, most willow flycatcher nests reported for the Sierra Nevada and other parts of northern California were found in willows, with occasional references to blackberry (*Rubus* spp.), aspen (*Populus tremuloides*), and alder (*Alnus* spp.) as nest substrates (Bendire and Brevet 1895, Bent 1942). Sierra Nevada nest records in the collection at the

Western Foundation of Vertebrate Zoology dated between 1898 and 1950 include 34 records that document the nest substrate: 2 were placed in alder, 3 in aspen, 4 in wild rose (*Rosa* spp.), and 25 in willow. More recent accounts usually describe willow as the most frequently used nest substrate. Sanders and Flett (1989) reported that all 20 nests found at two meadows on the Tahoe National Forest in 1986 and 1987 were placed in willow (*Salix lemmonii*, *S. geyeriana*, or *S. jepsonii*). Out of more than 250 nests found at 15 meadows in the north-central Sierra Nevada between 1997 and 2001, only three occurred in non-willow shrubs: two in mountain alder (*Alnus tenuifolia*) and one in creek dogwood (*Cornus stolonifera*) (Morrison et al. 2000, Bombay et al. 2001, Bombay and Morrison, unpubl. data). In most territories within this study area, willow is the only available riparian shrub (Bombay 1999, H. Bombay, pers. obs.). Recently, however, McCreedy and Heath (*in review*) discovered (or rediscovered) a population of willow flycatchers in Rush Creek (Mono Lake) where all nine discovered nests were in wild rose, despite the presence of suitable nesting willows.

Valentine (1987) reported that, although willow was the most abundant shrub type, and the most frequently used nest substrate in the Sierra National Forest study area, in Poison Meadow all four willow flycatcher nests located there between 1984 and 1986 were placed in creek dogwood. Similarly, King and King (*in press*) reported that, although willow made up more than half (57.3 percent \pm 26.5 percent) of the shrubby vegetation surrounding 10 nests in the extreme northern Sierra Nevada, all were placed in mountain alder.

Current nest records for other shrub substrates outside the Sierra Nevada, but within northern California, include mountain mahogany (*Cercocarpus* spp.) on the Modoc National Forest and blackberry along the Klamath River (Harris 1996). In other parts of the West, *adustus* and *brewsteri* subspecies are frequently reported to nest in cow parsnip (*Heracleum lanatum*) and bracken fern

(*Pteridium aquilinum*) (King 1955, Sedgwick 2000).

Territory/Willow Stand

Territory is the specific area within a meadow that a single male willow flycatcher defends for breeding and foraging resources. Because specific resources are being defended, and these resources may not be distributed uniformly across the meadow, habitat use within territories may vary from the general meadow habitat. To determine whether territory is a meaningful scale in relationship to willow flycatcher habitat use, Bombay (1999) compared habitat use within Sierra Nevada territories to the general meadow habitat. Similarly, Sedgwick and Knopf (1992) compared macroplots (roughly equivalent to the size of a territory) in Colorado between territorial and unoccupied areas. Both found the same results: willow flycatcher territories exhibited significantly more willow cover.

In the Sierra Nevada, Bombay (1999) found shrub cover (virtually all Lemmon willows [*S. lemmonii*]) within territories to average about 48 percent, while at many of the same sites studied by Bombay (1999), Sanders and Flett (1989) found shrub coverage in territories (0.34 ha mean size) to average 44 percent. Sedgwick and Knopf (1992) found virtually identical results in Colorado. Plots (0.32 ha) centered over nests averaged 49 percent willow coverage, while plots centered over song perches averaged 44 percent. Bombay (1999) also found that successful territories had more shrub cover than unsuccessful ones (52 percent versus 43 percent). At a recently discovered site near Mono Lake, McCreedy and Heath (*in review*) found nine nests centered on monotypic patches of wild rose.

Bombay (1999) found that the mean coverage of standing water, or highly saturated soils, was relatively high (44 percent) and much higher than that found by Sedgwick and Knopf (1992) in Colorado (10 to 11 percent). Neither study, however, indicated significant differences in water coverage between

occupied territories and unoccupied area. Bombay (1999) did, however, find significantly greater water depths in successful (0.6 m) than unsuccessful (0.5 m) territories. Greater water depths may improve nesting success by increasing food supply (Voigts 1976, Erman 1984, Gray 1993, Kelley and Wood 1996) and reducing predator access (Ammon and Stacey 1997, Cain 2001). In contrast, McCreedy and Heath (*in review*) found that willow flycatchers nesting along Rush Creek used wild rose stands in drier situations. On average, Rush Creek nests were more than 130 m from water (the creek itself), indicating different breeding ecologies in desert riparian versus mountain meadow habitats.

Meadow

The one consistency of Sierra Nevada willow flycatcher habitat use is that they nest in wet meadows with standing water and abundant willows (Serena 1982; Harris et al. 1987, 1988; Fowler et al. 1991). Thus, the meadow scale provides insights on meadow hydrology and distribution of willow stands. Bombay (1999) found occupied meadows to have a significantly higher percentage of meadow with a shrub component (60 percent versus 40 percent) and standing water or saturated soils (57 percent versus 41 percent) than unoccupied meadows. Bombay (1999) also found occupied meadows to contain 22.6 percent more foliar density in the lower 2 m of shrub, 1.8 ha more shrub, 20.2 percent more grass cover, more beaver use, and more small stream channels than currently unoccupied meadows.

Size of meadows is also important. Meadows used by nesting willow flycatchers in the Sierra Nevada have ranged in size from 0.4 to 290 ha (1 to 719 ac), with more than 80 percent of the territories occurring in meadows greater than 8 ha (20 ac) (Serena 1982; Harris et al. 1987, 1988; Bombay 1999).

Broad-scale

The broad scale enables conceptualizing about elevational limits, nearest neighbor distances, and dispersal needs. The elevational range of willow flycatchers in the Sierra Nevada bioregion, which includes *extimus* populations on the South Fork Kern River and Owens Valley, is 365 to 2,900 m. However, most meadows used for breeding by *brewsteri/adastus* are between 1,200 and 2,500 m (4,000 to 8,000 ft) elevation (Serena 1982, Harris et al. 1988, Stafford and Valentine 1985, Bombay 1999, Bombay et al. 2001). Research by Bombay (1999) suggests that there is an upper elevational limit to flycatcher use in the Sierra Nevada, which she attributed to the presence of snow and unleafed willows at the time of spring arrival. Late snowmelt at the higher elevations can delay nesting and shorten breeding seasons, both contributing to nesting success, or even nesting attempts.

Willow flycatcher nest sites are distributed along the length of the Sierra Nevada. However, multiterritory sites (excluding *extimus*) active since 1999 are clustered at five general locations: Lassen Peak, Truckee, Carson, Yosemite, and Mono Lake. Distances between these clusters range from 68 to 323 km (42 to 60 miles) and average about 84 km (52 miles). These locations may represent spruce populations, or isolated strongholds in an ever-shrinking distribution.

HABITAT ISOLATION

Habitat isolation in the breeding populations of Sierra Nevada willow flycatchers is inherent because of the very patchy nature of their breeding habitat. Grinnell and Miller (1944) described the range of the willow flycatcher in California as “Roughly, the entire length of the State...,” but “really much very restricted” in regard to breeding habitat. Meadows with willow riparian basically represent “islands” of habitat in a “sea” of forest avoided by this bird. As the number of meadows providing suitable habitat has declined, presumably from anthropogenic factors, the remaining meadows have become

even more isolated. Whether these expanded distances between breeding populations are greater than normal willow flycatcher dispersal distances remains to be determined.

MEADOW HYDROLOGY

The montane meadows used by willow flycatchers have formed in the low-gradient valleys of the Sierra Nevada over the last 10,000 years (Wood 1975). These meadows, products of alluvial processes (low-gradient deposits along streams), are characterized by their high saturation of water, especially during spring snowmelt runoff. These hydrological regimes, known as “wet meadows,” result in water budgets exceeding groundwater inflow and evapotranspirative water losses. Characteristic features are highly saturated soils, including standing water, and a community of hydrophytic plants able to withstand water saturation. Sawyer and Keeler-Wolf (1995) have classified Sierra Nevada wet meadows, with a shrub component dominated by willows (or other riparian deciduous shrubs), as “montane wetland shrub habitat.” At least nine species of willow and two alder can be found in this vegetation type.

The characteristics of shrub-dominated montane meadows important to willow flycatchers are the prevalence of willows and, during the nesting season, standing or flowing water, or highly saturated soils. As shown by Cain (2001; see also Cain et al., *in press*), wetness aids nesting success by inhibiting nest access of forest and edge predators and preventing establishment of lodgepole pine, which provides habitat for forest and edge predators. Wetness may also provide habitat for important willow flycatcher prey.

The primary cause of meadow desiccation in the Sierra Nevada has been identified as gullying (Hagberg 1995). Gullies form in meadows when the protective sod layer has been damaged or incised, resulting in erosive processes reaching the soil layer. Gullies alter groundwater hydraulics and hydrology by intercepting surface and groundwater (thereby cutting off water supply to downstream areas)

and by reducing the pressure head to zero at all exposed points along the gully (Reid 1989, Hagberg 1995). The result is a drop in the water table, leading to surface desiccation (Reid 1989). Interestingly, in his study of 15 gullied meadows on the Sierra National Forest, Hagberg (1995) used aerial photography to conclude that all gullies formed during either a 1937 or a 1950 rain-on-snow storm event. Essentially, gullies can be formed from a specific episodic (storm flood) event leading to a chronic condition (headcutting). Further, through a process of alternative hypothesis elimination and evidence gleaned from aerial photographs, Hagberg inferred that livestock trampling and chiseling were the likely causes at 12 of the meadows, and road building and mining coupled with grazing were the causes at the other 3. Regardless of the actual causes, many of these gullies remain and continue to stress meadow ecology.

While intensive grazing by livestock has damaged meadow resources in the Sierra Nevada (Ratliff 1985), and it is likely that livestock damage and road building may have resulted in gully formation leading to meadow desiccation, connecting grazing directly to willow flycatcher population declines remains speculative. Nevertheless, meadow restoration efforts and erosion mitigations leading to gully healing and an increase in habitat components important to willow flycatchers should benefit recovery of this species.

Chapter 6

Home Range and Territoriality

The breeding home range and territory are nearly synonymous in the willow flycatcher. Willow flycatcher territories generally fall within Nice's (1941) Type A classification where the mating, nesting, and foraging areas are all actively defended (McCabe 1991). KRCD's (1985b) observations in the Sierra Nevada confirm that most foraging and other activities occur within the territory. Breeding willow flycatchers will, on occasion, forage outside their defended territory, even crossing adjacent territories while doing so. Sanders and Flett (1989) found willow flycatchers on the Little Truckee River using foraging perches up to 30 m outside their defended territory and conducting forage bouts to 100 m beyond their territory. Once young begin fledging, territory boundaries begin breaking down, with both fledglings and adults extending their home ranges into adjacent territories (KRCD 1985b).

Territory size in willow flycatchers can vary widely depending on habitat structure, forage density, pressures from adjacent territories, and mating strategy. Sanders and Flett (1989) found average territory size of 22 pairs of willow flycatchers on the Little Truckee River to be 0.34 ha, or about twice the 0.18 ha average KRCD (1985b) found for 6 pairs at Dinkey Meadows on the Sierra National Forest. *E. t. extimus* in the Sierra Nevada Forest Plan Amendment area may defend even larger territories. Monogamous males on the South Fork Kern River defended

territories averaging 0.6 ha, and polygynous males averaged 1.1 ha (Whitfield and Placer 1994, Whitfield and Strong 1995, Whitfield and Enos 1996, Whitfield et al. 1997).

Information on home range use during the migration and wintering period is lacking, although a greater variety of habitats, including non-riparian vegetation, is used by willow flycatchers during migration than during breeding (Yong and Finch 1997, Finch et al. 2000). No information on territoriality during migration exists (Finch et al. 2000).

Territoriality by willow flycatchers on their wintering ground was suspected by a number of researchers (Gorski 1969, Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999), but was not confirmed until research conducted by Koronkiewicz and Sogge (2000). Koronkiewicz and Sogge (2000) monitored the behaviors of 40 wintering willow flycatchers in Costa Rica and found that they not only defended specific territories, they exhibited relatively high within-year (85 percent) and between-year (43 to 77 percent) site fidelity. Both males and females aggressively responded to simulated intrusions into their territories by other flycatchers and excluded conspecifics from their territories regardless of sex. Koronkiewicz and Sogge (2000) also captured and color-banded several non-territorial floaters, some of which quickly occupied and defended vacant territories after the original defender had disappeared.

Chapter 7 Movements

NATAL DISPERSAL

The frequency, patterns, and average distances of adult and natal dispersal for *E. t. adastus* and *E. t. brewsteri* in the Sierra Nevada are largely unknown. Between-meadow natal dispersal data are limited to 19 resighting records collected between 1997 and 2001 (Bombay et al. 2001, Bombay and Morrison, unpubl. data). These records consist of between-year, between-meadow movements only, and recorded distances range from 0.8 km to 19.8 km (median = 3.6 km; mean = 6.0 km; SD = 4.9 km). Eighteen of these dispersal events are from the eastern portion of the Tahoe National Forest, and one is from an area along the boundary between the Toiyabe and Eldorado National Forests. Dispersal distances reported here are the straight-line distance in kilometers between the center of the meadow where a bird was banded and the territory where it was resighted. Most of these dispersal events occurred downstream within the same drainage; however, four occurred upstream within the same drainage, and two occurred between different drainages (which all have ramifications for locating potential meadow restoration projects).

Similar between-patch, between-year natal dispersal distances are reported for *E. t. extimus* in Arizona (Luff et al. 2000, Kenwood and Paxton 2001). These natal dispersal distances ranged from 0.4 to 67 km for 5 hatching year birds 1999/2000 (median = 1.7 km, mean = 7.08 km, SD = 12.16 km) and 21 hatching year birds in 2000/2001 (median = 1.9 km, mean = 8.74 km, SD = 16.37 km) (Luff et al. 2000, Kenwood and Paxton 2001).

For the purpose of this document, a southwestern willow flycatcher habitat patch is defined as a distinct area of riparian vegetation supporting one or more territories, and separated from other breeding areas by areas of non-riparian vegetation, or riparian vegetation without the characteristics required

by willow flycatchers (Kenwood and Paxton 2001). For comparison, a southwestern willow flycatcher habitat patch is essentially synonymous with the Sierran habitat unit of a meadow.

ADULT DISPERSAL

On the Tahoe National Forest, Sanders and Flett (1989) reported that an adult male resettled approximately 1 km (0.6 mile) from his 1986 breeding territory in 1987. Among adult and juvenile willow flycatchers color-banded in the same study area in 1994, one was detected 2.4 km (1.5 miles) downstream in 1997 (J. Steele unpubl. data, Bombay and Morrison, unpubl. data). In the southern Sierra Nevada, Stafford and Valentine (1985) reported that one female willow flycatcher (banded as an adult) moved 14.5 km (9 miles) from her 1983 territory to a new territory, where she nested successfully in 1984.

Data collected for southwestern willow flycatchers in Arizona indicate that 13 to 17 percent of adults moved to new breeding sites each year (Busch et al. 2000, Paxton 2000, Paxton and Sogge 2000). Between 1997 and 1998, 19 between-site movements ranging from 0.4 to 190 km were documented for southwestern willow flycatchers (median = 16.0 km; mean = 31.8 km; SD = 46.6 km). Four of these records represent between-drainage movements (Netter et al. 1998). Between-patch, between-year movements by adults in Arizona ranged from 0.4 to 144 km for 1999/2000 (median = 12 km, mean = 13.67 km, SD = 14.30 km) and 2000/2001 (median = 1.9 km, mean = 19.46 km, SD = 36.74 km) (Luff et al. 2000, Kenwood and Paxton 2001). In 1999/2000, 1 of these 34 movements was between drainages, and 11 of 31 movements in 2000/2001 were between drainages. Whether the variation in dispersal distances reported for *adastus/brewsteri* in the Sierra Nevada and *extimus* in Arizona represents a regional or sub-specific

difference in dispersal behavior or habitat availability, or is the result of different levels of survey effort, is unknown at this time.

SURVIVAL AND RETURN RATES

Data on juvenile and adult return rates for the willow flycatcher population in the Sierra Nevada bioregion are preliminary. An ongoing willow flycatcher demographic study in the central Sierra Nevada reported a mean juvenile return rate of 14.5 percent annually (SE = 3.1) between 1998 and 2001, based on 217 banded fledglings (Bombay et al. 2001). In Oregon, the juvenile return rate was 7.5 percent of 1,271 *E. t. adastus* nestlings and fledglings banded (Sedgwick and Iko 1999, Sedgwick 2000), while it was 1.4 percent of 147 nestlings banded in Michigan (Walkinshaw 1966). Juvenile return rates for southwestern willow flycatchers in the extreme southern Sierra Nevada and Arizona are recorded as 34 percent of 38 banded nestlings and 8 percent of 12 banded nestlings, respectively (Stoleson et al. 2000). From 1996 to 2001, 36 of 189 *E. t. extimus* nestlings banded in Arizona were resighted from 1 to 4 years after banding, resulting in a pooled recruitment rate of 19 percent (Luff et al. 2000, Kenwood and Paxton 2001).

Juvenile return rates in the Sierra Nevada appear to be slightly lower than those currently reported for southwestern willow flycatchers, but higher than those reported for presumably stable populations of *E. t. adastus* and *E. t. traillii* in other parts of North America. Sierran juvenile return rates are also higher than the 2 to 5 percent reported for most other migratory passerines (Shields 1984, Blancher and Robertson 1985, Payne and Payne 1990, Sherry and Holmes 1992, Roth and Johnson 1993, Lemon et al. 1996, Netter et al. 1998). It is difficult to interpret how these recruitment values reflect on population trends because observed recruitment rates may depend largely on the amount and distribution of available habitat close to natal areas, as well as the extent to which available habitat is fully occupied.

These three factors regarding available habitat may affect how far away and in what pattern birds disperse and, therefore, the researchers' ability to detect all surviving young.

Willow flycatcher return rates are generally higher for adults. In the central Sierra Nevada, Bombay et al. (2001) reported that the pooled adult return rate was 66.7 percent from 1997 to 2001. At two of the same Tahoe National Forest study sites, Sanders and Flett (1989) found that 4 out of 14 (29 percent) banded adults returned the following year. In the southern Sierra, Stafford and Valentine (1985) had 4 of 12 (33 percent) adults return.

Estimates of life span for willow flycatchers come primarily from birds followed from 1988 to 1997 on the Malheur NWR in Oregon. Sedgwick and Iko (1999) reported that willow flycatchers in this study area had a mean life span (not taking dispersal into account) of 1.08 years \pm 0.11 SE for males, and 0.97 years \pm 0.10 SE for females. At this study area, the maximum age recorded was 11 years (Sedgwick 2000). Reports of birds 5 to 7 years of age are not uncommon in the literature (Walkinshaw 1966, Walkinshaw 1971, Clapp et al. 1983). In the Sierra Nevada a number of adults 4 to 5 years of age have been reported (Bombay et al. 1999, Bombay et al. 2001).

Adult survival for southwestern willow flycatchers in the southern Sierra Nevada and Arizona was estimated at roughly 52 percent for males and 34 percent for females based on 79 returning males and 255 returning females (Stoleson et al. 2000). In Michigan, 30 percent of 53 banded adults returned the following year (Walkinshaw 1966). Similarly, in Oregon, 45 percent of birds banded as adults returned annually over 8 years of study (Sedgwick and Klus 1997). After 10 years at the same Oregon study site, Sedgwick and Iko (1999) reported 53.6 percent of females (186/347) and 52.3 percent of males (138/264) returned to breed in the same general area. Based on somewhat limited sample sizes for Sierra Nevada willow flycatchers, it appears that adult survival, expressed as return rate, in the

bioregion falls within the range observed for other willow flycatcher populations in other bioregions.

PHILOPATRY

Although the previous discussion of survival indicates the proportion of willow flycatchers that survived and returned to any of a number of breeding locations, it does not indicate how many birds return to the same breeding site in sequential years. Philopatry, on the other hand, looks at how faithful willow flycatchers are to specific meadows or even territory locations. In the Sierra Nevada, little information is available. On the Tahoe National Forest in 1986 and 1987, three of four returning adult willow flycatchers returned to the same willow clump in which they bred in the previous year (Sanders and Flett 1989). Similarly, on the Sierra National Forest in 1983 and 1984, three of four known surviving adults returned to the same meadow used in the previous year (Stafford and Valentine 1985). Philopatry data for an ongoing demography study in the central Sierra Nevada are also limited. Of 61 resightings of known surviving “after second year” (ASY) willow flycatchers, 13 incidences (representing 12 individuals) of birds using the same or similar territory locations (within 100 m) in sequential years have been documented (J. Steele, unpubl. data; Bombay and Morrison, unpubl. data). A rough estimate of philopatry based on these data indicates that 20 percent of known adult survivors return to use the same location. Because willow flycatchers in this study were not color-banded to identify individual birds (color-coded for year and location only), this value is based on the assumption that if a bird with the same cohort and natal site color bands is detected on the same territory in sequential years it is most likely the same individual.

Of the adult southwestern willow flycatchers in Arizona known to survive between years, a mean of 71 percent (SE = 4.8 percent) returned to the same habitat patch during the 1996 through 2001 period. Of the birds

returning to the same patch, a mean of 64 percent (SE = 10.5) returned to within 50 m of their previous year’s territory (Luff et al. 2000, Kenwood and Paxton 2001). Between 1996 and 1998, 32 percent of adults displayed breeding site/patch philopatry in Arizona (Busch et al. 2000). In extreme southern Sierra Nevada, 61.6 percent of adult male southwestern willow flycatchers (n = 138) and 51.8 percent of adult females (n = 137) returned to one of the patches within the study area (M. Whitfield pers. comm.). More than half of the breeding adults captured in a 1988 to 1997 study in Oregon returned to the same general area to breed in subsequent years (females: 186/347 [53.6 percent]; males: 138/264 [52.3 percent]) (Sedgwick and Iko 1999, Sedgwick 2000). At this same study site, the median distance for returning males (n = 362) and females (n = 349) from the previous years’ nest site was 25 and 26 m (82 and 85 ft), respectively (males: mean = 193 m, SE = 29 m, range = 0 to 4,662 m; females: mean = 233 m, SE = 37 m, range = 0 to 5,926 m) (Sedgwick 2000). When compared to willow flycatcher populations in other regions, it appears that Sierra Nevada willow flycatchers may exhibit slightly lower philopatry.

Within-year Movements - For the Sierra Nevada, no information is available relative to movements of adult willow flycatchers within a single breeding season. Bombay et al. (2001) reported that many males annually disappear from what appear to be defended territories after only a few weeks. While the fate of these individuals is unknown, it is assumed that at least some are settling elsewhere later in the season. Recent data from southwestern willow flycatcher populations in Arizona support this assumption and suggest more mate switching and within season dispersal than previously assumed (Luff et al. 2000). In 2000, Luff et al. (2000) reported five incidences of adult birds moving between habitat patches during the breeding season. Three unpaired males moved 0.4, 1.7, and 4 km to new sites where they successfully found mates. Two females moved 13 and 29 km between successive

nesting attempts. Additionally, four more unmated males moved to new territory locations within the same habitat patch and secured mates. Similarly, Kenwood and Paxton (2001) reported that 17 flycatchers moved more than 50 m within the same habitat patch; 20 moved between different habitat patches within the same drainage, and 11 moved between different drainages. One

of these was a female that moved 117 km between two within-year nesting attempts, and two males moved 144 km between years. These data for southwestern willow flycatchers suggest that it may not be uncommon for males to move to new locations if they cannot find a mate and that females may move to new locations after failed nest attempts (Luff et al. 2000).

Chapter 8

Population Ecology and Risks

DEMOGRAPHY

Demographic studies of populations are often conducted to determine whether populations are increasing, decreasing, or remaining stable. This is done by calculating the annual rate of population change, termed Lambda (λ). A λ value of 1.0 means the population abundance is stable, a value lower than 1.0 means it is declining, while a value greater than 1.0 means it is increasing. For example a λ of 0.96 indicates that the population is annually declining by 4 percent. Three parameters define λ : adult survival, juvenile recruitment, and fecundity.

Adult Survival

Adult survival is usually estimated from banding studies to assess annual return rates of individual cohorts. At Malheur National Wildlife Refuge in Oregon, Sedgwick and Klus (1997) reported an average adult return rate of 45.1 percent, while Sedgwick and Iko (1999) found adult returns rates between 48.9 and 55.6 percent, depending on sex and whether nests had been parasitized by cowbirds. In the central Sierra Nevada, Bombay et al. (2001) reported a pooled average survival rate of 66.7 percent over 4 years of study. These rates are at or near the 50 to 70 percent adult return rates generally reported for long-distance migrants (Ricklefs 1992, Sherry and Holmes 1992, 1995).

Survivorship may differ between sexes. In Michigan, Walkinshaw (1966) found the return rate for male willow flycatchers to be twice that of females in the first year after they were banded (40.9 percent versus 22.6 percent). Paxton et al. (1997) reported *extimus* male return rates (52.0 percent) to be much higher than that of females (34.0 percent). Sedgwick and Iko (1999) also found slightly higher survival rates for male *adastus* in Oregon and attributed this to possible higher energetic cost for breeding females (Nur 1988). However, Sedgwick and

Klus (1997) reported a higher return rate for females (46.9 percent) than males (43.3 percent) at the same study site in Oregon (Malheur National Wildlife Refuge) as Sedgwick and Iko's study site (1999).

Juvenile Recruitment

Bombay et al. (2001) found willow flycatcher juvenile recruitment to average 14.5 percent (range 11.6 to 18.6 percent) over 4 years of banding study in the Sierra Nevada, which is similar to the 13.2 percent return rate reported by Sedgwick and Klus (1997) from the Malheur National Wildlife Refuge in eastern Oregon. However, Sedgwick and Iko (1999) reported juvenile return rates of exactly half (6.6 percent) that of Sedgwick and Klus (1997), even though the study sites were the same. Sedgwick and Iko (1999), however, questioned the credibility of their observed juvenile return rates because they were too low for the population to persist unless it is a sink population maintained by other sources. These rates, all from birds in the range of *adastus*, are similar to rates for *extimus* in Arizona (8 percent: Paxton et al. 1997), but are much lower than Kern River *extimus* (34 percent: Whitfield, unpubl. data) and not nearly as low as from Walkinshaw (1966) in Michigan (1.4 percent).

Sedgwick and Iko (1999) also found substantial differences in return rates relative to fledgling dates. Young fledged on or before 15 July (10 percent of total fledglings) were nearly six times more likely to return the following year than young fledged at later dates.

Fecundity

Fecundity is a measure of production based on individual (generally female) or population performance. Fecundity is the product of the probability of breeding, clutch size, hatching success, nesting success, and number of

nesting attempts per season (USFWS 2001). Female willow flycatchers breed in their first year, and there is no evidence of reproductively viable females going unmated. If sex ratios are skewed towards females, females appear to choose sharing males with other females (polygyny) rather than going unmated.

Clutch size information was provided in detail in Chapter 3. Of relevance here are the Sierra Nevada data from Bombay and Morrison (unpubl. data) showing a mean clutch size of 3.52 eggs for first nestings and 2.96 eggs for renestings.

Reported hatching success rates for willow flycatchers have ranged from 55 percent (Holcomb 1972) to 93 percent (King 1955, Berger 1967). McCabe (1991) reported a composite average of 74 percent from five different studies.

Reported nesting successes (number of successful nests/number of nests ratio) in the Sierra Nevada have ranged from 24.4 percent (Harris 1991) to 44 percent (Bombay et al. 2001). Whitfield et al. (1999) found nesting success of South Fork Kern River *extimus* to increase from 23 to 41 percent after brown-headed cowbird control measures were instituted. Table 8-1 provides reported nesting successes from a number of locations.

Sierra Nevada willow flycatchers frequently renest if earlier attempts fail. Bombay et al.

(2001) reported that 27 percent of all nesting over a 5-year period consisted of renests, with a 3 percent third nesting attempt. There is no evidence in these populations of producing two successful broods in the same year.

Bombay et al. (2001) estimated that central Sierra Nevada willow flycatcher females (n = 39) produced 1.74 fledglings on average (or 0.87 female fledglings) in 2001. They did, however, suggest that the true fledglings produced per female were closer to 1.57, taking into account losses of some individual nestlings to predation in the few days immediately before fledging. Bombay et al.'s (2001) estimate of 0.87 female produced per female in 2001 is much higher than the lifetime performance of 0.5 female per female Williams and Craig (1998) calculated for Sierra Nevada populations based on data from KRCD (1985b) and Sanders and Flett (1989).

Population Rate of Change

Bombay et al. (2001) calculated a range of λ estimates based on varied adult survival estimates (pooled versus unpooled) and juvenile recruitment estimates (observed versus estimate from another population accounting for dispersion). The three estimates of annual rate of change (0.768, 0.839, and 0.869) that were calculated all indicate annual declines of between 13 and 23 percent, although sample sizes were small.

Table 8-1. Nest success for willow flycatchers across various studies.

Nesting Success	Sources	Location
18.0%	Sogge et al. 1997	Grand Canyon, AZ
24.4%	Harris 1991	South Fork Kern River, CA
23.0%	Whitfield et al. 1999 (pre-BHCO removal)	South Fork Kern River, CA
39.0%	Whitfield et al. 1999 (post-BHCO removal)	South Fork Kern River, CA
40.0%	Bombay 1999	Central Sierra Nevada, CA
40.7%	Sedgwick and Knopf 1988	Colorado
42.0%	Sanders and Flett 1989	Central Sierra Nevada, CA
44.0%	Bombay et al. 2001	Central Sierra Nevada, CA
44.6%	King 1955	Eastern Washington
65.6%	Walkinshaw 1966	Michigan

This study is ongoing, and these estimates should be considered preliminary.

Sedgwick and Iko (1999) did not calculate a population rate of change for eastern Oregon willow flycatchers because they could not demonstrate a credible estimate for juvenile

mortality. They did, however, use known data to calculate the juvenile survival value needed to maintain a stable population, and they found this value to be much higher than the observed values. They concluded that their population is either in decline, or is a sink population.

ECOLOGICAL INFLUENCES ON SURVIVAL AND REPRODUCTION

Predators and Predation

Adult Predators – Little information is available in the literature regarding predators of adult willow flycatchers. Presumably, avian predators specializing in hunting passerines (e.g., Cooper’s hawk [*Accipiter cooperii*], northern goshawk [*A. gentilis*], sharp-shinned hawk [*A. striatus*], and American kestrel [*Falco sparverius*]) occasionally prey on willow flycatchers.

Nest Predators – Published willow flycatcher predation rates have ranged from 11 percent (McCabe 1991) to 51 percent (Holcomb 1972), indicating potential for high variability as well as significant influence on population viability. Nest predation is likely the factor most affecting willow flycatcher population viability in the Sierra Nevada (Bombay 1999, Cain 2001). Over 9 years of study in the South Fork Kern River, Whitfield et al. (1999) observed a loss of 36 percent of the southwestern willow flycatcher nests to predation. Sanders and Flett (1989), Bombay (1999), and Cain (2001) all conducted willow flycatcher demographic studies in the Little Truckee River drainage. Sanders and Flett (1989) recorded evidence of predation at 6 of 21 nests studied, but in only 1 was the entire brood lost. Bombay (1999) observed a loss of 32 (36 percent) of 90 nests monitored, and Cain (2001) recorded 22 (45 percent) of 49 nests lost to predation where the clutch initiation was confirmed. Morrison et al. (2000) estimated that 72 percent of the total nest failures in the central Sierra Nevada from 1997 through 2000 were a result of nest predation.

Nest predation is rarely directly observed. Documented willow flycatcher nest predators include milk snake (*Lampropeltis triangulum*; McCabe 1991), common kingsnake (*Lampropeltis getulus*), red-tailed hawk (*Buteo jamaicensis*; Whitfield and Lynn 2001), and Cooper’s hawk (Paxton et al. 1997, McCarthy et al. 1998). Other nest predators have been inferred, but not confirmed. They include long-tailed weasels (*Mustela frenata*) and house wrens (Stafford and Valentine 1985).

The most illuminating study on predation of willow flycatcher nests was conducted by Cain (2001) in the Sierra Nevada. First, he correlated predator activity with nest success and found negative correlations with Douglas squirrel (*Tamiasciurus douglasii*), long-tailed weasel and short-tailed weasel (*M. erminea*), Cooper’s hawk, and brown-headed cowbird presence depending on the nesting stage. Douglas squirrels in particular were highly negatively correlated, especially during the incubation stage. Clark’s nutcracker (*Nucifraga columbiana*) activity during the willow flycatcher incubation stage also appeared to influence nesting success.

Second, using sympatric yellow warbler (*Dendroica petechia*) nests baited with zebra finch (*Taeniopygia guttata*) eggs as surrogates, Cain (2001) photo-documented 14 depredation events on his study site. The most common predators recorded were chipmunks (*Tamias* spp.; five events), followed by Douglas squirrels (four events), short-tailed weasels (three events), and a deer mouse (*Peromyscus maniculatus*; one event).

Cain (2001) also believed that predation pressure from squirrels and chipmunks was reduced for nests farthest from the forest edge and surrounded by standing water. Bombay (1999), too, found that nest success increased as distance to the closest tree increased. Both Bombay (1999) and Cain (2001) suggested that trees provide habitat, especially foraging perches, for a number of mammalian and avian predators that, otherwise, would not penetrate the meadow interior. Meadow interior nesting flycatchers, therefore, may

exhibit higher nesting success because they are pressured only by the few predators not discouraged by a lack of trees or presence of standing water (e.g., weasels) (Cain 2001; Cain et al., *in press*).

Cain (2001) concluded that nest predation was the likely limiting factor controlling reproductive success of willow flycatchers in the Sierra Nevada. The implication is that degradation of meadows from factors such as past intensive grazing and water diversions has led to increased habitat components (i.e., less standing water and more encroaching forest) used by predators of willow flycatcher nests (Bombay 1999, Cain 2001). Fire exclusion, too, may play a role in forest encroachment. Meadow restoration strategies favoring return of meadows to natural hydrological regimes, as well as mitigation of current erosive forces, and, concurrently, stemming forest encroachment (especially lodgepole pine [*Pinus contorta*]), may prove the best techniques for reducing predation pressures and improving population viability.

Brood Parasitism

As they did with American bison (*Bison bison*) populations in the Midwest, brown-headed cowbirds developed a commensal relationship with domestic livestock (Friedmann 1929). As livestock grazing rapidly spread across North America, so did the range of the cowbird (DeSante and George 1994). Consequently, new populations of passerines became brood parasitism hosts. Brood parasitism refers to the laying of eggs by one species in the nest of another. Cowbirds have invaded the Sierra Nevada in only the last 60 to 70 years (Rothstein et al. 1980).

In the Sierra Nevada, the prevalence of cowbirds, and the associated incidence of brood parasitism, relates to a number of factors that are not mutually exclusive (Verner and Ritter 1983, Purcell and Verner 1999). At lower elevations, where the environment is more open and livestock, agriculture, and human disturbance areas are more prevalent,

the incidence of brood parasitism is higher. Whitfield and Sogge (1999) reported the highest reported percentage of brood parasitism (66 percent) for *E. t. extimus* on the South Fork Kern River (elevation 800 m). A meta-analysis by Lorenzana and Sealy (1999) showed that cowbirds had a very large effect on flycatcher productivity based on Harris's (1991) and Whitfield's (pers. comm.) study results at the South Fork Kern River. In contrast, Bombay et al. (2001) reported an annual parasitism rate of 8.3 percent (range = 4 to 15 percent) for central Sierra Nevada populations (1,700 to 2,500 m). Higher elevation forests simply may not provide a full component of habitat requisites for cowbirds, and/or most cowbirds may arrive (with cattle) too late in the nesting season to greatly impact breeding willow flycatchers. Further, these values are well below the 30 percent parasitism rate where conservation concerns begin (Mayfield 1977, Laymon 1987). Nevertheless, most of the parasitism reported by Bombay et al. (2001) occurred at three adjacent sites in the Upper Truckee River drainage where the maximum parasitism rate was 47 percent between 1998 and 2001. Consequently, even at high elevations, cowbirds can greatly influence flycatcher productivity on a local level.

Purcell and Verner (1999) did not find cowbirds on their detection plots above 2,000 m in the southern Sierra Nevada, and cowbird abundance in the ponderosa pine zone (below 1,300 m) was eight times higher than the mixed conifer zone (1,700 to 2,000 m). Also, Verner and Ritter (1983) did not find cowbirds at remote meadows without cattle except when supplemental food sources were nearby. Telemetry studies have shown that feeding sites of individual cowbirds are tightly linked to locations of grazing livestock and to pack stations (or other livestock facilities) (Verner and Ritter 1983, Verner and Rothstein 1988, Goguen and Mathews 1999, Halterman et al. 1999, Shapiro et al. 1999). In addition, the influence of supplemental feeding (e.g., pack station grain spillage and bird feeders) may not be trivial. On June 1, 2002, approximately a dozen brown-headed

cowbirds were observed at a sunflower seed feeding station at Red Lake on the Toyaibe National Forest (G. Green, pers. obs.). Red Lake sits at 2,400 m (7,900 ft) elevation and annually supports about five willow flycatcher nesting territories. It has not experienced brown-headed cowbird parasitism in 5 years (1997 to 2001) of monitoring (Bombay et al. 2001). Cain (2001), however, did report the presence of brown-headed cowbirds and the parasitism of yellow warbler nests at Red Lake.

The willow flycatcher is probably a poor host for the brown-headed cowbird. Whitfield and Sogge (1999) reported that only 14 percent of the parasitized nests on the South Fork Kern River successfully fledged cowbirds. This is lower than the 18 percent McGeen (1972) reported for the yellow warbler, a significantly smaller host (9.5 g versus 13.4 g; Dunning 1993). Bombay et al. (2001) reported that 71 percent of the parasitized nests in their central Sierra Nevada study site were either abandoned by their host or depredated. Note, however, that nest desertion in least Bell's vireos (*Vireo bellii pusillus*) does not appear to be an adequate natural defense against cowbird parasitism, largely because subsequent nests of deserting pairs are also parasitized (Kus 2002). Morrison et al. (2000) and Kus (2002) showed, however, that human removal of cowbird eggs is effective in improving host nesting success. Cowbird eggs are removed as part of the willow flycatcher demography study in the Sierra Nevada (Bombay and Morrison, unpubl. data). Recent work by Kilpatrick (2002) suggests that raising 1 cowbird nestling is energetically equivalent to willow flycatchers raising 2.5 of their own nestlings.

EFFECTS OF HABITAT LOSS AND DEGRADATION

Nesting willow flycatchers in the Sierra Nevada appear to occupy a narrowly defined niche. Based on available data, willow flycatchers nest in willow patches averaging about 1 ha (Bombay 1999) but are more

frequently associated with meadows greater than 6 ha (Serena 1982, Harris et al. 1988, Stefani et al. 2001). Once willow patches are degraded, possibly due to past direct grazing by cattle or indirect meadow desiccation from natural (climate change, drought) and other anthropogenic causes (water diversions, adjacent timber harvest and fuels treatments, fire suppression, mining, roads, recreation), the ability of these patches to support nesting flycatchers is lost, and the birds do not have the plasticity to nest in other habitat types. Evidence for this is the large number of meadow sites that no longer support breeding willow flycatchers.

Habitat degradation in the montane meadow systems appears to follow a pattern beginning with the expanded use by humans beginning in the mid- to late 1800s. As reviewed elsewhere in this document, grazing, mining, recreation, roads, adjacent timber harvest and fuels treatments, fire suppression, water diversion, and other factors have all combined to degrade meadows. It is inferred that grazing cattle can directly impact flycatchers by removing willow cover (browsing, grazing, and trampling) (Taylor 1986) and occasionally knocking down nests (King 1955, Valentine et al. 1988). Concomitantly, cattle-attending, brown-headed cowbirds may arrive and parasitize a number of willow flycatcher nests. Further, some of the meadows have suffered from past livestock damage such that the vegetation layer has been breached, followed by erosion of underlying soils. During episodic heavy rain events, these erosion sites form deep gullies that alter the hydrology (Hagberg 1995). The water table drops and desiccation ensues (Reid 1989). Drier meadows result in a reduction of hydrophytic willows and allow expansion of forest conifers, especially lodgepole pine, into meadows. Drier meadow surfaces, expanded forest edge, and intrusion of conifer into the meadow proper may allow forest nest predators, especially squirrels and chipmunks, access to flycatcher nests (Cain 2001). Increased predation due to meadow desiccation may prove to be one of the factors

most responsible for the decline of willow flycatchers in the Sierra Nevada. Also, the initial actions that precipitated meadow desiccation may have occurred decades earlier (Hagberg 1995).

D. Cluck (Entomologist, Forest Health Protection, Susanville, California) observed *Salix* dieback, apparently caused by a fungi (most likely *Cytospora chyrsosperma*, *Venturia saliciperda*, and *Glomerella miyabeana*). These fungi cause dieback of willow stands through infection that is scattered on stems throughout an individual plant. Woodboring beetles may then become active within the dead and dying stems. In the area of observed willow mortality, water stress may predispose the willows to infection.

POPULATION SIZE AND TREND

Current estimates of the willow flycatcher population in the Sierra Nevada bioregion range from 300 to 400 individuals, with 120 to 150 individuals on National Forest lands

(Serena 1982; Harris et al. 1987, 1988; Ritter and Roche 1999).

In general, the willow flycatcher has experienced declines throughout its North American range. Between 1966 and 1996, willow flycatchers annually declined 1.2 percent in North America, 2.3 percent in the western region, 5.8 percent in western Oregon and Washington (*brewsteri*), and 2.5 percent in eastern Oregon and Washington (*adastus*) (Sauer et al. 1997). There are not enough data to calculate current trends for the Sierra Nevada, based on surveys. However, Bombay et al. (2001) did calculate annual population rates of change based on demographic data from central Sierra Nevada indicating 13 to 23 percent annual decline rates (although sample sizes were small).

Another indicator of decline is that 53 of 135 (39 percent) breeding locations were found unoccupied in subsequent surveys (Table 8-2), including 46 of 128 (36 percent) known to be active since 1982. A number of

Table 8-2. Declines in willow flycatcher breeding sites and territories in the Sierra Nevada Forest Plan Amendment area (USDA Forest Service, unpubl. data).

Forest	Sites			Territories ^b		
	Total	Active ^a	Change	Total	Active ^a	Change
Modoc	7	6	14%	11	10	9%
Lassen	19	14	26%	63	52	18%
Plumas	18	12	33%	25	18	28%
Tahoe	18	14	22%	61	55	10%
LTCMU	7	2	71%	12	4	67%
Eldorado	1	0	100%	1	0	100%
Toiyabe	7	4	43%	12	6	50%
Stanislaus	8	3	63%	15	7	53%
Inyo	17	12	29%	35	28	20%
Yosemite NP	5	4	20%	12	11	8%
Sierra	13	2	85%	21	4	81%
Sequoia	10	5	50%	41	35	15%
Sequoia/Kings Canyon NP	5	4	20%	6	4	33%
Total	135	82	39%	315	234	26%

^a Breeding sites or territories active on the last year they were surveyed.

^b Total of the mean number of territories at each site.

these inactive sites, however, included only one or two territories. Using the mean number of territories per site, the number of territories has declined from 315 to 234 (26 percent) (Table 8-2). Although these data should be viewed with caution due to the variability in past survey efforts, they do reflect a consistent decline across the Sierra Nevada.

The largest mean territory declines have occurred on the Sierra (81 percent), Stanislaus (53 percent), and Toiyabe (50 percent) National Forests and the Lake Tahoe Basin Management Unit (67 percent) (Table 8-2). Also, the Eldorado National Forest has apparently lost its only territory. The Stanislaus National Forest loss may be even greater (93 percent) as six of its territories are records from the 1930s. The least decline is from Yosemite National Park at 8 percent; however, removing one old record of five territories from 1966 brings the loss to 50 percent.

Relatively light losses have occurred on the Modoc (9 percent), Tahoe (10 percent), Sequoia (15 percent), and Lassen (18 percent) National Forests (Table 8-2). However, 32 of the 35 territories remaining in the Sequoia National Forest area are *extimus* nesting along the South Fork Kern River (South Fork Wildlife Area and Kern River Preserve) and at Bloomfield Ranch. Half the sites on the Sequoia National Forest thought to be occupied by *brewsteri/adastus* are no longer viable.

In general, sites currently supporting multiple territories of *brewsteri* occur only in the Lassen Peak region (including Warner Valley) of the Lassen National Forest and in Yosemite National Park (e.g., Hodgdon Meadows) (USDA Forest Service, unpubl. data). Relatively large numbers of *adastus* are found only in the Little Truckee River drainage, although a few multiple territory sites are still found in the Carson region (e.g., Red Lake) and near Mammoth/Mono Lake. Interestingly, two of the healthier populations (South Fork Kern River and Owens Valley,

Bishop) of willow flycatcher are endangered *extimus*.

DIRECT HUMAN EFFECTS

Direct human effects on willow flycatchers in the Sierra Nevada are, for the most part, those that affect flycatcher habitat, resulting in reduced breeding opportunity or success. Finch et al. (2000) listed a number of human activities that could directly impact willow flycatchers, including livestock management, water developments, recreation, and pesticide use. Each is addressed below.

Livestock Management

In their critical assessment of the management recommendations and literature regarding willow flycatcher conservation in the Sierra Nevada, Dahm and Pittroff (n.d.) concluded that, "There is currently no sound scientific knowledge basis which justifies the assertion that livestock grazing is the primary factor driving willow flycatcher abundance in the Sierra Nevada." Their report, based on an investigation of a small subset of the literature used in the Sierra Nevada Forest Plan Amendment DEIS regarding livestock impacts to willow flycatchers, indicates that much of the evidence they reviewed was based on inference and/or circumstantial evidence. While they concede that livestock may, in certain instances, based on the literature, be detrimental to willow flycatchers, none of the grazing-related findings in the 10 published and unpublished papers reviewed in their report is statistically robust. While concurring with Dahm and Pittroff's assertion of inconclusive scientific evidence in the role of livestock grazing on willow flycatcher status, the fact that meadow resources have, in the past, been severely impacted by livestock (Ratliff 1985, Menke et al. 1996) cannot be ignored. If past livestock damage has led to chronic conditions (such as gullies) that continue to alter habitat components important to willow flycatchers, then restorative actions to correct these conditions are highly appropriate, regardless of the initial cause. Because it is impossible

to travel back in time, causes from the past must be inferred.

Current grazing schemes that allow grazing within willow flycatcher breeding habitat may upset flycatcher nests (Stafford and Valentine 1985), alter willow habitat including shrub vigor and spatial pattern (Taylor and Littlefield 1986, Stanley and Knopf 2002), facilitate cowbird brood parasitism, and exacerbate chronic conditions (gullies). Preliminary results from grazing studies in the Sierra Nevada indicate that there are impacts from contemporary livestock grazing (B. Allen-Diaz, pers. comm.), though preliminary range monitoring results from meadows on five National Forests in the Sierra Nevada suggest a slight upward trend in ecological condition on key range sites (D. Weixelman, pers. comm.). A recently published study of historically grazed pastures in a high elevation floodplain of Colorado (Stanley and Knopf 2002) suggested that habitat for grazing-sensitive birds may be restored while still allowing late-season grazing, although the rate at which species are recovered will be slower than if all cattle are removed. They have strong statistical evidence that bird densities of the stenotopic (grazing-sensitive) guild, which included the willow flycatcher, increased more on ungrazed pastures than on grazed pastures. The contemporary influence of managed livestock grazing on willow flycatcher status in high-quality (i.e., good ecological condition) habitat is unknown. Further research, directed at livestock impacts on willow flycatchers and their habitat in the Sierra Nevada, is needed before sound conclusions can be drawn. Two issues should be highlighted: (1) the past causes of meadow drying must be determined to ensure that they have stopped (if they can be controlled); and (2) regardless of the causes, meadow condition must be improved (i.e., increase meadow wetness throughout the breeding cycle).

Water Developments

Water diversions have also impacted willow flycatchers, especially those populations using

streamside riparian zones. In the Owens Valley, riparian vegetation downstream of the intake to the Los Angeles aqueduct has dramatically changed to a more xeric condition due to the lack of water (Brothers 1984) and no longer provides habitat for nesting willow flycatchers. Stine et al. (1984) documented the destruction of the riparian systems (e.g., Lee Vining and Rush Creeks) draining into Mono Lake due to water diversion to Los Angeles. Several hundred acres of willow-dominated habitat was either inundated by impoundments or dried up from diversions. Today, these riparian zones support eight territories (C. McCreedy, pers. comm.), but as a result of recent restoration activities.

Recreation

Recreational activity can have varying impacts to nesting birds (Knight and Gutzwiller 1994). Potential activities occurring at Sierra Nevada meadows include hiking, camping, picnicking, fishing, bird watching, mountain biking, and off-road vehicle use. The magnitude of these activities may not be high where Sierra willow flycatcher are known to breed; however, given the small size of some breeding populations, any incident resulting in disturbance may be significant. Food scraps and garbage left at recreational use areas can also attract jays, squirrels, and other wildlife known to prey on willow flycatcher nests (Johnson and Carothers 1982, Blakesley and Reese 1988, Marshall and Stoleson 2000).

Pesticides

Pesticide contamination has not been raised as a major threat to Sierra Nevada willow flycatcher populations, probably because these populations are not close to agricultural areas where pesticide use is most prevalent.

However, recent research (Zabik and Seiber 1993, Aston and Seiber 1997, McConnell et al. 1998, Le Noir et al. 1999) has shown that considerable pesticide loads are transported by prevailing summertime wind patterns to the central and southern Sierra Nevada from the Central Valley, and such loads have been implicated in the dramatic population declines of anurans in the Sierra Nevada (Sparling et al. 2001). Further, pesticide use has been documented in Central and South American wintering grounds (Koronkiewicz et al. 1998, Koronkiewicz and Whitfield 1999, Lynn and Whitfield 2000). Consequently, pesticide contamination remains a potential, but unknown, threat.

Roads

Roads, whether they are dirt-surfaced or paved, provide a near impervious wall, intercepting surface and subsurface hydrological flow (Furniss et al. 1991, Kattelmann 1996). When natural meadow hydrological flows are intercepted and redirected, meadow drying occurs. Runoff from road surfaces can also collect and then discharge as erosive flows, greatly increasing sediment yields below the roads, especially during the wet season (Kattelmann 1996). Erman et al. (1977) found, during a study of logging impacts on stream invertebrates (potential willow flycatcher prey), that failures of poorly designed roads, leading to increased sediment yields, had the greatest impact to aquatic invertebrates. Roads also provide access for other activities that might impact willow flycatchers or their habitat (e.g., recreation, timber harvest) (Kattelmann 1996).

POPULATION DYNAMICS

Metapopulations are essentially populations within populations. They occur as large populations distributed in patches separated by distances farther than individuals typically disperse, but not so far apart that there is no significant demographic interchange (Gutierrez and Harrison 1996). Metapopulations function as separate

populations, but maintain demographic and genetic affinity with other populations. Metapopulations also tend to maintain equilibrium (Wilson 1975).

Population patterns of Sierra Nevada willow flycatchers do not fit the metapopulation model very well. Although little is presently known about willow flycatcher dispersal patterns, as neotropical migrants, willow flycatchers are wholly capable of traveling great distances over unsuitable habitat. In particular, birds breeding in the northern portion of their range obviously travel each year past habitat used by other populations. Finally, if the Sierra Nevada population in general is declining, as appears to be the case, it does not meet Wilson's (1975) equilibrium criteria. There is no evidence to suggest that Sierra Nevada populations of willow flycatchers operate as a metapopulation(s).

Breeding populations of willow flycatchers in the Sierra Nevada are, however, patchily distributed, and in a manner perhaps explained by source/sink dynamics. Source populations are growing populations that occupy high-quality habitat and produce emigrants (Pulliam 1988, Gutierrez and Harrison 1996). Sink populations are those occupying low-quality habitat that cannot maintain themselves without immigration from source populations. Certain large meadows in the Sierra Nevada (e.g., Lacey, Little Truckee, and Warner Valley) are consistently occupied by multiple territories with apparently enough success to persist. They may, therefore, be viewed as source meadows. There is also a relatively large number of meadows that have been occupied in the past, generally just by one territory, and might be viewed as sinks.

Given the lack of consistency in willow flycatcher survey methodologies between known sites and years, as well as unknowns in willow flycatcher detection probabilities and site occupancy trend patterns, categorizing known sites as sources or sinks based upon the number of reported territory holders is premature and could be counterproductive (i.e., a site with one to two territory holders

could provide high quality habitat and later prove to be a “source”). An alternative explanation is that willow flycatchers currently may not be habitat-limited, but increased mortality and decreased productivity levels (e.g., increased nest predation, decline in prey quality or quantity, problems on the wintering ground) have caused a general decline in the population. Sites supporting few territories are more likely to be impacted by the resulting demographic stochasticity (localized extinction) than meadows supporting multiple territories. Eventually, the sites occupied by multiple territories (although fewer territories) tend to dominate. Only a third of all meadows known to be occupied since 1999 support a single territory.

If the current population declines are a result of recent extrinsic factors (anthropogenic factors), it is possible that the Sierra Nevada populations operated under source/sink dynamics before the existence of these factors. Regardless, insufficient information is currently available to ascertain or classify willow flycatcher population dynamics. Long-term monitoring and continued demographic study, however, should lead in this direction.

POPULATION GENETICS

Only very recently have the genetics of willow flycatchers begun to be investigated. Before Paxton’s (2000) genetic study, understanding of willow flycatcher taxonomy was based on song, behavior, and morphology. While genetically determined song (Kroodsma 1984) and behavior were used to separate willow flycatchers from alder flycatchers, plumage color and wing formula have been the dominant criteria used to separate subspecies (Unitt 1987). However, Barrowclough (1982) has questioned whether assigning subspecies status based solely on morphological characters is valid. Given the controversy over the possible existence of a fifth subspecies, *campestris*, and whether major intergrade zones occur at subspecies

intercepts (Browning 1993), Barrowclough raises a valid point.

Genetic studies of willow flycatchers began with Seutin and Simon (1988) and Winker (1994). Both teams investigated potential hybridization in sympatric populations of willow and alder flycatchers by using electrophoretic techniques. Although both cautioned that further research was needed to validate their results, neither group found conclusive evidence of hybridization.

Using both nuclear and mitochondrial DNA analysis, the latter an improvement over earlier electrophoretic techniques, Paxton (2000) examined structuring of willow flycatcher populations based on genetics. A primary purpose of his study was to determine whether a molecular genetic study would support the distinction of *E. t. extimus* as a valid subspecies. The U.S. Fish and Wildlife Service’s 1995 listing of the southwestern willow flycatcher as an endangered species assumed *extimus* was a valid taxon, but this assumption was based on earlier morphometric studies where subspecies differences are often very subtle.

After collecting genetic samples from 232 adult willow flycatchers from 49 sites across the species’ range, Paxton (2000) concluded that highly significant genetic variability occurred between *extimus* and other subspecies based both on mitochondrial (*cytochrome-b*) and nuclear (amplified fragment length polymorphism) DNA analysis. His results also showed that the willow flycatcher population in the Owens Valley north of Bishop is *extimus*. Paxton (2000), however, found no significant genetic difference between *adastus* and *brewsteri* using either technique, lending support to Miller (1941) and Behle (1948), who posited that the two groups are not taxonomically distinct. However, Paxton (2000) did state that his sample size for *brewsteri* was small and perhaps biased towards *brewsteri*’s range along an intergradation zone with *adastus*. Of interest to this assessment were the *cytochrome-b* sequence data that indicated Perazzo Meadow (north of Lake Tahoe)

adastus were more closely related to Warner Valley (Lassen) *brewsteri* than Red Lake (south of Lake Tahoe) *adastus*, again suggesting intergradation between the two subspecies. Further research on whether

adastus and *brewsteri* populations in the Sierra Nevada are truly distinct is warranted, especially if continuing declines in populations necessitate conservation status changes or management strategies based on taxon separation.

Chapter 9

Conservation Status

INTRODUCTION

The previous chapters provide a technical review of the biology and ecology of the willow flycatcher, as well as its prey and the habitats in which it is found. This technical review is the basis for assessing whether the species is likely to persist within its Sierra Nevada range over the long term, or whether management intervention may be required to prevent extirpation. A number of conservation questions are addressed below, which lead to one of three possible conclusions: (1) populations of willow flycatchers are secure in the Sierra Nevada and will likely remain so, given current land management practices, (2) populations of Sierra Nevada willow flycatchers are in peril or are likely to be in peril in the near future under current land management practices, and (3) there is insufficient evidence to determine the species' conservation status in the Sierra Nevada.

Is the Distribution and Abundance of the Willow Flycatcher Declining in the Sierra Nevada?

Both *E. t. extimus* and *E. t. brewsteri* have experienced significant population declines in California. *E. t. brewsteri* has been virtually eliminated from its former range within the central valley of California, and the range of *extimus* has been reduced to a very few locations (e.g., South Fork Kern River, Owens Valley). Breeding populations of *brewsteri/adastus* remain in a few strongholds in the Sierra Nevada, but 53 of 135 known sites (Table 8-2) were found to no longer support willow flycatchers during recent surveys. The distances between current sites are expanding, and this may have implications regarding dispersal.

Do Habitats Vary in Their Capacity to Support Willow Flycatcher Populations?

The breeding habitat for willow flycatchers in the Sierra Nevada is quite narrowly defined as willow patches forming meadow or streamside riparian habitat. This habitat type provides almost all of the requisites for nesting, perching, and foraging. An element of standing water or wetness is also important and may serve as both a deterrent to nest predators and as breeding habitat for aquatic insect prey. The ability of these habitats to support willow flycatchers is likely reduced under degraded conditions.

What Are the Important Characteristics of Those Habitats?

Height and density of willow and the amount of standing water or meadow wetness are the important characteristics in meadows and streamside riparian habitat.

Do Habitats Vary in Their Capacity to Support Principal Prey Species?

Willow flycatchers forage on a variety of invertebrate prey species, many of which have aquatic life stages (e.g., deer flies, damselflies, and mayflies), or larval dependence on riparian vegetation (e.g., willow sawflies and certain wasps) (Sumner and Dixon 1953, H. Bombay, pers. obs.). Desiccated meadows lack habitat for aquatic invertebrates and reduce the standing crop of riparian vegetation available for willow sawflies. Consequently, degradation of the meadow habitat via desiccation can profoundly affect flycatcher prey, as well.

If the Willow Flycatcher or Its Prey Select Particular Habitats, Are These Habitats Declining or Being Stressed by Current Management?

The primary breeding habitat for willow flycatchers and their prey is declining and stressed where past and current management continues to manifest long-term desiccation of willow habitat. Drought or climate change may create or further compound these effects. Management intervention (restoration of meadow hydrology and attendant erosion mitigations) probably will be needed to stem population declines.

Do the Life History and Ecology of the Willow Flycatcher Suggest That Populations Are Vulnerable to Habitat Change?

Willow flycatchers are vulnerable to changes in their willow riparian habitat that lead to desiccation. Past grazing, road building, and water diversion projects have resulted in more mesic or xeric conditions within traditional flycatcher breeding habitat. Drought, climate change, fire suppression, mining, recreation, roads, or current overgrazing also may create or exacerbate these conditions, which can result in vegetational changes away from willow-dominated riparian habitat and allow encroachment of conifers or sagebrush into meadows. Increased conifers and sagebrush and lack of standing water allow greater access of forest predators into the wetland

environment, especially rodents such as Douglas squirrels and chipmunks.

What is the Current and Projected Conservation Status of the Willow Flycatcher?

The current conservation status of the willow flycatcher in the Sierra Nevada is that of a population in peril. Many former breeding sites are no longer used, probably due to habitat degradation. Populations are experiencing high nest predation rates, likely caused by meadow desiccation, itself a possible result of past or current natural events and anthropogenic activities. Populations are being impacted by a new threat: brood parasitism by brown-headed cowbirds. Small populations have experienced stochastic environmental events (e.g., summer snowstorm) with severe consequences.

Available demographic information suggests that the current Sierra Nevada population of 300 to 400 individuals (Ritter and Roche 1999) is declining (Bombay et al. 2001). If the primary reason for population decline of willow flycatchers in the Sierra Nevada is meadow desiccation, then willow flycatchers are likely to continue to decline towards extirpation unless management intervention is successful in restoring the hydrological functions of, and concomitantly mitigating, the erosive activities affecting these meadows.

Chapter 10

Management Considerations and Uncertainties

Indirect evidence brought forth in the previous chapters suggests that past livestock grazing may have been the prime factor leading to willow flycatcher declines in the Sierra Nevada, although there is no hard evidence to confirm this. Livestock could directly impact willow flycatchers by knocking down nests, affecting prey base by trampling and foraging, and removing nesting cover, as well as, indirectly, by promoting brood parasitism from brown-headed cowbirds, a bird species associated with livestock. Neither nest disruption or brood parasitism, however, appears to be a prevalent impact in this population. Meadow desiccation, which may indirectly be caused by livestock trampling (but also by roads, recreation, adjacent timber harvest or fuels treatments, fire suppression, water diversions, mining, climate changes, and drought), appears to be the single-most important proximate factor in willow flycatcher decline in the Sierra Nevada. Drier meadows result in a reduction of willow cover and standing water, leading to encroachment by conifers. The presence of conifers and the lack of standing water allow forest predators easier access to willow flycatcher nests. The increased predation rates on these nests may be the primary cause most influencing willow flycatcher population decline in the Sierra Nevada.

Obviously, management efforts leading to restoration of meadow hydrological regimes and reestablishment of healthy willow stands may prove the best options for restoring willow flycatcher populations. The magnitude of the problem is exemplified in the Feather River watershed where 98 percent of the 100,000 ha of meadow and small mountain valleys are considered degraded (Lindquist and Wilcox 2000). The impact of drought may further degrade these habitats (for example by reducing willow flycatcher prey base, leading to nestling deformities [H. Bombay, pers. obs.]) and also increase

livestock grazing pressure on shrubs. The Aquatic Conservation Strategy Meadow Study Plan, currently being developed for Sierra Nevada aquatic, riparian, and meadow (ARM) ecosystems, is the first step leading towards willow flycatcher conservation and should be coordinated appropriately.

A major uncertainty is the genetic relationship among the three subspecies, but most especially between *brewsteri* and *adastus*. Genetic work by Paxton (2000) suggests that *brewsteri* and *adastus* populations in the Sierra Nevada are not genetically distinct and, therefore, may be intergrades.

The importance of genetic understanding to management relates to whether, for instance, Little Truckee River *adastus* can be considered a source population for recovery of Middle Fork Feather River *brewsteri* populations 25 km away. Or are declining populations of *brewsteri* in the southern half of the Sierra Nevada more likely to be supplemented by Mono Lake *adastus* 40 km to the east, or Warner Valley *brewsteri* nearly 300 km to the north? The potential to discover additional occurrences of federally endangered *extimus* subspecies brings additional, legally mandated, management requirements. Thus, a clearer understanding of the genetic distinction among the three subspecies in the Sierra Nevada has a bearing on whether recovery efforts target subspecies differently.

Another uncertainty is the possible role windborne pesticides from the Central Valley and pesticide use on the wintering grounds may have on willow flycatcher immune response systems and egg viability. Circumstantial evidence from studies of other Sierra Nevada riparian and aquatic vertebrates (Sparling et al. 2001) suggests that pesticides may pose a threat to willow flycatchers, although significance has yet to be determined.

Chapter 11

Recommendations for Management

This Conservation Assessment has identified meadow degradation, which results in meadow drying, loss of nesting and foraging substrates, increased predator access to meadow interiors, and potentially cowbird parasitism as among the key factors likely responsible for the decline of the willow flycatcher. Although few rigorous, quantitative, cause-effect studies are available, the weight of evidence indicates that improving meadow conditions is the most likely step that will enhance flycatcher breeding success. Because each meadow is impacted by each negative factor to varying degrees, management activities must also be tailored on a meadow-specific basis. In this section desired outcomes are identified that should lead to improved habitat conditions for willow flycatchers. The primary Forest Service management activities are as follows:

- Manage meadow hydrology so that meadows remain wet throughout the breeding cycle of flycatchers.
- Implement a willow flycatcher monitoring program investigating nesting success and habitat conditions.
- Restore degraded meadows to nesting habitat conditions that increase opportunities for willow flycatcher population expansion.
- Lessen the influence of brown-headed cowbird brood parasitism on willow flycatcher populations.

MEADOW CONDITION

As reviewed in this document, meadows have been negatively impacted by a variety of factors that, together, have apparently caused a decline in habitat conditions for breeding and foraging flycatchers. Thus, management should be instituted that leads to an improvement in the stature (height and foliar cover) and recruitment of willow and

maintains wet conditions throughout the flycatcher breeding cycle.

A number of grazing alternatives, proposed by the USDA Forest Service and outside groups, were developed in the Sierra Nevada Forest Plan Amendment FEIS. They range from elimination of grazing in suitable habitat within 5 miles of meadow and riparian ecosystems occupied by willow flycatchers to developing buffer zones and limiting operating periods (LOPs) based on willow flycatcher nesting phenology and habitat use. Even under the no-action alternative, some forests are adopting their own LOP standards to protect nesting willow flycatchers. Forest managers must make meadow-specific determinations of what, if any, impact livestock are having on willow flycatcher habitat and take appropriate corrective actions. Whatever alternative is selected, additional research and monitoring are needed to address potential livestock impacts under current management regimes in the Sierra Nevada.

For example, if drought increases livestock grazing pressure on shrubs through premature drying of herbaceous forage, livestock could be taken off of the grazing allotment when shrub browse exceeds a certain percent as determined in collaboration with permit holders. Such standards should allow recruitment of riparian deciduous shrubs (that provide willow flycatcher nesting substrate) and are consistent with current management directions in the Sierra Nevada (SNFPA ROD 2001, p. A-59).

Roads also may have a negative influence on meadow condition, especially those that bisect meadows and have associated drainage structures to maintain road conditions. The SNFPA ROD (P A-57) recommended road redesign and no new roads in flycatcher habitat as a means of alleviating the negative effects of roads on meadow hydrology and, thus, on flycatcher habitat.

MONITORING

Continued monitoring of willow flycatcher populations and habitat is necessary to identify the factors limiting population recovery. Protocol-based detection surveys annually indicate where breeding willow flycatchers do and do not occur. They allow detection of changes in numbers and distribution of breeding pairs. Demographic studies identify the elements influencing population change such as nest success, dispersal, and overwinter survival. Monitoring of predation and parasitism rates should be built into the population monitoring and demographic studies. Nest predation by natural predators is likely to be a significant factor controlling Sierra Nevada willow flycatcher nesting success (Morrison et al. 2000, Cain 2001). Photo-documentation of nest predators to help evaluate the proportion of avian, snake, and mammalian predators will inform strategies to mitigate willow flycatcher nest predation. Habitat monitoring allows detection of annual changes to the most significant habitat features for willow flycatchers, including meadow wetness and willow coverage. In addition, evaluating the prevalence and monitoring the spread of recent *Salix* species dieback, believed to be caused by fungi (D. Cluck, pers. comm.), will yield valuable information. Coupled with demographic information, habitat studies can be used to define suitable habitat, quantity of value when identifying potential restoration sites, define restoration targets, and determine desired management conditions.

Obtain site soil profiles to determine soil characteristics, soil moisture, and site capability to support desired wetness, shrub cover, and foliar density at a site. Use these data to evaluate the influence of livestock, as well as the restoration potential, at a site.

HABITAT RESTORATION

Among the factors that may ultimately prove to be responsible for the decline of willow flycatcher populations (e.g., livestock grazing, increased predation rates, overwinter mortality), many are either an agent, or a

result, of habitat change. Consequently, restoration efforts are important tools in recovery of willow flycatcher populations. Without a sanctioned restoration strategy for willow flycatcher habitat, however, restoration efforts might be implemented without knowing whether the project will contribute to willow flycatcher recovery (Stefani et al. 2001).

Presumably, restoration efforts should focus on restoring meadow hydrology where activities have resulted in desiccation as well as mitigating current erosion sources. Meadows with restored hydrological regimes may provide greater soil saturation later in the summer season. Wetter soils may prevent forest predators from accessing nest sites and encroachment of lodgepole pines, a habitat feature for forest and avian predators (Cain 2001, Cain et al., *in press*).

Because of limited funding, a priority list of meadows that are candidates for restoration should be developed. Initially, efforts should be focused within willow flycatcher dispersal distance towards or near those meadows already supporting a high percentage of the Sierra Nevada willow flycatcher population. With ramifications for locating potential restoration projects, most willow flycatcher dispersal events have occurred downstream within the same drainage; however, four have occurred upstream within the same drainage, and two have occurred between different drainages (Bombay and Morrison, unpubl. data).

Restoration efforts elsewhere cannot succeed without first securing the source populations (and their habitat). Source populations produce the birds that are expected to expand

elsewhere. If flycatchers are lost at primary-use meadows such as Perazzo, Lacey, and Warner Valley, sustaining populations anywhere else in the Sierra Nevada is unlikely.

Meadow restoration work should also be guided by a conservation strategy developed jointly by the USDA Forest Service and U.S. Fish and Wildlife Service. The strategy should include site planning, action accountability, budgeting, and implementation and monitoring schedules. This strategy has to quantify minimum hydrological thresholds, or habitat components, that meadows should meet once restoration is completed. Consequently, the desired attributes of hydrology (meadow wetness) and habitat (such as willow coverage and structure, willow patch distribution, herbaceous species composition, and meadow distribution) have to be defined and incorporated into restoration and management plans. Finally, to help ensure the success of these expensive endeavors, peer-review of plans is advised.

COWBIRDS

Brood parasitism by brown-headed cowbirds does occur with Sierra Nevada willow flycatcher populations, but does not appear to be a significant problem (except with Kern River populations of *extimus*).

Observed parasitism rates (Bombay and Morrison 2001) are below levels believed to

be biologically harmful (Mayfield 1977, Laymon 1987). Nevertheless, localized high brood parasitism rates have been observed in the central Sierra Nevada, warranting that monitoring for parasitism should continue. The removal of cowbird eggs in parasitized nests in the endangered least Bell's vireo (*V. b. pusillus*) (Kus 2002) and Arizona Bell's vireo (*V. b. arizonae*) (Morrison and Averill-Murray 2002) increased productivity and has been implemented in the willow flycatcher demography study in the Sierra Nevada (Bombay and Morrison, unpubl. data).

To reduce the incidence of cowbird brood parasitism, conduct a GIS analysis should be conducted to evaluate the location of all existing foraging areas throughout the Sierra Nevada and to identify vulnerable flycatcher sites for monitoring. A bioregional level analysis would address cumulative effects/threats to flycatchers and ensure consistent approaches across forest boundaries. Monitoring and mitigation could then be prioritized and scheduled.

Periodic reviews, incorporating updated willow flycatcher and cowbird data, are recommended to evaluate mitigation success and consider new proposals. Such analyses should include the influence of dispersed and developed recreation effects, cowbird use and movements relative to livestock concentrations, the use by cowbirds of harvested sites, and other factors related to cowbird abundance and behavior.

Chapter 12

Research Needs

The following research needs are not listed in any order of priority.

1) Continue monitoring of willow flycatcher sites.

Willow flycatcher population status in the Sierra Nevada is precarious, especially in the southern half. Continuous monitoring, following protocols (Bombay et al. 2000), is required to ascertain the distribution and abundance of willow flycatchers, track trends in the general population and in response to management activities (grazing, recreation), and evaluate mitigation or restoration strategies.

2) Using willow flycatcher protocol, investigate detection probability and observer bias.

Determining population trends depends on accurate detection of nesting pairs that might be present. Poor detection rates or variation in an observer's ability to detect birds can result in underestimating the nesting population and a subsequent exaggeration of estimated population decline. By testing for detection probabilities and observer bias, correction factors can be developed that will lead to more accurate estimates of population change.

3) Continue demographic studies measuring λ .

Recent demographic studies by Bombay et al. (2001) have helped identify which segments of the population (i.e., sex-age) are most important in the observed annual rates of change. Strong correlations between nesting success and recruitment suggest that future efforts should focus on factors influencing nest success (e.g., nest predation). These studies are preliminary, however, and are based on small sample size. In particular, better estimates of dispersion patterns and overwinter survival (return rates) are needed to improve the reliability of population change estimates (λ). Continued study will

improve estimates of λ , identify suitable habitat criteria through linked research on habitat use and reproductive fitness, and confirm appropriate management direction. Furthermore, these data may address whether nestling sex ratios (e.g., female; see Paxton et al. 2002, Janota et al. 2002) and/or mating systems (e.g., polygyny; see Paxton et al. 2002) at a site provide clues about habitat quality. In the case of polygyny, it may either indicate that the particular site is outstanding or, alternatively (if available), that the other available unmated male territories are poor quality. Additional recommendations include expanding the geographic scope of the willow flycatcher demography study to include the Warner Valley Wildlife Area population and better understand source/sink dynamics in the Sierra Nevada.

4) Investigate further role of meadow wetness on predation rates.

Research by Cain (2001, see also Cain et al., *in press*) has shown that predation rates, especially from forest predators, may be the most or an, important factor leading to willow flycatcher population decline in the Sierra Nevada. Continued investigation into the relationship of standing water and encroaching conifers to predation rates should lead to refinement in developing meadow restoration strategies. In addition, the predator release hypothesis, which predicts an increase in mammalian predation pressure where declines of top forest carnivores (e.g., fisher, marten, northern goshawk) have occurred, could be evaluated.

5) Evaluate existing willow flycatcher habitat conditions and inventory potential restoration meadows, including meadows formerly occupied by willow flycatchers.

Using a consistent protocol or monitoring study plan (Morrison et al., *in prep.*), evaluate existing conditions and limiting factors within

willow flycatcher habitat to establish baseline data and to determine trends in meadow conditions for supporting or sustaining willow flycatchers.

Large meadows potentially suitable for restoration should be inventoried and classified as to current hydrological regime (wetness). Restoring meadow wetness where it has been lost and managing or mitigating erosive activities (e.g., roads, mining, adjacent timber harvest and fuels treatments, grazing, recreation) may prove to provide the greatest benefit to willow flycatcher recovery.

There are more than 50 identified sites that formerly supported breeding populations of willow flycatcher. Those sites no longer supporting breeding territories should be examined to determine whether habitat components remain, or if options for restoration are viable.

There are also sites known to support flycatchers the last year they were surveyed that have not been surveyed for at least 5 years. These sites should be resurveyed to determine status and condition of habitat.

6) Investigate the effects of weather events on willow flycatcher nesting success.

Reliable weather data are needed to quantify the relative contribution of habitat factors to nesting success (Dahm and Pittroff n.d.). The ongoing demographic study (Bombay and Morrison, unpubl. data) does, however, evaluate the cause of nesting failures. A single summer storm event could have a profound influence on annual nesting success, overriding all other factors. Further, meadow wetness, already identified as an important habitat component, is directly influenced by annual snow-pack. Consequent annual weather patterns and episodic events have to be factored in when correlating cause and effects with nesting success.

7) Measure response of willow flycatchers to meadow restoration efforts.

Meadow restoration is costly and labor-intensive. Where restoration efforts are planned, measurements of willow flycatcher habitat requisites should be included to quantify flycatcher response to revegetation and restoration efforts.

8) Identify subspecies distributions and determine if there is a genetic distinction between west slope *brewsteri* and east slope *adastus*.

As mentioned in Chapter 10, subspecies status, especially whether *brewsteri* and *adastus* are genetically distinct, should be clarified further for conservation and management of the species. If central Sierra Nevada *brewsteri* and *adastus* populations are fully intergraded and provide source/sink populations for each other, then they can be managed as one population. However, if east slope and west slope populations are genetically (or at least behaviorally) distinct, and do not intergrade, then *brewsteri* and *adastus* might have to be managed separately. These considerations also apply to *extimus*. At least, potential origins of source populations for recovery should be investigated.

There are four ways to define subspecies status:

- 1) Determine whether east slope and west slope populations can be differentiated using coloration following the methods of Unitt (1987).
- 2) Conduct genetic analysis specifically comparing central Sierra Nevada populations (similar to work by Paxton [2000]).
- 3) Conduct sonographic analyses to determine whether populations can be differentiated by vocal signatures (similar to Sedgwick 2001).
- 4) Intensify banding efforts and tracking dispersal.

A willow flycatcher born in one population found later breeding in another provides the strongest evidence for intergradation. Quantifying dispersal can also identify which meadows may prove to be good candidates for restoration, based on known dispersal distances from nearby occupied sites.

9) Investigate pesticide burdens in willow flycatchers.

Although there is no current evidence to show clearly that Sierra Nevada willow flycatchers are threatened by pesticides, the facts that 1) DDE burdens have been found in eggs (Valentine, pers. comm. *in* Williams and Craig 1998), 2) they winter where pesticide use is known, and 3) airborne pesticides from the Central Valley may impact other riparian- and meadow-associated vertebrates (Sparling et al. 2001), indicate that the threat might be real. Further, as Dahm and Pittroff (n.d.) pointed out in their critical assessment of the willow flycatcher literature (e.g., Taylor and Littlefield 1986), results implicating one stress or stressor (e.g., grazing) may be confounded by the presence of another (e.g., pesticides). Therefore, opportunistic analysis of non-viable eggs for pesticides should be considered.

10) Investigate the effects of major management activities that occur in

Sierra Nevada willow flycatcher habitat.

For example, investigate the effects of roads and road drainage, recreation, and livestock grazing on vegetation (shrub and herbaceous layer structure), plant species composition, predator and prey species composition and abundance, hydrology, and brown-headed cowbird brood parasitism rates. Relate these factors to willow flycatcher reproductive success to evaluate the effects of these activities on willow flycatcher population productivity.

11) Establish the relationship between willow flycatcher productivity and prey.

Explore the effects of willow flycatcher prey species composition and abundance and adult foraging activities across a gradient of meadow conditions.

12) Determine the impact of parasitism on willow flycatcher nest success and population trends.

Quantify cowbird parasitism rates and evaluate the responses of flycatcher success to cowbird control (i.e., egg addling and nestling removal, adult trapping).

Chapter 13

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