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Chapter 8:

Demographic Characteristics and Population Modeling

An understanding of the basic demography of a species is necessary to estimate and evaluate population trends. The relative impact of different demographic parameters on growth rates can be assessed through a sensitivity analysis, in which different parameters are altered singly to assess the effect on population growth. Identification of critical parameters can allow managers to focus their efforts on factors most likely to increase populations.

In this chapter, we describe the demography of the southwestern willow flycatcher. Our objectives are to (1) describe basic population characteristics of the subspecies, (2) summarize and estimate vital demographic parameters of the flycatcher, (3) use those parameters in a life table and population projection model, and (4) use an elasticity analysis to determine which parameters have the greatest impact on population growth rates, and therefore offer the greatest potential for management. Much of these data come from the only two well-studied populations of *E.t. extimus*, in the Kern River Preserve in California (data from Whitfield 1990, Whitfield and Strong 1995, Whitfield and Enos 1996, and Whitfield unpublished) and the Grand Canyon in Arizona (data from Sogge et al. 1997 and Sogge unpublished). Information from the Kern River Preserve that lacks a citation represents previously unpublished data of M. Whitfield. To provide perspective, we present

additional data from other willow flycatcher subspecies as well as other *Empidonax* flycatchers.

Populations Characteristics _____

Age Classes

Because of the lack of age-specific plumages, there are only two discernible age classes for the willow flycatcher: hatching year (HY) and after hatch-year (AHY).

Sex Ratio

There is no sexual dimorphism in this species; therefore inferences about sex ratios are necessarily circumstantial. Fledgling sex ratios are likely to be 1:1, as is true for almost all birds (Clutton-Brock 1986, Breitwisch 1989). Although facultatively monogamous, the sex ratio of adults in some populations of this subspecies appears to be male-biased, as suggested by the substantial proportion of unmated males observed. However, the proportion of unmated males, and therefore the sex ratio, varies greatly among sites. For example, in the Grand Canyon from 1993-1996, 44% of territorial males were unpaired (Sogge et al. 1997). In contrast, at the Kern River Preserve, generally 2-4 of 28-35 males (6-14%) are unpaired in any year, while in the upper Gila Valley, New Mexico, a maximum of 8 of

195 singing males (4.1%) may have been unpaired in 1997 (Parker 1997; S. Stoleson and D. Finch, unpublished data). The apparent skewed sex ratio in some populations may be due to higher mortality among females (see Survivorship section below). Alternatively, in very small populations, such as the Grand Canyon, sex ratios skewed in either direction can result from demographic stochasticity (Burgman et al. 1993). Polygyny has been recorded in this species, which may result from an excess of females in a population (Sedgwick & Knopf 1989, M. Whitfield unpublished data). However, mating systems in this species may be more complex than previously thought, as both unmated and polygynous males can occur in the same population (M. Whitfield, unpublished data).

Population Growth Rates

Few, if any, populations of *E.t. extimus* have been monitored for a sufficient time to quantify long-term population trends. Former populations in Arizona on the lower Salt River, Santa Cruz River, and lower Colorado River near Yuma are believed to have been extirpated. In California, a large population on the Santa Ana River in San Bernadino County mentioned by Hanna (1928) is gone although some suitable habitat remains (R. McKernan, personal communication). Similarly, a population at the mouth of the Santa Clara river appears to have been extirpated (M. C. Badger, cited in Unitt 1987).

In the short term, most monitored populations of the southwestern willow flycatcher have declined or shown no trend. For example, between 1993 and 1997, two small populations (3 to 4 pairs) in the Verde Valley, Arizona, have disappeared. Two small populations in the White Mountains of Arizona have decreased steadily over the past five years (Langridge and Sogge 1997). Between 1989 and 1993, the population in the Kern River Valley, California, dropped from 44 to 27 pairs (Whitfield 1993), but since then has remained relatively stable at about 32 to 34 pairs (Whitfield et al., in review). Similarly, the overall population in the Grand Canyon has not shown any consistent trend in the years 1982 to 1997, although there have been local extirpations and recolonizations at all the small breeding patches (Brown 1988, Sogge et al. 1997). Surveys conducted from 1994 to 1999 along the upper Gila River in New Mexico suggest that flycatcher numbers there may be increasing (Parker 1997, Stoleson & Finch unpublished data).

Fecundity

Fecundity is the measure of rate of reproduction in a population. Seasonal (or annual) fecundity is difficult to quantify in the field, especially for species that can attempt multiple nests in a season (Clobert &

Lebreton 1991). In bird populations, average seasonal fecundity is the product of the average probability of an individual breeding in a given season, the average number of eggs produced per clutch, the average number of nesting attempts per season, and the overall hatching and fledging success rates of nesting attempts within a season. We address these components individually below.

Probability of Breeding

Willow flycatchers apparently begin to breed in their second calendar year, i.e., on their first return to the breeding grounds (M. Whitfield, unpublished data, Paxton et al. 1997). At the Kern River, all females of all age classes appear to breed every year, perhaps as a result of a skewed adult sex ratio. The same is likely to be true for other populations as well. As noted above, in many populations a significant portion of territorial males may remain unpaired. Whether or not a male remains unmated during a season appears to be independent of age (M. Whitfield, unpublished data).

Clutch Size

The modal clutch size is three eggs throughout most of the range of *E.t. extimus*, and varies from 1 to 5 (although one-egg clutches are likely the result of predation or disturbance). Clutch sizes at the Kern River appear to be larger than in Arizona or New Mexico (Table 8-1). Four-egg clutches are common among first nesting attempts of a season at the Kern ($\bar{x} = 3.64 \pm 0.68$ eggs [mean \pm SD], $n = 96$). Elsewhere in the southwest, clutches of four eggs are rare (Sferra et al. 1997, Sogge et al. 1997, S. Stoleson and D. Finch, unpublished data). Among other subspecies of the willow flycatcher, clutches of four are not uncommon, and mean clutch size is generally larger than that of *E.t. extimus* (Table 8-1).

In general, clutch sizes of other flycatchers in the genus *Empidonax* tend to be larger than those of *E.t. extimus* (Table 8-1). Clutches of four eggs are common, and clutches of five eggs occur in several species (e.g., Briskie & Sealy 1989, Sedgwick 1993, Bowers & Dunning 1994). This difference may be related to habitat or latitude. Unlike the shrub and riparian woodland inhabiting willow flycatcher, several of the other *Empidonax* listed in Table 8-1 occupy closed forest habitats (Bent 1942). Forest interior birds may experience lower predation rates, and consequently may have evolved relatively larger clutch sizes than sister taxa in more open habitats or edges (Martin 1993, 1995). In general, clutch sizes of birds increase with increasing latitude (Lack 1968, Klomp 1970). The southwestern willow flycatcher breeds further south than any other subspecies of *E. traillii* (Unitt

Table 8-1. Clutch sizes of willow flycatchers and other *Empidonax* species.

Taxon ^a	Site	Mean	N	Range	Source
<i>E.t. extimus</i>	Kern River, CA (1987)	NA	16	1-4 ^b	Harris 1991
	Kern River, CA (1989-97)	3.33	154	1-5 ^b	M. Whitfield unpub. data
	Grand Canyon, AZ	3	3	3	Sogge et al. 1997
	Arizona, statewide	2.34	67	1-4 ^b	Sferra et al. 1997
	San Luis Rey, CA	2.69	29	1-4 ^b	W. Haas pers. comm.
	Cliff-Gila Valley, NM	2.67	21	2-4	Skaggs 1996, Stoleson and Finch unpub. data
<i>E.t. adastus</i>	WA	3.42	33	3-4	King 1955
<i>E.t. brewsteri</i>	Truckee R., CA	2.82	11	2-3	Flett & Sanders 1987
<i>E.t. traillii</i>	MI	3.28	92	3-5	Walkinshaw 1966
	OH, NE	3.41	91	2-5	Holcomb 1972, 1974
	WI	3.59	415	3-5	McCabe 1991
<i>E. difficilis</i>	Monterey, CA	4.00	23	NA	Davis et al. 1963
<i>E. fulvifrons</i>	AZ	3.37	12	2-5	Bowers & Dunning 1994
<i>E. minimus</i>	MI	3.95	46	3-5	Walkinshaw 1961
	Manitoba	3.92	192	2-5	Briskie & Sealy 1989
<i>E. oberholseri</i>	MT	4.00	21	2-5	Sedgwick 1993
<i>E. virescens</i>	MI	2.54	66	NA	Walkinshaw 1961
	MI	2.92	25	2-4	Mumford 1964

^a *E. traillii* = willow flycatcher, *E. difficilis* = Pacific-slope flycatcher, *E. fulvifrons* = buff-breasted flycatcher, *E. minimus* = least flycatcher, *E. oberholseri* = dusky flycatcher, *E. virescens* = acadian flycatcher.

^b Clutch sizes of one are likely the result of disturbance or predation.

1987), and further south than most of the other species listed in Table 8-1. Therefore, *E.t. extimus* may be expected to have smaller clutches, on average, than other subspecies or other *Empidonax* species. It may be noteworthy that the Kern River population is further north than populations in Arizona and New Mexico and tends to have larger clutch sizes. The Acadian Flycatcher (*E. virescens*), whose breeding range extends further south in the United States than any other *Empidonax* (Bent 1942), also tends to have smaller clutch sizes than its congeners (Table 8-1).

Clutch size in the southwestern willow flycatcher does not increase or decrease as a function of age (M. Whitfield, unpublished data). However, clutch size does tend to decrease with successive nesting attempts within a year (Holcomb 1974, M. Whitfield, unpublished data). For example, at the Kern River, mean clutch size declined from 3.64 for first attempts to 2.87 for second and 2.67 for third attempts. Least Flycatchers (*E. minimus*) show a similar pattern of decreasing clutch size in successive nesting attempts (Briskie & Sealy 1989), as do many other passerines (Rowe et al. 1994, Young 1994).

Number of Nesting Attempts per Season

Willow flycatchers often respond to cowbird parasitism, nest destruction, or other severe disturbance by abandoning their nests and reneating. Consequently,

females will frequently attempt several nests per season following the failure of earlier nests (Holcomb 1974, Whitfield 1990, Harris 1991). At the Kern River, females averaged 1.82 ± 0.89 nesting attempts per season from 1989 to 1997. Some females in Arizona and New Mexico have been suspected of initiating up to four clutches in a season, although this is uncertain because the birds were unbanded (T. McCarthey, S. Stoleson and D. Finch, unpublished data). The highest documented number of nesting attempts within a season occurred at the Kern River during a year of intense cowbird parasitism, where one pair built six nests (Harris 1991). In general, a high incidence of cowbird parasitism leads to an increased number of nesting attempts per season because many flycatchers will quickly abandon and reneat. For example, at the Kern River, females averaged 2.04 ± 0.99 ($n=82$) attempts per year prior to cowbird trapping, and only 1.66 ± 0.78 ($n=118$) attempts afterwards.

Other than reneating after nest failure or parasitism, multiple nesting attempts within a season are rare. McCabe (1991) considered willow flycatchers to be single-brooded. However, double brooding (raising a second brood after successfully fledging the first) has been documented or suspected at several sites in the southwest (Whitfield 1990, Griffith & Griffith 1995, Sferra et al. 1997, S. Stoleson and D. Finch, unpublished data). For example, at the Kern River, 3.8% of successful females attempted to raise second

broods. Double brooding is relatively rare in other *Empidonax* flycatchers as well, although reported at least occasionally in most species (e.g., Walkinshaw 1961, Davis et al. 1963, Sedgwick 1993, Bowers & Dunning 1994, Briskie 1994). Briskie and Sealy (1987) suggested that the Least Flycatcher may double brood infrequently because delaying fall migration to raise a second brood may prevent birds from establishing and maintaining winter territories. This may apply to willow flycatchers as well: females seem to double brood only when the young from their first brood have fledged by late June or very early July.

Hatching Success

Hatching success of southwestern willow flycatcher eggs varies among populations. The overall hatching rate in unparasitized nests for all monitored sites in Arizona in 1996 was 66% (Sferra et al. 1997). At the Kern River and San Luis Rey River populations in California, 63% and 86% of eggs hatched in unparasitized nests, respectively (Whitfield and Sogge 1999, W. Haas personal communication). Hatching rates for other subspecies vary widely among populations, from a low of 54.8% ($n=272$) in Ohio and Nebraska (Holcomb 1972) to a high of 92.6% ($n=67$) in Washington (King 1953). Thus, populations at the Kern River and in Arizona appear to experience relatively low hatching success, although comparable rates have been reported for both Acadian

(Walkinshaw 1961) and Dusky Flycatchers (*E. oberholseri*; Sedgwick 1993).

Nesting Success

Nesting success for the southwestern willow flycatcher varies greatly among sites (Table 8-2). Areas with high levels of cowbird parasitism exhibit very low success (e.g., the Grand Canyon, the Kern River prior to cowbird trapping). In contrast, other sites experience relatively high levels of nesting success. For example, at some sites in Arizona and in the Gila Valley of New Mexico, 50 to 55% of nests successfully fledged one or more young (Sferra et al. 1997, Skaggs 1996, S. Stoleson and D. Finch, 1999). At the San Luis Rey River in California, nesting success has reached 70% in an area of intensive cowbird trapping (W. Haas, personal communication). In general, nesting success rates for cup-nesting passerines in North America range from about 38 to 70%, with a median value of 52% (Nice 1957, Martin 1993). Thus, some populations of *E.t. extimus* (listed in Table 8-2) experience poor nesting success compared to other cup-nesting songbirds.

Nesting success in Tyrannid flycatchers tends to be relatively high for the size of the bird, perhaps because of their aggressive nature (Murphy 1983). Studies of other willow flycatcher subspecies have generally indicated higher nesting success rates than are typical for *E.t. extimus*, from lows of about 40% to almost 70%

Table 8-2. Measures of nesting success in willow flycatchers and other *Empidonax* species.

Taxon ^a	Site	% nest success ^b	No. of nests	Fledglings per nest	Fledglings per female	Source
<i>E.t. extimus</i>	Kern River, CA (1987)	15.8	19	0.62	1.25	Harris 1991
	Kern River, CA (1989-1997)	36.4	324	1.27	1.44	Whitfield unpub. data
	Grand Canyon, AZ	18.0	17	NA	0.70	Sogge et al. 1997
	statewide ave., AZ	42.9	163	0.93	0.99 ^c	Sferra et al. 1997
	Cliff-Gila Valley, NM	55.2	97	NA	NA	Skaggs 1996; Stoleson & Finch unpub. data
	San Luis Rey R., CA (1994)	64.0	11	2.09	NA	Griffith & Griffith 1995
	San Luis Rey R., CA (1995-97)	66.0	70	1.54	2.45	Haas pers. comm.
<i>E.t. adastus</i>	North Park, CO	40.7	27	0.89	NA	Sedgwick & Knopf 1988
	Malheur N.W.R., OR	NA	876	NA	1.81	Sedgwick & Iko 1999
<i>E.t. brewsteri</i>	Truckee R., CA	54.5	11	1.27-1.36	1.40-1.50	Flett & Sanders 1987
<i>E.t. traillii</i>	MI	69.5	209	NA	NA	Berger 1967
	MI	65.2	92	2.15	NA	Walkinshaw 1966
	OH, NE	39.5	91	1.11	1.88	Holcomb 1972
	WI	68.6	459	2.13	NA	McCabe 1991
<i>E. difficilis</i>	Monterey, CA	73.9	43	1.92	NA	Davis et al. 1963
<i>E. fulvifrons</i>	AZ	NA	12	2.08	NA	Bowers & Dunning 1994
<i>E. minimus</i>	MI	56.3	16	3.80	NA	Walkinshaw 1961
	Manitoba	58.6	273	1.25	NA	Briskie & Sealy 1989
<i>E. oberholseri</i>	MT	58.3	24	1.60	1.90	Sedgwick 1993
<i>E. virescens</i>	MI	59.1	66	1.36	NA	Walkinshaw 1961

^a See Table 8-1 for common names of taxa.

^b Percentage of nests of known outcome that produced at least one flycatcher fledgling; not Mayfield estimates (Mayfield 1975).

^c $n = 102$ females

(Table 8-2). Nesting success among other *Empidonax* species tends to be somewhat higher yet, usually well over 55% (Table 8-2). Willow flycatchers may have somewhat lower success than their congeners because their riparian habitats tend to be patchy, fragmented, linear, and with a high proportion of edge, especially in the Southwest. Birds in such habitats are likely to be more vulnerable to predation or parasitism than in more contiguous wooded habitats (Robinson et al. 1995). As mentioned above, most of the other species in Table 8-2 are species of contiguous forest, which tend to have higher rates of nesting success than species that nest in more open or fragmented habitats (Martin 1993). In addition, most forests in the west are higher in elevation and further from concentrations of livestock than are floodplain riparian woodlands, so there may be an elevational component to the difference in nest success as well.

Seasonal Fecundity

Fecundity can be measured as the number of young fledged on a per nest or per pair basis. The number of fledglings produced per nest is much more easily determined. At most sites where data are available, southwestern willow flycatchers fledge less than one chick per nest, including nests that fail or are abandoned (Table 8-2). In contrast, studies of other willow flycatcher subspecies have usually reported more fledglings per nesting attempt, ranging from 1.11 to over 2 (Table 8-2). One exception was in North Park, Colorado, where heavy cowbird parasitism on *E.t. adastus* reduced per-nest productivity to 0.89 fledglings (Sedgwick & Knopf 1988). Because cowbird parasitism often provokes nest abandonment, it can greatly reduce the average nest productivity. For example, at the Kern River, an intensive cowbird control program increased the average per-nest productivity from 1.04 fledglings to 1.72 fledglings (Whitfield et al., in review). The effects of cowbird parasitism on productivity are discussed in depth in the following chapter. Other *Empidonax* show higher per-nest productivity than *E.t. extimus* as well (Table 8-2).

Because flycatchers may renest multiple times during a breeding season, per-nest productivity does not

necessarily equate with seasonal fecundity. Rather, the best measure is the number of chicks fledged per pair per year (Clobert & Lebreton 1991). Recent evidence suggests low levels of mate fidelity in the willow flycatcher, even within a season (Paxton et al. 1997). Because female fecundity is much easier to assess accurately than male fecundity, we will use the number of fledglings per female per year as the measure of seasonal fecundity. Unfortunately, this rate has been calculated in very few studies, in part because it requires having color-banded birds, and because of the difficulty of following individual females through the course of an entire breeding season (Pease & Grzybowski 1995).

Seasonal fecundity of *E.t. extimus* ranges from a low of 0.7 fledglings per female in the Grand Canyon to 2.45 fledglings per female (3 year average) at the San Luis Rey River (Table 8-2). The low rate of reproduction in the Grand Canyon suggests a sink population. In contrast, the fecundity of the San Luis Rey population, where cowbirds are controlled, exceeds that of most populations of other subspecies and other *Empidonax* species (Table 8-2).

Survivorship

Data on survivorship for willow flycatchers are sparse. Information that does exist comes from return rates of banded birds. Estimates of survivorship based on resighting or recapture of banded individuals are necessarily conservative because they do not discriminate between mortality and emigration (Lebreton et al. 1992, Noon & Sauer 1992). Individuals of *E.t. extimus* have been color-banded systematically for more than three years only at the Kern River Preserve, although in 1996 the Colorado Plateau Field Station began a statewide banding effort in Arizona (Paxton et al. 1997).

Return Rates of Banded Birds

Return rates of banded adult flycatchers from the two color-marked populations of *extimus* were very similar: about 52% for males and 35% for females (Table 8-3). In contrast, studies of other subspecies

Table 8-3. Return rates of color-banded willow flycatchers in four areas.

Site	HY ^a	AHY: male ^a	AHY: female ^a	Source
Kern River, CA	34.2% (38)	51.7% (29)	33.8% (207)	Whitfield unpub. data
Arizona	8% (12)	52.0% (50)	34.0% (48)	Paxton et al. 1997
Michigan	1.4% (147)	40.9% (22)	22.6% (31)	Walkinshaw 1966
Malheur NWR, OR	13.2% (214)	43.3% (192)	46.8% (211)	Sedgwick & Klus 1997

^a HY = hatch year (from fledging through first breeding season), AHY = after hatch year.

showed lower return rates. Whether this represents lower survival rates or greater dispersal due to more available habitat is unclear. In general, return rates of female flycatchers were lower than those of males. Because adult female willow flycatchers are thought to show high site fidelity (Walkinshaw 1966, Sedgwick & Knopf 1989, but see Paxton et al. 1997), lower return rates probably indicate lower survival rates than for males. Male-biased survival rates are common among passerines (Breitwisch 1989). The population at Malheur National Wildlife Refuge, Oregon, is exceptional in that females returned to the site at about the same rate as males (Sedgwick & Klus 1997). In general, annual survival rates for small migratory passerines range from 0.3 to 0.6 (Dobson 1990, Karr et al. 1990), so the estimates based on resighting probabilities presented in Table 8-3 seem reasonable for birds the size of willow flycatchers.

Estimates of survivorship for first year birds based on return rates to their natal region are usually biased because first year birds normally disperse from their natal area, and it is impossible to differentiate mortality from permanent emigration (Clobert & Lebreton 1991, Noon & Sauer 1992). Relatively low return rates for Michigan and Oregon populations (Table 8-3) almost certainly reflect high rates of natal dispersal. A relatively high proportion of first year birds returned to the Kern River Preserve (Table 8-3), perhaps because very little suitable riparian habitat exists in that region into which birds can disperse, so more return to their natal area and are detected. For that reason, return rates of first year birds to the Kern may be our best estimate of first year survival. The situation is likely to be similar in Arizona, but small sample sizes (1 of 12 individuals banded in 1996 returned in 1997) make the reported 8% figure suspect (Paxton et al. 1997). Data are equally scant for related species. Of 410 fledgling Least Flycatchers banded in Manitoba, only 4.2% were ever recaptured (Briskie 1994).

The between-season survival rate of fledglings appears to decline as the breeding season progresses. Whitfield and Strong (1995) found significantly higher return rates for young fledged before July 21 than for young fledged afterwards. This pattern has been reported in numerous other avian species as well (e.g., Hochachka 1990, Verhulst et al. 1995, Brinkhof et al. 1997). Therefore, there are two reasons why cowbird parasitism can affect seasonal fecundity even when birds are successful after abandoning early parasitized nests. Second (or later) clutches will be smaller, and fledglings from later attempts will be less likely to survive to breeding age. At the Kern River, observed return rates for fledglings were greater following the initiation of cowbird control in 1992, exceeding 0.50 in 1996 and 1997, although this may reflect increased resighting effort in those years (see Chapter 8).

Lifespan

Apart from a few anecdotal accounts, there is little information available on the longevity of willow flycatchers. In Oregon, one of 537 birds banded as adults survived at least eleven years after its first capture (J. Sedgwick, personal communication). One of 22 males banded as adults survived at least five years in Michigan (Walkinshaw 1966). For *E.t. extimus*, one male survived at least six years after banding, and three females and a male were still alive five years after banding at the Kern River (Whitfield and Enos 1996). Similarly, little is known of lifespans of other *Empidonax* flycatchers. The maximum known age for any other species, based on banding recoveries, is 8 years for a Dusky Flycatcher (Sedgwick 1993).

The average life span of a bird can be estimated from mortality rates using the formula:

$$L = \frac{2 - m}{2m}$$

where L = average lifespan and m = the average annual mortality rate (Gill 1990). Substituting 0.66 for m (based on minimum annual survival = 0.34, see Table 8-3) yields an average lifespan of 1.02 years; using 0.47 for m (based on maximum annual survival = 0.53, see Table 8-3) gives a lifespan of 1.63 years. Thus, the average lifespan of southwestern willow flycatchers is likely to be somewhere between 1.02 and 1.63 years.

Lifetime Reproductive Success

Lifetime reproductive success (LRS) has been estimated for very few passerines, in part because of the logistical difficulties in following individual females through the course of their lifetimes. Long term studies of *E.t. adastus* in Oregon have revealed that females reared, on average, 3.60 young over their lifespans (Sedgwick and Iko 1999). LRS varied with whether or not females were parasitized in their first breeding year, but was not affected by parasitism in subsequent years.

Immigration and Emigration

To date, what little is known of movement among populations of *E.t. extimus* comes from recent work in Arizona (Paxton et al. 1997). Rates of immigration and emigration varied considerably among populations, perhaps based on the relative degree of isolation of the population. Overall, of 48 birds that bred in 1996 and were resighted in 1997, 13 (27%) returned to a different site. It is likely that immigration rates are lower where available breeding sites are limited, such as at the Kern River (Paxton et al. 1997). Also, site fidelity tended to be lower for sites with lower overall

nesting success, suggesting higher emigration rates (Paxton et al. 1997). Information on sex-biased dispersal is sparse, but recent data from color-banded birds in Arizona suggest that males emigrate more frequently than females, contrary to the normal pattern among passerine birds (Greenwood & Harvey 1982). It is yet unclear whether females disperse further than males, as in other birds.

Life Table Analyses

A life table summarizes the vital rates of age-specific survivorship and fecundity for a population. As mentioned above, because of the difficulty in determining fecundity rates for males, life tables are normally female-based. Observed rates of fecundity are divided in half to indicate the rate of production of female fledglings, and assume an equal sex ratio at fledging (Noon & Sauer 1992).

It is evident from previous sections of this chapter that estimates of demographic parameters for the southwestern willow flycatcher are available from very few sites, and that estimates vary considerably, both among sites, and within sites depending on year and management practices. For no population (with the possible exception of the Kern River) is there sufficient knowledge of demographic parameters to create a complete life table. Therefore we present two composite life tables, using estimates of parameters from various populations. One table is conservative, and uses minimum estimates of survival and fecundity. It may be thought of as a worst case scenario. The second table is more optimistic, uses the highest recorded parameter estimates, and represents a best case scenario. The two tables bracket the likely range of demographic parameters for the majority of willow flycatcher populations.

Life Table Parameters

In the conservative life table, we used 0.34 as the survival rate (p_x) for both the HY age class, based on the observed return rate of HY birds at the Kern River, and for the AHY age class, based on observed return rates for adult females in Arizona (Table 8-3; Paxton et al. 1997). The fecundity rate, or maternity function m_x , denotes the expected number of female fledglings produced by a female of age x . We used the observed rate of 0.7 fledglings per female per season from the Grand Canyon (Sogge et al. 1997), divided by two to account for female offspring only. In the optimistic life table, HY birds were assigned a survival rate of 0.50 (M. Whitfield, unpublished data), and AHY birds a rate of 0.47 (Sedgwick & Klus 1997). We used an optimistic fecundity rate of 1.28 female fledglings per female per season, based on 1997 data from San Luis Rey, California (W. Haas, personal communication).

Other parameters in both life tables are x , which denotes age class expressed in years; p_x , the probability of survival from age class x to age class $x+1$; l_x , the probability that an individual aged 0 will survive to enter age class x ; and $l_x m_x$, the age-specific reproductive rate. The latter term multiplied by age x is used for calculating population parameters (see below). Life tables assumed no reproductive senescence, but were truncated at eight years, the maximum recorded lifespan for willow flycatchers. Fecundity and survival were assumed to be constant after the hatching year.

Life tables are presented as tables 8-4 and 8-5. They show that for either scenario, a very small proportion

Table 8-4. Life table of the southwestern willow flycatcher based on conservative^a parameter values^b.

x	p_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	0.340	1.000	0.00	0.000	0.000
1	0.340	0.340	0.35	0.119	0.119
2	0.340	0.116	0.35	0.040	0.081
3	0.340	0.039	0.35	0.014	0.041
4	0.340	0.013	0.35	0.005	0.019
5	0.340	0.005	0.35	0.002	0.008
6	0.340	0.002	0.35	0.001	0.003
7	0.340	0.001	0.35	0.000	0.001
8	0.340	0.000	0.35	0.000	0.000
SUM:				0.180	0.272

^a Conservative scenario uses the lowest value recorded among all willow flycatcher populations for each parameter.

^b Table parameters are: x = age class in years; p_x = probability of survival from age class x to $x+1$; l_x = probability that an individual aged 0 will survive to enter age class x ; m_x = average number of female offspring by a female of age x ; $l_x m_x$ = product of l_x and m_x , the age-specific reproductive rate; and $x l_x m_x$ = product of $l_x m_x$ and x (used for calculation of population parameters).

Table 8-5. Life table for the southwestern willow flycatcher based on optimistic^a parameter values^b.

x	p_x	l_x	m_x	$l_x m_x$	$x l_x m_x$
0	0.500	1.000	0.00	0.000	0.000
1	0.470	0.500	1.28	0.640	0.640
2	0.470	0.235	1.28	0.301	0.602
3	0.470	0.110	1.28	0.141	0.424
4	0.470	0.052	1.28	0.066	0.266
5	0.470	0.024	1.28	0.031	0.156
6	0.470	0.011	1.28	0.015	0.088
7	0.470	0.005	1.28	0.007	0.048
8	0.470	0.003	1.28	0.003	0.026
SUM:				1.205	2.250

^a Optimistic scenario uses the highest value recorded among all willow flycatcher populations for each parameter.

^b Refer to Table 8-4 for definitions of parameters.

of any cohort will survive beyond 3 years of age. Consequently, females in the 1 and 2 year age classes make the greatest contribution to reproduction (as indicated by the $l_x m_x$ terms).

Population Parameters Calculated from the Life Table

The life table enables calculation of R_0 , the net reproductive rate, and generation time T . The net reproductive rate is calculated as the sum of the $l_x m_x$ terms, and measures the expected production of female fledglings by a female during the course of its lifetime. Table 8-4 indicates that in the worst-case scenario, a female willow flycatcher will produce, on average, 0.18 female fledglings in its lifetime, or 0.36 fledglings of both sexes assuming an equal sex ratio. This rate is clearly well below the replacement rate of 1 female fledgling per female, and indicates a rapidly declining population. The best case scenario suggests a net reproductive rate of 1.21 female fledglings per female, and indicates a population growing at a relatively rapid rate.

Generation time T is a measure of the mean interval between the birth of a female and the birth of her offspring (Caughley 1977). T is calculated as

$$T = \frac{\sum x(l_x m_x)}{R_0}$$

Generation time calculated from the conservative life table is 1.51 years, and from the optimistic life table 1.87 years. The life table based on optimistic values yields a longer generation time because the expected reproductive lifespan of females is greater due to higher survival rates. In either case, the very short generation time suggests considerable potential for rapid population growth as well as considerable vulnerability to rapid population decline.

Population Projection Model

Effective management and recovery of a threatened or endangered species depend on identifying and correcting the factors that limit population growth. Demographic modeling can indicate probable population trends under current or future conditions if model parameters are well known. Sensitivity analyses can be used to indicate which life history components are the most likely to affect population growth rates, and hence provide the most potential for management. Because the southwestern willow flycatcher occurs in assemblages of local breeding populations that occupy dynamic habitat patches scattered across the landscape, it would be an ideal candidate for a metapopulation or spatially-explicit model (Hanski 1998). However, these types of models are data-intensive,

and require reasonable estimates of dispersal and patch-specific demographic rates, among other data, to produce meaningful results (Beissinger and Westphal 1998). Those data do not yet exist; therefore the use of a spatially structured demographic model would be premature at this time.

Instead, we present a simple stage-based matrix projection model for the southwestern willow flycatcher (Caswell 1989, McDonald & Caswell 1993). As with the life tables, we use estimates of demographic parameters from various populations. Accordingly, the model will not represent the dynamics of any particular population of willow flycatchers, but rather will provide a crude measure of range-wide population dynamics. The model was used to estimate lambda (λ), the finite rate of population growth, which indicates the factor by which a population grows over the projection interval. A lambda less than one indicates a declining population, and a lambda greater than one a growing population.

Model Structure

In the absence of age-specific vital rates (see Life Table Analyses above), a simple model was created based on the two life stages that are identifiable in the field: hatching year and after-hatch year. The population life cycle diagram is presented in Figure 8-1, and is based on post-breeding censuses and a one-year projection interval. This life cycle is typical of many birds (McDonald & Caswell 1993). Post-breeding censuses are used for the model because parameters are

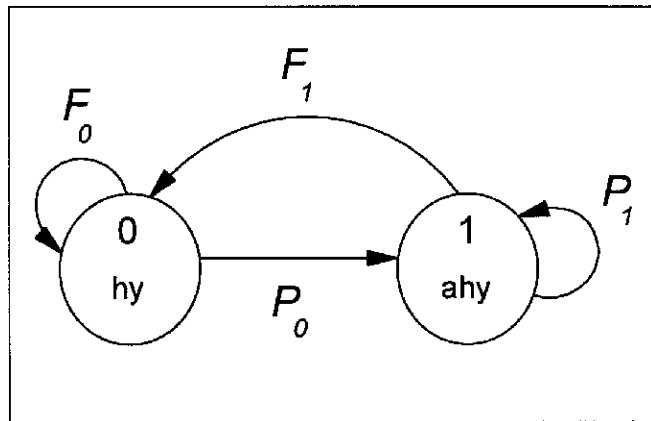


Figure 8-1. A simple life cycle diagram for the southwestern willow flycatcher used to create a stage-based population model. P_0 = probability of a fledgling surviving through the following breeding season; P_1 = annual survival probability for adults; F_0 = fecundity (i.e., the number of fledglings produced per female per breeding season) of birds in their first year of life; F_1 = annual fecundity of birds one or more years old; hy = hatch year; ahy = after hatch year.

more easily estimated from field data than is true for pre-breeding censuses. Pre-breeding censuses also confound estimates of fecundity and first year survival (Noon and Sauer 1992). Note that the timing of the census for the purposes of this model is not meant to address questions of field methodology.

In the model, P_0 is the probability that a fledgling will survive to the next breeding season. P_1 is the annual survivorship of adults. The annual fecundity (number of female fledglings per female per year) is given as F_0 for hatch-year birds and F_1 for adults. Note that because this is a post-breeding model, the fecundity value for HY birds indicates the productivity of birds in their first breeding attempt, after their return to the breeding grounds but before the census. The flow of events in the model is (1) birds are censused at the close of the breeding season, (2) birds survive to the next season, (3) individuals are aged one year, (4) survivors breed, and (5) birds are censused again. The model is completely deterministic, as there are no data available on the variance of parameters within a population. Because in this model birds must survive to the next season before breeding, F values are the product of the maternity rate (m_x) from the life tables and the stage-specific survival rates P .

The model assumes that: (1) males do not affect survival and reproduction of females, (2) rates of survival and fecundity are constant among individuals within a stage class and among years, (3) breeding occurs in a single birth-pulse, (4) the population is near a stable age distribution, and (5) parameters are not density dependent (Noon & Sauer 1992). None of these assumptions are likely to be strictly true for a passerine bird. In particular, both survival and fecundity can vary greatly among years at some sites. However, slight violations of these assumptions are unlikely to affect the qualitative results of the model (Noon & Sauer 1992). As with the life tables, we examined the model using both optimistic and conservative parameters. We also added an intermediate set of values as perhaps more typical of most populations. Because data are available for very few populations, we used simple means of the extreme parameter values in the intermediate scenario. The vital rates used for the conservative and optimistic models were the same as in the life tables (Table 8-6).

Populations were projected over a 25 year time span, arbitrarily starting with 100 pairs of flycatchers. Lambda was calculated for each scenario analytically as N_t/N_{t-1} at $t=25$ years, where N is the total population size. For all three scenarios, lambda had stabilized after 20 years.

Population Projection Results

Under the optimistic scenario, the hypothetical population grew exponentially (Figure 8-2). Lambda was

Table 8-6. Values used for demographic parameters^a in a conservative, an intermediate and an optimistic population projection model^b.

Model	P_0	P_1	m_x	F_0	F_1
Conservative	0.34	0.34	0.35	0.12	0.12
Intermediate	0.42	0.41	—	0.38	0.36
Optimistic	0.50	0.47	1.28	0.64	0.60

^a See Figure 8-1 for definitions of parameters; maternity function, m_x = number of female fledglings per female (see Tables 8-4, 8-5).

^b Conservative and optimistic models defined as in Table 8-4; intermediate model uses means of extreme values.

calculated to be 1.11, which indicates an annual increase of 11%. This rapid population growth is based on actual rates measured in the field, and illustrates that under optimal conditions, willow flycatchers have the potential for rapid recovery. In contrast, populations declined to extinction under both the intermediate and conservative scenarios. In the worst-case scenario, lambda was 0.46, which indicates a precipitous population decline of 54% per year. The population still declined at an annual rate of 22% under the intermediate scenario. Estimates of lambda derived from this model should not be considered as representing the growth rate of any population of willow flycatcher, nor should they be used to predict future population sizes. However, if the parameter values used are considered to be representative of the extremes found in flycatcher populations, then the trajectory of any particular population is likely to be

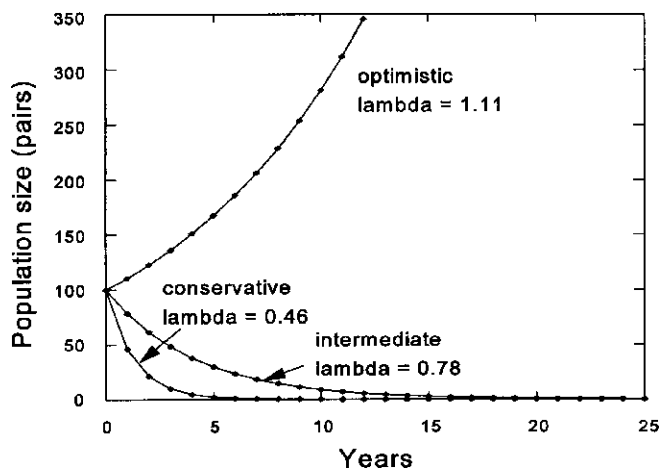


Figure 8-2. Hypothetical population trajectories for the south-western willow flycatcher using conservative (lowest values among all populations), optimistic (highest values among all populations), and intermediate (mean of conservative and optimistic values) parameters for fecundity and survival. Initial population size was 100 pairs. See text for details of model.

Table 8-7. Elasticity of lambda to changes in demographic parameters for three different scenarios. See Table 8-6 for parameter definitions and values used in each of the scenarios.

Model	P_0	P_1	F_0	F_1
Conservative	0.19	0.56	0.07	0.19
Intermediate	0.24	0.28	0.24	0.24
Optimistic	0.24	0.21	0.31	0.24

within the extremes presented. Further, if the intermediate values used are indeed typical of most flycatcher populations, then the prospect for all but a few populations is bleak.

Elasticity of Demographic Parameters

Elasticity is a measure of the proportionate effect of a parameter on lambda. Parameters showed different elasticity among the three scenarios (Table 8-7). Under the conservative scenario, lambda was most strongly affected by adult survival (P_1), and little affected by other parameters. This suggests that prolonging the reproductive lifespan of breeding females would have a greater effect on population growth than would increasing seasonal fecundity, perhaps since fecundity is low. In contrast, under the optimistic scenario, lambda was most strongly affected by HY fecundity (F_0), and moderately affected by the other parameters about equally. From Table 8-5 it is evident that first time breeders make the largest contribution to reproduction (as indicated by the $l_x m_x$ term), and increasing their fecundity would have a disproportionate effect on population growth. Under the intermediate scenario, the effect of all parameters on lambda was similar.

Implications for Management

The effectiveness of management actions can be maximized by concentrating efforts on those demographic components that have the greatest effect on population growth rates. However, which demographic component to manage depends on which scenario is used. With the conservative scenario, increasing the population growth rate would be best accomplished by increasing adult survivorship. Better data are needed on the causes and timing of adult mortality to accomplish this task. On the other hand, the optimistic scenario suggests increasing fecundity may be the best strategy. This might be accomplished by reducing cowbird parasitism or nest predation. In reality, it is probably much easier to improve fecundity through management than it would be to increase survival

rates, in part because this species is a neotropical migrant with overwinter survival constrained by factors outside of the United States, and therefore difficult to manage. In addition, demographic rates, and hence the best management strategies, are likely to be site-specific.

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