



R. & N. Bowers

SOUTHWESTERN WILLOW FLYCATCHER SURVEYS, DEMOGRAPHY, AND ECOLOGY ALONG THE LOWER COLORADO RIVER AND TRIBUTARIES, 2003 and 2004

Contract No. 03-CS-30-0093

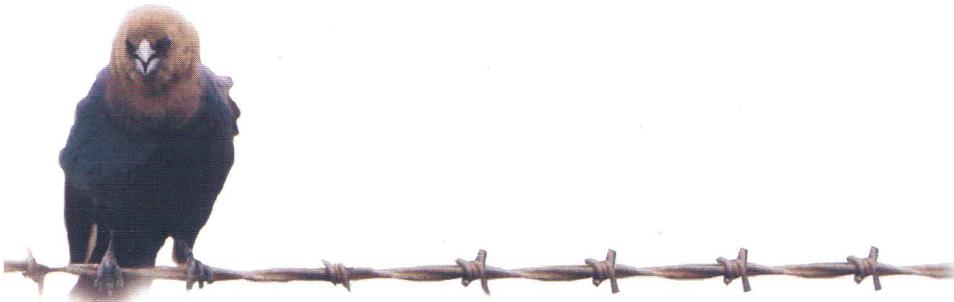
Addendum



Submitted to
U.S. Bureau of Reclamation
Lower Colorado Region
400 Railroad Avenue
Boulder City, NV 89005

Submitted by
SWCA
Environmental Consultants
114 N. San Francisco Street
Suite 100
Flagstaff, Arizona
86001

March 2005



**SOUTHWESTERN WILLOW FLYCATCHER SURVEYS, DEMOGRAPHY, AND
ECOLOGY ALONG THE LOWER COLORADO RIVER AND TRIBUTARIES,
2003 and 2004**

Contract # 03-CS-30-0093

Addendum

Submitted to

U.S. BUREAU OF RECLAMATION

Lower Colorado Region
400 Railroad Avenue
Boulder City, NV 89005

Submitted by

Mary Anne McLeod
Thomas J. Koronkiewicz
Bryan T. Brown
Steven W. Carothers

SWCA ENVIRONMENTAL CONSULTANTS

114 N. San Francisco St., Suite 100
Flagstaff, Arizona 86001
(928) 774-5500

March 21, 2005

This page intentionally left blank.

Recommended citation:

McLeod, M.A., T.J. Koronkiewicz, B.T. Brown, and S.W. Carothers. 2005. Southwestern Willow Flycatcher surveys, demography, and ecology along the lower Colorado River and tributaries, 2003 and 2004. Addendum submitted to U.S. Bureau of Reclamation, Boulder City, NV, by SWCA Environmental Consultants, Flagstaff, AZ. 11 pp.

This page intentionally left blank.

TABLE OF CONTENTS

Preface.....	VII
CHAPTER 3 ADDENDUM, 2003 AND 2004. COLOR-BANDING AND RESIGHTING ..	8
NUMBER OF UNBANDED FLEDGLINGS	1
CHAPTER 4 REPLACEMENT, 2003. NEST MONITORING.....	2
INTRODUCTION	2
METHODS	2
RESULTS	3
Nest Monitoring.....	3
Nest Failure.....	4
Brood Parasitism.....	5
Mayfield Nest Success and Nest Productivity	5
DISCUSSION	7
Nest Success.....	7
Brood Parasitism.....	8
Mayfield Nest Success and Nest Productivity	8

List of Tables

3.1. Fates of banded nestlings and number of unbanded fledges at the life history sites and Bill Williams, 2003.....	1
3.2. Fates of banded nestlings and number of unbanded fledges at the life history sites and Bill Williams, 2004.....	1
4.1. Summary of willow flycatcher nest monitoring results at the four life history study areas and Bill Williams, 2003.	4
4.2. Summary of willow flycatcher nest failure at the four life history study areas and Bill Williams, 2003.	4
4.3. Summary of fates of willow flycatcher nests parasitized by Brown-headed Cowbirds, 2003.....	5
4.4. Daily survival rates and Mayfield survival probabilities (MSP) for willow flycatcher nest stages at the four life history study areas and Bill Williams in 2003..	6

This page intentionally left blank.

PREFACE

This addendum provides revised and updated information for Southwestern Willow Flycatcher studies completed in 2003 and 2004 along the lower Colorado River and its tributaries by SWCA[®] Environmental Consultants (SWCA) under Contract # 03-CS-30-0093 with the U.S. Bureau of Reclamation (USBR). The chapter numbers in this addendum correspond with the chapter numbers in the 2003 and 2004 annual reports previously submitted by SWCA to USBR.

We present supplemental material in Chapter 3 regarding the fate of banded nestlings and the number of unbanded fledges in 2003 and 2004. Chapter 4 in this addendum replaces Chapter 4 of the 2003 annual report. In the original report we were inconsistent in reporting the number of fledglings. In most cases we reported the number of fledglings that were actually observed. In the case of a few nests, we reported the number of fledglings that were suspected, based on the number observed and additional fledglings heard, or on the behavior of the adults. This revised chapter reports only the number of fledglings visually confirmed, and thus presents a more conservative estimate of nest success. In the 2004 annual report, we consistently reported only the number of fledglings visually confirmed, and revisions to the 2004 data are not needed.

This page intentionally left blank.

COLOR-BANDING AND RESIGHTING

NUMBER OF UNBANDED FLEDGLINGS

We have previously reported the number of nestlings banded at each study area (Chapter 3) as well as the number of young fledged at each study area (Chapter 4). However, we have not reported the number of banded nestlings that were known to have fledged or the number of unbanded fledges. Some banded nestlings were known to have died before fledging, and the fate of others was unknown. Other young fledged without being banded, either because the nest was too high to reach or because some nestlings were underdeveloped relative to their siblings and were too small to retain bands at the time the other nestlings were banded. A simple comparison of the number of banded nestlings to the number of fledglings may produce erroneous conclusions; e.g., 18 nestlings were banded at Mesquite West in 2003, and 16 young were known to have fledged. The most obvious assumption is that 2 of the nestlings died and all 16 that fledged were banded. However, two of the banded nestlings were known to have died, two had unknown fates, and two fledglings were unbanded. To clarify these ambiguities, we present the details of banded and unbanded fledges for 2003 and 2004 in Tables 3.1 and 3.2, respectively.

Table 3.1. Fates of banded nestlings and number of unbanded fledges at the life history sites and Bill Williams, 2003.

Study Area ¹	Nestlings Banded	Banded Nestlings			Unbanded Fledglings	Total Confirmed Fledglings
		Known to Have Died	Fate Unknown	Known to Have Fledged		
PAHR	22	0	3	19	5	24
MESQ	18	2	2	14	2	16
MOME	1	1	0	0	0	0
TOPO	16	0	5	11	2	13
BIWI	6	3	3	3	0	3
Total	63	3	13	47	9	56

¹ PAHR = Pahrnagat National Wildlife Refuge, MESQ = Mesquite, MOME = Mormon Mesa, TOPO = Topock Marsh, BIWI = Bill Williams National Wildlife Refuge

Table 3.2. Fates of banded nestlings and number of unbanded fledges at the life history sites and Bill Williams, 2004.

Study Area ¹	Nestlings Banded	Banded Nestlings			Unbanded Fledglings	Total Confirmed Fledglings
		Known to Have Died	Fate Unknown	Known to Have Fledged		
PAHR	30	3	0	27	8	35
LIFI	2	0	0	2	0	2
MESQ	14	3	0	11	0	11
MOME	8	2	0	6	0	6
GRCA	3	0	3	0	0	0
TOPO	32	1	10	21	4	25
Total	89	9	13	67	12	79

¹ PAHR = Pahrnagat National Wildlife Refuge, LIFI = Littlefield, MESQ = Mesquite, MOME = Mormon Mesa, GRCA = Grand Canyon, TOPO = Topock Marsh

NEST MONITORING

INTRODUCTION

Documentation of nest success and productivity is critical to understanding local population status and demographic patterns of the Southwestern Willow Flycatcher. In 2003, at all sites where willow flycatcher breeding activity was suspected, we conducted intensive nest searches and nest monitoring. Specific objectives of nest monitoring included identifying breeding individuals (see color-banding, Chapter 3) for subsequent fecundity studies, calculating nest success and failure, documenting causes of nest failure (e.g., abandonment, desertion, depredation, and brood parasitism), and calculating nest productivity. Nest monitoring results from 2003 were compared with those at the study areas in previous years (McKernan and Braden 1998–2001). Although aspects of willow flycatcher breeding ecology can vary widely across its broad geographical and elevational ranges throughout the Southwest (Whitfield et al. 2003), we compared monitoring results with range-wide data to identify specific variables that may contribute to the characterization of flycatcher breeding ecology throughout the lower Colorado and Virgin River riparian systems.

METHODS

Upon locating territorial willow flycatchers, regardless of whether a possible mate was observed, we conducted intensive nest searches following the methods of Rourke et al. (1999). Nest monitoring followed the methods described by Rourke et al. (1999) and a modification of the Breeding Biology Research and Monitoring Database (BBIRD) protocol by Martin et al. (1997).

Nests were located primarily by observing adult flycatchers return to a nest or by systematically searching suspected nest sites. Nests were monitored every two to four days after nest building was complete and incubation was confirmed. During incubation and after hatching, nest contents were observed directly using a telescoping mirror pole to determine nest contents and transition dates. Nest monitoring during nest building and egg laying stages was limited to reduce any chance of abandonment during these periods. To reduce the risk of depredation (Martin et al. 1997), brood parasitism by the Brown-headed Cowbird, and premature fledging of young (Rourke et al. 1999), we observed nests from a distance with binoculars once the number and age of nestlings were confirmed. If no activity was observed at a previously occupied nest, the nest was checked directly to determine nest contents and cause of failure. If no activity was observed at a nest close to or on the estimated fledge date, we conducted a systematic search of the area to locate possible fledglings.

We considered a willow flycatcher nest successful only if fledglings were observed near the nest or in surrounding areas. The number of young fledged from each nest was counted based on the number of fledglings actually observed and thus is a conservative estimate. We considered a nest to have failed if (1) the nest was found empty or destroyed more than two days prior to the

estimated fledge date (depredated); (2) the nest fledged no willow flycatcher young, but contained Brown-headed Cowbird eggs or young (parasitized); (3) the nest was deserted with eggs remaining (deserted); (4) the nest was abandoned prior to egg laying (abandoned); (5) the nest was destroyed due to weather (weather); or (6) the entire clutch was incubated for an excess of 20 days (infertile/ addled).

During each nest check, we recorded date and time of the visit, observer initials, monitoring method (observation via binoculars or mirror pole), nesting stage, nest contents, and number and behavior of adults and/or fledges present onto standardized data forms (Appendix A) that included the nest or territory number and UTM coordinates. We calculated flycatcher nest success using both simple nesting success (number of successful nests/total number of nests) and the Mayfield method (Mayfield 1961, 1975), which calculates daily nest survival to account for nests that failed before they were found. We assumed one egg was laid per day, and incubation was considered to start the day the last egg was laid (per Martin et al. 1997). The nestling period was considered to start the day the first egg hatched and end the day the first nestling fledged. If exact transition dates were unknown, we estimated the transition date as halfway between observations. To calculate Mayfield survival probabilities (MSP), we used 2.6, 12, and 12.5 days as the length of the egg laying, incubation, and nestling stages, respectively (per Rourke et al. 1999). We also calculated the average number of days in each nest stage using nests where transition dates were known. These averages are presented below, but we did not use these numbers in calculating MSP because of low sample size and possible year-to-year variability. Average length of each nest stage at the Virgin and lower Colorado River study areas may be used to calculate MSP in future years when additional data on stage lengths are available from subsequent years of study. Nest productivity was calculated as number of young fledged per nesting attempt. Only willow flycatcher nests that contained at least one flycatcher egg were used in calculating nest success and productivity. Fecundity was calculated as number of young produced per female over the breeding season.

RESULTS

NEST MONITORING

We documented 57 willow flycatcher nesting attempts at the four life history study areas and Bill Williams, 50 of which contained eggs and were used in calculating nest success and productivity. Twenty-six (52%) nests were successful and fledged young, 23 (46%) failed, and the fate of 1 (2%) nest was undetermined (Table 4.1). Thirty-nine females were followed through all of their nesting attempts. Of the 37 females who produced at least one egg, 26 had one nesting attempt, 10 had two nesting attempts, and 1 had three nesting attempts. Of the 11 females who had multiple nesting attempts, 4 renested after successfully fledging young, and 7 renested after unsuccessful nests.

NEST FAILURE

Depredation was the major cause of nest failure, accounting for 57% of all failed nests (Table 4.2) and 74% of nests that failed after flycatcher eggs were laid. Six nesting attempts (20%) were abandoned prior to willow flycatcher eggs being laid and four (13%) were deserted after 13 or 14 days incubation. Cause of failure could not be determined at three nests (10%). No nests failed because of weather.

Table 4.1. Summary of willow flycatcher nest monitoring results at the four life history study areas and Bill Williams, 2003. Only nests with at least one flycatcher egg were used in calculations.

Study area	Site	Pairs	Nests	Successful nests (%)	Failed nests (%)	Nests with unknown fate (%)	Parasitized nests (%)
Pahrnagat	Pahrnagat North	7	10	9 (90%)	1 (10%)	0	0
	Pahrnagat South	1	1	1 (100%)	0	0	0
	Total	8	11	10 (91%)	1 (9%)	0	0
Mesquite	Mesquite West	13	18	7 (39%)	10 (56%)	1(5%)	4 (22%)
	Total	13	18	7 (39%)	10 (56%)	1(5%)	4 (22%)
Mormon Mesa	Mormon Mesa North	3	4	0	4 (100%)	0	1 (50%)
	Virgin River #1 North	3	4	0	4 (100%)	0	0
	Virgin River Delta #4	2	2	0	2 (100%)	0	0
	Total	8	10	0	10 (100%)	0	1 (10%)
Topock	In Between	6	6	4 (67%)	2 (33%)	0	1 (17%)
	800M	2	2	2 (100%)	0	0	0
	Glory Hole	1	1	1 (100%)	0	0	1 (100%)
	Total	9	9	7 (78%)	2 (22%)	0	2 (22%)
Bill Williams	Site 3	3	2	2 (100%)	0	0	0
	Total	3	2	2 (100%)	0	0	0
Overall Total		41	50	26 (52%)	23 (46%)	1 (2%)	7 (14%)

Table 4.2. Summary of willow flycatcher nest failure at the four life history study areas and Bill Williams, 2003. All nesting attempts are included.

Study area	Total # of Nests	Depredated	Deserted	Abandoned	Infertile/ Addled Eggs	Unknown
Pahrnagat	12	1	0	1	0	0
Mesquite	19	7	3 ^a	0	0	1 ^b
Mormon Mesa	13	9	0	3 ^c	0	1 ^d
Topock	11	0	1 ^a	2	0	1 ^e
Bill Williams	2	0	0	0	0	0
Totals All Sites	57	17	4	6	0	3

^aAll nests deserted after 13 or 14 days incubation.

^bNest abandoned during building or depredated during egg-laying.

^cOne nest was abandoned with one cowbird egg in the nest.

^dNest probably depredated during incubation, but nest was too high to mirror pole to confirm fate.

^eNest unattended when found with one flycatcher egg and one cowbird egg.

BROOD PARASITISM

Seven of 50 nests (14%) with flycatcher eggs were brood parasitized by Brown-headed Cowbirds (Table 4.1). Parasitism may have resulted in nest desertion at one nest at Topock that was first discovered unattended with one flycatcher egg and one cowbird egg. One additional flycatcher nest at Mormon Mesa was abandoned prior to egg laying after being parasitized. Only one nestling mortality at Topock could potentially be attributed to brood parasitism (Table 4.3). Brood parasitism at all sites ranged from 0 to 22% and was highest at Mesquite and Topock.

Table 4.3. Summary of fates of willow flycatcher nests parasitized by Brown-headed Cowbirds, 2003.

Study area	Parasitized Nests	Outcome
Mesquite	4	2–depredated; 1–deserted after 13 days incubation (1 flycatcher egg, 1 cowbird egg); 1– cowbird nestling disappeared at four days of age, fledged flycatcher nestling (two flycatcher eggs addled/infertile)
Mormon Mesa	2	1–depredated; 1–abandoned with one cowbird egg before flycatcher eggs were laid
Topock	2	1–nest unattended when found with one cowbird egg and one flycatcher egg; 1–fledged cowbird and flycatcher nestling, another flycatcher nestling disappeared before fledge date

MAYFIELD NEST SUCCESS AND NEST PRODUCTIVITY

MSP at the four life history study areas and Bill Williams ranged from 6 to 100% and was 56% for all sites combined (Table 4.4). At all sites, 56 nestlings were confirmed to have fledged from 50 nests (mean number of nestlings/nest=1.12, SE=0.18; Table 4.5). This total does not include at least two additional fledglings that were detected at Topock, where a re-nest of a color-banded female was suspected but never found. Fecundity ranged from 0.0 to 3.00 young per female and averaged 1.40 across all study sites (Table 4.5).

Table 4.4. Daily survival rates and Mayfield survival probabilities (MSP) for willow flycatcher nest stages at the four life history study areas and Bill Williams in 2003. Mayfield survival probability was calculated using 2.6-day egg laying, 12-day incubation, and 12.5-day nestling stages.

Study Area	Nest Stage ¹	Nest Losses/ Observation Days	Daily Survival Rate	Mayfield Survival Probability
Pahranagat	1	0/22	1.000	1.000
	2	1/112	0.991	0.898
	3	0/139	1.000	1.000
MSP all stages = 0.898				
Mesquite	1	2/32	0.938	0.846
	2	5/201	0.975	0.739
	3	3/120	0.975	0.728
MSP all stages = 0.454				
Mormon Mesa	1	0/18	1.000	1.000
	2	7/81	0.913	0.336
	3	3/24	0.875	0.188
MSP all stages = 0.063				
Topock	1	0/13	1.000	1.000
	2	1/99	0.990	0.885
	3	0/96	1.000	1.000
MSP all stages = 0.885				
Bill Williams	1	0/2	1.000	1.000
	2	0/12	1.000	1.000
	3	0/22	1.000	1.000
MSP all stages = 1.000				
Totals All Sites	1	2/87	0.977	0.941
	2	14/504	0.972	0.713
	3	6/401	0.985	0.828
MSP all stages = 0.556				

¹Nest Stages: 1=egg laying, 2=incubation, 3=nestling

Table 4.5. Willow flycatcher nest productivity and fecundity at the four life history study areas and Bill Williams, 2003.

Site	Young Fledged (Total # Nests)	Mean # of Young Fledged/Nest	Fecundity (Young Fledged per Female)
Pahranagat	24 (11)	2.18 (SE=0.35)	3.00 (SE=0.42)
Mesquite	16 (18)	0.89 (SE=0.30)	1.23 (SE=0.51)
Mormon Mesa	0 (10)	0.00	0.00
Topock	13 (9)	1.44 (SE=0.34)	1.44 (SE=0.34)
Bill Williams	3 (2)	1.50 (SE=0.50)	1.00 (SE=0.58)
Totals All Sites	56* (50)	1.12 (SE=0.18)	1.40 (SE=0.25)

*=Total does not include at least two additional fledglings detected where a re-nest was suspected but never found.

DISCUSSION

NEST SUCCESS

Nest success at Pahrnagat (91%) was the highest recorded at the site since monitoring began there in 1998, with 37, 56, 52, and 33% nest success recorded at the site in 1998 to 2001, respectively (McKernan and Braden 2002). Nest success at Mesquite West (39%) differed little from results recorded at the site in previous years, with 56 and 47% nest success recorded in 2000 and 2001, respectively. Topock showed an increase in nest success (78%), rebounding from a continuous downward trend recorded in 1997 to 2001 (78, 43, 35, 28, and 25%, respectively). Nest success at Bill Williams in 2003 was high (100%), consistent with results reported from 2000 (100%; Paradzick et al. 2001), 2001 (60%; Smith et al. 2002), and 2002 (50%; Smith et al. 2003). Nest success at Mormon Mesa (0%) was the lowest recorded since monitoring began at that study area in 1997, with a downward trend recorded in 1997 to 2001 (100, 55, 50, 31, and 35%, respectively).

Of 10 flycatchers exhibiting between-year, between-site movements (see Chapter 3), 7 moved approximately 40 km from Mormon Mesa to Mesquite West. A continual downward trend in nest success combined with the relatively high degree of flycatcher emigration and little immigration is highly suggestive that the Mormon Mesa study area may be a population sink. However, differences in nest success among study areas and the annual fluctuations of nest success at sites are difficult to interpret as it has been shown that demographic patterns of passerine populations often vary year to year, and sometimes to a very large degree (Wiens 1989a). Factors driving the continual downward trend in flycatcher nest success at Mormon Mesa are unidentified at this time. The different patterns of nest success observed at the study areas reinforce the variability of the demographic traits of the willow flycatcher and further demonstrate the need for long-term data.

Depredation was the major cause of willow flycatcher nest failure in 2003, accounting for 57% of all failed nests at the four life history study areas and Bill Williams. These results are consistent with those reported at the life history study areas from 1997 to 2001 (McKernan and Braden 2002) and with all monitored sites in Arizona from 2000 to 2002 (Paradzick et al. 2001, Smith et al. 2002, 2003), with depredation accounting for the majority of all willow flycatcher nest failures. Nest depredation at Pahrnagat in 2003 (9%) was the lowest since monitoring began there in 1998, with 63, 31, 19, and 44% nest depredation recorded at the site in 1998 to 2001, respectively. Nest depredation at Mesquite West has increased since monitoring began there in 2000, with 22, 32, and 39% nest depredation recorded at the site in 2000, 2001, and 2003, respectively. In 2003, Topock exhibited the lowest rate of nest depredation (0%) since monitoring began there in 1997, with 11, 33, 55, 44, and 35% nest depredation recorded at the site in 1997 to 2001 (McKernan and Braden 2002). Bill Williams exhibited 0% nest depredation for the fourth consecutive year since year 2000 (Paradzick et al. 2001, Smith et al. 2002, 2003). Over half (53%) of all depredated nests at the four life history study areas in 2003 were documented at Mormon Mesa, with nest depredation accounting for 90% of all nest failures at the site. Nest depredation at Mormon Mesa in 2003 was the highest since monitoring began there in 1997, with 0, 36, 31, 31, and 30% recorded at the site in 1997 to 2001, respectively (McKernan and Braden 2002). Factors influencing the sharp increase in nest depredation at the

Mormon Mesa site and decreases in nest depredation at Pahranaagat and Topock in 2003 are inherently complex and at this time remain undetermined. However, the large variation in nest depredation rates we observed among study areas in 2003 (0 to 90%) and the annual fluctuations in nest depredation recorded at the sites since 1998 (McKernan and Braden 2002) are not unusual for open cup nesting species. For open cup nesting passerines, it has been shown that nest depredation rates can vary year to year, and sometimes substantially, with depredation of eggs and young ultimately linked to fluctuations in predator densities, abundance, and richness (Howlett and Stutchbury 1996, Robinson 1992, Wiens 1989b). As direct observations of nest predation events are rare during nest monitoring, studies specifically designed to address willow flycatcher nest predator management strategies are therefore warranted.

BROOD PARASITISM

Brood parasitism by Brown-headed Cowbirds at the four life history study areas and Bill Williams ranged from 0 to 22% in 2003. One nest abandonment, one desertion, and one nestling mortality were potentially associated with parasitism. These results are consistent with those reported from 1998 to 2001, with brood parasitism averaging 10, 19, 23, 22 and 20% for Pahranaagat, Mesquite, Mormon Mesa, Topock and the Bill Williams, respectively (Paradzick et al. 2001, McKernan and Braden 2002, Smith et al. 2002). Because the incidence of brood parasitism reported for the willow flycatcher is highly variable, ranging from less than 10% at some sites to over 60% at others (Sedgwick 2000), 2003 results are difficult to interpret. However, our results indicate a minimal effect of brood parasitism on reproductive output of flycatchers at the life history study areas in 2003. Because it is still unclear how brood parasitism rates affect flycatcher population sizes (Rothstein et al. 2003), baseline nesting studies need to be continued to determine whether brood parasitism presents a serious problem for populations at the life history study areas.

MAYFIELD NEST SUCCESS AND NEST PRODUCTIVITY

Comparing MSP with those from previous years is somewhat problematic because of differences in methods. Average lengths of the egg laying, incubation, and nestling stages used to calculate MSP at the study areas in previous years were 2, 14, and 13 days, respectively (McKernan and Braden 2002), and were calculated assuming that incubation commenced with the penultimate egg. We used the average lengths of the nest stages (2.6, 12, and 12.5 days, respectively) reported in Rourke et al. (1999), which were calculated assuming incubation commenced with the final egg, as recommended by Martin et al. (1997). These differences in methods may result in differences in overall MSP of few percentage points. Therefore, MSP should be used to evaluate broad trends and not fine-scale differences between years.

MSP at the four life history study areas and Bill Williams (56%) differed little from results reported in previous years, with an average MSP of 44.3% reported from 1997 to 2001 across the four life history sites (McKernan and Braden 2002). MSP in 2003 was also within the range of MSP values reported for all monitored sites in Arizona, with an MSP of 55.0, 64.6 and 28.4% reported for 2000–2002, respectively (Paradzick et al. 2001, Smith et al. 2002 and 2003). Except for Mormon Mesa in 2003, we observed an increase in MSP at each of the study areas compared to previous years, with Pahranaagat and Topock exhibiting the greatest increases.

Chapter 4 Replacement, 2003

MSP at Pahrnagat averaged 48.1% from 1997 to 2001 and was 89.8% in 2003, while Topock went from an average MSP of 33.3% in 1997–2001 to 88.5% in 2003. However, these increases in MSP must be interpreted cautiously because annual MSP are unavailable for each of the life history study areas prior to 2003, and we are therefore unable to assess annual variation in MSP.

MSP in 2003 for the egg laying (94.1%), incubation (71.3%), and nestling stages (82.8%) also differed little from results reported in previous years, with an MSP of 75.0, 72.0, and 82% for the egg laying, incubation, and nestling stages, respectively, reported at the four life history study areas from 1997 to 2001 (data not available for Bill Williams).

Nest productivity at all sites ranged from 0 to 2.55 young per nest. Nest productivity for all sites combined was 1.30 young per nest. These results are consistent with those at monitored sites in Arizona, with nest productivity reported at 0.50, 1.66, and 1.02 young per nest from 2000 to 2002, respectively (Paradzick et al. 2001, Smith et al. 2002, 2003). Fecundity at all sites ranged from 0.0 to 3.50 and averaged 1.63. From 1996 to 2001, fecundity at the life history study areas and the Grand Canyon averaged 1.27 (SE=0.52) (McKernan and Braden 2002). As stated above, the demographic traits of the willow flycatcher are highly variable and difficult to interpret based on limited data.