

CHAPTER 4

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 2004, 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 Chapter 3, Color-banding and Resighting) 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 2004 were compared with those at the study areas from 1996 to 2003 (McKernan 1997; McKernan and Braden 1998, 1999, 2001a, 2001b, 2002; Koronkiewicz et al. 2004; Braden and McKernan, unpubl. data). 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 the 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 abandoned prior to egg laying (abandoned); (2) the nest was deserted with flycatcher eggs or young remaining (deserted); (3) the nest was found empty or destroyed more than two days prior to the estimated fledge date (depredated); (4) the nest was destroyed due to weather (weather); or (5) the entire clutch was incubated for an excess of 20 days (infertile/addled). For nests containing flycatcher eggs, parasitism was considered the cause of nest failure if (1) cowbird young outlived any flycatcher eggs or young, or (2) the nest was parasitized during egg laying and the disappearance of flycatcher eggs coincided with the appearance of cowbird eggs.

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 or dates of depredation events were unknown, we estimated the transition date as halfway between observations. To calculate Mayfield survival probabilities (MSP), we used the average length of each nest stage (2.22, 12.65, and 13.65 days for laying, incubation, and nestling stages, respectively) as observed in this study in 2003 and 2004 for nests where transition dates were known. Nest productivity was calculated as the 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 91 willow flycatcher nesting attempts at the four life history study areas, Littlefield, and Grand Canyon; 81 of these nests were known to contain flycatcher eggs and were used in calculating nest success and productivity. Thirty-eight (47%) nests were successful and fledged young, and 41 (51%) failed. The fates of two nests (2 %) were undetermined (Table 4.1). In these two cases, field personnel heard vocalizations suspected to be fledglings begging, but no fledglings could be visually confirmed. Nest success ranged from 24% at Mesquite to 76% at Pahrangat. For a comparison of nest success at all monitoring sites from 1998 to 2004, see Table 4.2.

Sixty-two nesting females were followed through all of their nesting attempts; sixty of these females produced at least one egg each. Two additional females were detected for which no nesting attempt could be confirmed. Of the 62 nesting females, 38 had one nesting attempt, 19 had two nesting attempts, and 5 had three nesting attempts. Of the 24 females who had multiple nesting attempts, 4 renested after successfully fledging young, and 20 renested after unsuccessful nests.

Table 4.1. Summary of Willow Flycatcher Nest Monitoring Results at the Four Life History Study Areas, Grand Canyon, AZ, and Littlefield, AZ, in 2004*

Study Area ¹	Site	# Pairs	# Nests	# Nests with 1+ WE ²	# Successful Nests (%)	# Failed Nests (%)	# Nests with Unknown Fate ³	# Parasitized Nests ⁴ (%)
PAHR	Pahrnagat North	13	15	15	12 (80%)	3 (20%)	0	0
	Pahrnagat South	1	2	2	1 (50%)	1 (50%)	0	0
	Total	14	17	17	13 (76%)	4 (24%)	0	0
LIFI	North	1	3	2	1 (50%)	1 (50%)	0	0
	Total	1	3	2	1 (50%)	1 (50%)	0	0
MESQ	Mesquite West	12	20	17	4 (24%)	13 (76%)	0	8 (47%)
	Total	12	20	17	4 (24%)	13 (76%)	0	8 (47%)
MOME	Mormon Mesa North	1	1	1	1 (100%)	0	0	0
	Virgin River #1 North	4	5	4	1 (25%)	3 (75%)	0	1 (25%)
	Delta West	2	1	1	1 (100%)	0	0	0
	Total	7	7	6	3 (50%)	3 (50%)	0	1 (17%)
GRCA	RM 274.5	1	1	1	0	0	1 (100%)	0
	Total	1	1	1	0	0	1 (100%)	0
TOPO	Pipes 3	3	5	4	1 (25%)	3 (75%)	0	2 (50%)
	PC6-1	4	6	5	1 (20%)	4 (80%)	0	2 (40%)
	Pig Hole	1	1	1	1 (100%)	0	0	0
	In Between	8	15	14	6 (43%)	8 (57%)	0	4 (29%)
	800M	2	3	3	2 (67%)	1 (33%)	0	0
	Pierced Egg	2	2	2	2 (100%)	0	0	0
	250M	1	1	1	1 (100%)	0	0	1 (100%)
	Hell Bird	3	3	2	1 (67%)	1 (33%)	0	1 (50%)
	Glory Hole	5	7	6	2 (33%)	3 (50%)	1 (17%)	2 (33%)
Total	29	43	38	17 (45%)	20 (53%)	1 (2%)	12 (32%)	
Overall Total		64	91	81	38 (47%)	41 (51%)	2 (2%)	21 (26%)

* Only nests with at least one flycatcher egg were used in percentage calculations.

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

² WE = willow flycatcher egg.

³ No fledglings were visually located but nests are suspected to have fledged.

⁴ Parasitized nests include all nests that contained at least one flycatcher egg and one cowbird egg, regardless of nest fate. Nests that contained at least one cowbird egg but no flycatcher eggs are addressed under Brood Parasitism later in this chapter.

Table 4.2. Willow Flycatcher Percent Nest Success Recorded at Breeding Sites along the Virgin and Lower Colorado Rivers from 1997 to 2004*

Year	Pahrnagat (# nests)	Littlefield (# nests)	Mesquite ¹ (# nests)	Mormon Mesa ² (# nests)	Grand Canyon (# nests)	Topock (# nests)	Bill Williams (# nests)
1996	Nm ³	Nm ³	Nm ³	Nm ³	57 (7)	100 (1)	Nm ³
1997	Nm ³	Nd ⁴	40 (5)	38 (16)	29 (14)	78 (9)	Nd ⁴
1998	37 (19)	Nd ⁴	0 (7)	58 (13)	Nd ⁴	43 (21)	Nd ⁴
1999	56 (16)	Ns ⁵	Nm ³	50 (12)	Nc ⁶	35 (20)	Nd ⁴
2000	52 (21)	Nd ⁴	56 (9)	31 (16)	Nc ⁶	28 (18)	100 ⁷ (1)
2001	33 (27)	Nd ⁴	47 (19)	35 (20)	nc ⁸	25 (20)	60 ⁷ (5)
2002	29 (21)	Nd ⁴	53 (19)	0 (10)	Nd ⁴	25 (12)	50 ⁷ (11)
2003	91 (11)	Nd ⁴	44 (18)	0 (10)	Nd ⁴	78 (9)	100 (2)
2004	76 (17)	50 (2)	24 (17)	50 (6)	bc ⁹	45 (38)	Nd ⁴

* Data from 1997 to 2002 are from McKernan 1997, McKernan and Braden (2002), and Braden and McKernan (unpubl. data) unless noted otherwise; data from 2003 are from Koronkiewicz et al. (2004); data from 2004 can be found in this document. Total number of nests is indicated in parentheses.

¹ Study area includes both the Mesquite East and West sites.

² Study area includes the Virgin River Delta at Lake Mead.

³ Study area not monitored.

⁴ Study area surveyed, no breeding documented.

⁵ Study area not surveyed.

⁶ Breeding suspected, nest success not calculated.

⁷ Nest success calculated by Paradzick et al. (2001), and Smith et al. (2002, 2003).

⁸ Breeding confirmed, nest success not calculated.

⁹ Breeding confirmed, undetermined if nestlings from a single nest fledged.

NEST FAILURE

Depredation was the major cause of nest failure, accounting for 47% (24 of 51) of all failed nests (Table 4.3) and 59% (24 of 41) of nests that failed after flycatcher eggs were laid.

Table 4.3. Summary of Causes of Willow Flycatcher Nest Failure at the Four Life History Study Areas, Grand Canyon, AZ, and Littlefield, AZ, in 2004*

Study Area ¹	Total # Nests	All Failed Nests	Abandoned (% failed nests)	Deserted (% failed nests)	Depredated (% failed nests)	Parasitized (% failed nests)	Unknown (% failed nests)
PAHR	17	4	0 (0%)	0 (0%)	3 (75%)	0 (0%)	1 ² (25%)
LIFI	3	2	1 (50%)	0 (0%)	1 (50%)	0 (0%)	0 (0%)
MESQ	20	16	2 ³ (13%)	4 ⁴ (25%)	3 (19%)	5 (31%)	2 ⁵ (13%)
MOME	7	4	1 ³ (25%)	0 (0%)	3 (75%)	0 (0%)	0 (0%)
GRCA	1	0	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
TOPO	43	25	5 ³ (20%)	1 ⁶ (4%)	14 (56%)	4 (16%)	1 ⁷ (4%)
Total	91	51	9 (18%)	5 (10)	24 (47%)	9 (18%)	4 (8%)

* All nesting attempts (those with and without flycatcher eggs) are included.

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

² Nest probably depredated during incubation, but nest was too high to mirror pole to confirm fate.

³ One nest abandoned after being parasitized.

⁴ One nest deserted with one flycatcher egg and one cowbird egg; one nest deserted with a flycatcher egg that appeared addled (discolored) and chipped; one nest deserted with nestlings in the nest, female not detected post desertion; one nest female built over eggs and reused nest structure after nest was parasitized.

⁵ One nest found on ground with shell fragments nearby; unknown if cowbird or flycatcher egg fragments. One nest parasitized after 6 days of incubation; remaining flycatcher egg failed to hatch after 14 days of incubation, then disappeared; nest subsequently deserted with one cowbird egg remaining.

⁶ Nest deserted with one flycatcher egg and one cowbird egg.

⁷ Nest contained a dead nestling.

Nine nesting attempts (17% of all failed nests) were abandoned prior to willow flycatcher eggs being laid and five nests (10%) were deserted. Nine nests (18%) failed because of Brown-headed Cowbird parasitism (see below for more details on parasitism). Cause of failure could not be determined at four nests (8%). No nests failed because of weather or infertile/addled eggs.

BROOD PARASITISM

Twenty-one of 81 nests (26%) with flycatcher eggs were brood parasitized by Brown-headed Cowbirds. An additional three nests (one each at Mesquite, Mormon Mesa, and Topock) were parasitized prior to flycatcher eggs being laid and were subsequently abandoned (Tables 4.3 and 4.4). For nests containing flycatcher eggs, parasitism caused nest failure at nine nests. Five of these fledged cowbird young, and four instances of parasitism coincided with the disappearance of any flycatcher eggs in the nest. Three nesting attempts were deserted with flycatcher and cowbird eggs in the nest; in one of these instances, the female built over the eggs and reused the nest structure. Four nests were depredated with both flycatcher and cowbird eggs or young in the nest. Three parasitized nests fledged flycatchers but no cowbirds, and one nest fledged two flycatchers and one cowbird. The cause of failure at one nest was undetermined. Brood parasitism at all sites ranged from 0 to 47% and was highest at Mesquite (Table 4.1). Nests that contained flycatcher eggs and were brood parasitized were less likely to fledge flycatcher young than nests that were not parasitized (Chi-square = 8.87, $P = 0.003$).

Table 4.4. Fates of Willow Flycatcher Nests Parasitized by Brown-Headed Cowbirds, 2004*

Study Area	Nest ID Code	Outcome
MESQ	1A	Fledged a cowbird
	1B	Parasitized (one flycatcher egg disappeared and cowbird egg appeared) after 6 days of incubation; remaining flycatcher egg failed to hatch after 14 days of incubation, then disappeared; nest subsequently deserted with one cowbird egg remaining
	2B	Fledged a cowbird
	3A	Deserted during egg laying with one flycatcher egg and one cowbird egg
	5A	Parasitized after one flycatcher egg was laid; flycatcher egg disappeared when cowbird egg appeared; nest abandoned
	5B	Abandoned with one cowbird egg before flycatcher eggs were laid
	9A	Parasitized after one flycatcher egg was laid; flycatcher egg found on ground when cowbird egg appeared; nest abandoned
	22A	Fledged a cowbird
	32A	Female built over one cowbird egg and one flycatcher egg and reused nest structure
MOME	10B	Abandoned with one cowbird egg before flycatcher eggs were laid
	32A	Fledged one flycatcher; cowbird nestling disappeared at approximately 7 days of age
TOPO	1A	Fledged one flycatcher; cowbird egg did not hatch
	9A	Fledged one cowbird and two flycatchers
	11C	Fledged a cowbird
	16A	One flycatcher egg disappeared from nest and another found on ground. Third egg disappeared when cowbird egg appeared.
	18A	Nest deserted with one flycatcher egg and one cowbird egg

Table 4.4. Fates of Willow Flycatcher Nests Parasitized by Brown-Headed Cowbirds, 2004*, continued

Study Area	Nest ID Code	Outcome
TOPO	22B	Depredated with one cowbird egg and one flycatcher egg
	23A	Depredated with one cowbird egg and two flycatcher eggs
	24B	Parasitized after two flycatcher eggs were laid; both eggs disappeared when cowbird egg appeared
	34A	Fledged a cowbird
	44A	Depredated with one flycatcher egg and one cowbird egg
	72B	Depredated with one dead cowbird nestling, one flycatcher nestling, and one flycatcher egg
	74A	Fledged one flycatcher; cowbird egg did not hatch
	77A	Abandoned with one cowbird egg before flycatcher eggs were laid

* All nesting attempts are included.

¹ MESQ = Mesquite, MOME = Mormon Mesa, TOPO = Topock Marsh.

MAYFIELD NEST SUCCESS AND NEST PRODUCTIVITY

Mayfield survival probability (MSP) at the four life history study areas and Littlefield ranged from 0.24 to 0.73 and was 0.44 for all sites combined (Table 4.5). At all sites, 79 nestlings were confirmed to have fledged from 79 nests of known outcome (mean number of nestlings/nest = 1.00, SE = 0.14). Fecundity across study areas ranged from 0.92 to 2.5 young per female and averaged 1.32 (SE = 0.18) (Table 4.6).

Table 4.5. Daily Survival Rates and Mayfield Survival Probabilities (MSP) for Willow Flycatcher Nest Stages at the Four Life History Study Areas, Littlefield, AZ, and Grand Canyon, AZ, in 2004*

Study Area	Nest Stage ¹	Nest Losses/ Observation Days	Daily Survival Rate	Mayfield Survival Probability
Pahranagat	1	0/32	1.000	1.000
	2	2/165	0.988	0.857
	3	2/165.5	0.988	0.847
	MSP all stages = 0.73			
Littlefield	1	0/5	1.000	1.000
	2	1/16	0.938	0.442
	3	0/11	1.000	1.000
	MSP all stages = 0.44			
Mesquite	1	5/30	0.833	0.667
	2	2/139.5	0.986	0.833
	3	5/84	0.940	0.433
	MSP all stages = 0.24			
Mormon Mesa	1	1/12	0.917	0.824
	2	1/56	0.982	0.796
	3	1/51	0.980	0.736
	MSP all stages = 0.50			

Table 4.5. Daily Survival Rates and Mayfield Survival Probabilities (MSP) for Willow Flycatcher Nest Stages at the Four Life History Study Areas, Grand Canyon, AZ, and Littlefield, AZ, in 2004*, continued

Study Area	Nest Stage ¹	Nest Losses/ Observation Days	Daily Survival Rate	Mayfield Survival Probability
Grand Canyon ²	1	0/2	1.000	1.000
	2	0/12	1.000	1.000
	3	--	--	--
Topock	1	4/39	0.897	0.786
	2	12/276.5	0.957	0.571
	3	4/259	0.985	0.809
	MSP all stages = 0.36			
TOTAL	1	10/120	0.917	0.824
	2	18/665	0.973	0.707
	3	12/570.5	0.979	0.748
	MSP all stages = 0.436			

* Mayfield survival probability was calculated using 2.22-day egg laying, 12.65-day incubation, and 13.65-day nestling stages.

¹ 1 = egg laying, 2 = incubation, 3 = nestling

² No values are given for the nestling stage or all stages combined because nest fate was undetermined.

Table 4.6. Willow Flycatcher Nest Productivity (Young Fledged per Nest) and Fecundity (Young Fledged per Female) at the Four Life History Study Areas and Littlefield, AZ, in 2004*

Study Area	# Young Fledged (# Nests)	Productivity Mean (SE)	Fecundity Mean (SE)
Pahrnagat	35 (17)	2.06 (0.34)	2.50 (0.47)
Littlefield	2 (2)	1.00 (1.00)	2.00 (1.48)
Mesquite	11 (17)	0.65 (0.30)	0.92 (0.40)
Mormon Mesa	6 (6)	1.00 (0.52)	1.00 (0.52)
Topock	25 (37)	0.68 (0.14)	0.93 (0.17)
Total	79 (79)	1.00 (0.14)	1.32 (0.18)

* Calculations include nests that contained flycatcher eggs and had a known outcome.

DISCUSSION

In 2004, willow flycatcher nesting was documented at the four life history study areas, Littlefield, and Grand Canyon. In 2003, nesting was documented at the four life history study areas and Bill Williams, and although surveys were conducted at Littlefield and Grand Canyon, no nesting was documented at either study area (Koronkiewicz et al. 2004). Although resident willow flycatchers were detected at Bill Williams in 2004, all were unpaired, non-breeding individuals (see Chapter 3). Flycatcher nesting at Littlefield this year is the first to be documented since surveys began in 1997, and nesting at Grand Canyon has not been recorded since 2001 (McKernan and Braden 2002). We recorded the highest number of nests to be

documented at Topock Marsh since monitoring began in 1997. The high number of nesting flycatchers recorded at Topock in 2004 compared to 2003 is the result of both improved coverage of survey areas and the presence of breeding flycatchers in areas that were surveyed and found to be unoccupied in 2003. Given that southwestern riparian ecosystems experience dynamic change and are not ecologically static (Periman and Kelly 2000), willow flycatcher occupancy and nesting are likely to be affected by changes in habitat suitability, with breeding flycatchers detected in one year and not in another. Between-year variability in flycatcher occupancy and breeding is also likely to be exhibited more at relatively small sites, such as those found in Grand Canyon, which appear to be more subject to ecological change.

NEST SUCCESS

As in 2003, Pahranaagat continued to exhibit high nest success in 2004, with 76% recorded in 2004 and 91% recorded in 2003 (see Table 4.2 for nest success at study areas from 1997–2004). Conversely, we recorded the lowest nest success at Mesquite since monitoring began in 1997, though success rate did not differ significantly from those recorded in 2000–2002 (Chi-square = 4.04, $P = 0.4$; small sample size in 1997–1998 precluded inclusion of these years in the analysis). At Mormon Mesa we observed few nesting attempts but the highest nest success (50%) since 1999. Nest success at Topock (45%) was in the middle of the range of success rates reported at the site since 1997. The increase in nest success at Mormon Mesa is of particular importance because no flycatchers have been reported to successfully fledge young at the site since 2001, and recent multi-year trends in low nest success and high emigration suggested that the site may be a population sink (Koronkiewicz et al. 2004). Nest success results at Mormon Mesa emphasize that the demographic patterns of passerine populations often vary year to year, and sometimes to a very large degree (Wiens 1989a). The different patterns of nest success observed at the study areas over many years reinforce the variability of the demographic traits of the willow flycatcher and further demonstrate the need for long-term data.

NEST FAILURE

Depredation was the major cause of willow flycatcher nest failure in 2004, accounting for 47% of all failed nests at the four life history study areas and Littlefield (Table 4.3). Depredation accounted for 75, 50, 19, 75, and 56% for all failed nests at Pahranaagat, Littlefield, Mesquite, Mormon Mesa and Topock, respectively. These results are consistent with those reported at the life history study areas from 1998 to 2003 (McKernan and Braden 2002; Koronkiewicz et al. 2004; Braden and McKernan, unpubl. data) and with monitored sites across Arizona from 2000 to 2003 (Paradzick et al. 2001; Smith et al. 2002, 2003, 2004), which report depredation as accounting for the majority of all willow flycatcher nest failures. Factors influencing the increases and decreases in nest depredation at the life history study areas are inherently complex and at this time remain undetermined. However, the large variation in nest depredation rates observed among the study areas over time 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 (Wiens 1989b, Robinson 1992, Howlett and Stutchbury 1996).

BROOD PARASITISM

Brood parasitism by Brown-headed Cowbirds across all study areas ranged from 0 to 47% and averaged 26% (Table 4.1). These results are consistent with those reported at the study areas from 1998 to 2003 (McKernan and Braden 2002; Koronkiewicz et al. 2004; Braden and McKernan, unpubl. data; see Table 5.2 in Chapter 5). These parasitism rates are higher than those reported at monitored sites across Arizona, which averaged 4, 5, 11, and 2% in 2000, 2001, 2002, and 2003, respectively (Paradzick et al. 2001; Smith et al. 2002, 2003, 2004). We observed the second consecutive year of no brood parasitism at Pahrnagat. Cowbird trapping and removal studies were initiated at all the life history studies in 2003, and we discuss trends in brood parasitism rates in detail in Chapter 5.

The effect of parasitism on nest fate was variable, but parasitism reduced the likelihood that a nest that contained flycatcher eggs would fledge flycatcher young. We observed seven nests in which the disappearance of flycatcher eggs coincided with the parasitism event. In these cases, cowbirds were suspected in ejecting the eggs. Female Brown-headed Cowbirds are known to physically attack willow flycatcher nestlings (Woodward and Stoleson 2002), remove single eggs, and occasionally destroy entire broods after laying is complete or after hatching (Lowther 1993 as cited in Woodward and Stoleson 2002). Therefore, it is also possible that some depredation events on eggs and nestlings are attributable to cowbirds. We also observed three nests that were parasitized prior to flycatcher eggs being laid and were subsequently abandoned. Thus, cowbird brood parasitism negatively affects overall flycatcher productivity by multiple mechanisms including interspecific nestling competition, depredation, and causing female flycatchers to expend energy renesting following parasitism events. Moreover, given that adult flycatchers exhibit high site fidelity to breeding areas (McKernan and Braden 2002, Koronkiewicz et al. 2004, this document) and renest most often after failed nests (Sedgwick 2000), females returning to sites with high brood parasitism are likely to reduce lifetime fecundity because they are expending energy on multiple failed nesting attempts over many years. Cowbird impacts to flycatcher populations may therefore be more severe than parasitism rates alone suggest. Because it is still unclear how brood parasitism rates affect flycatcher population sizes (Rothstein et al. 2003), baseline nesting studies in conjunction with cowbird control experiments 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

As presented in Koronkiewicz et al. (2004), comparing Mayfield survival probabilities (MSP) at the study areas with results from other studies may be somewhat problematic because of differences in the duration of nest stages (egg laying, incubation, and nestling stage) used in calculations. To determine the degree to which MSP comparisons can be made with other studies, we first calculated 2004 MSP at all study areas using the average flycatcher nest stages calculated by Rourke et al. (1999) and used by the Arizona Game and Fish Department (2.6, 12, and, 12.5 days for egg laying, incubation, and nestling stages, respectively). We then calculated 2004 MSP using the average flycatcher nest stages calculated at all study areas for 2003–2004 (2.22, 12.65, and 13.65 days for egg laying, incubation, and nestling stages, respectively), and compared the results. At each study area, the different methods resulted in differences in overall

MSP of less than two percent. Therefore, MSP comparisons between different study areas or across years in which different average nest stages are used can be used to evaluate broad trends in MSP.

Overall MSP (0.436) was similar to the overall MSP (0.383) reported at the life history study areas for 1997–2002 for the egg laying, incubation, and nestling stages (Braden and McKernan, unpubl. data). Overall MSP in 2004 was slightly lower than in 2003 (0.556) but was more consistent across study areas in 2004 than in 2003.