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EFFECTS OF MONOGAMY AND POLYGYNY ON REPRODUCTIVE SUCCESS IN SOUTHWESTERN WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII EXTIMUS*) IN ARIZONA

REBECCA F. DAVIDSON AND LINDA J. ALLISON

Abstract. We analyzed the reproductive consequences of a mixed mating strategy for the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) in central Arizona. We monitored 286 birds in 1998 and 1999; 243 active nests (including renests) were located. Of these, 124 (51%) were built by polygynously paired females. In 1998, 52% of all monitored females and 29% of monitored males were mated polygynously. In 1999, 59% of monitored females and 37% of monitored males were mated polygynously. Because sources of variability in reproductive success can be crucial in understanding the ability of endangered species to maintain stable or increasing populations, we examined whether mating status affected the probability of fledging one or more young or the number of young fledged. For females, none of our measures of reproductive success differed as a function of mating tactic; instead, female annual success showed significant between-year variability. The odds of a polygynous male fledging at least one young were 17.8 times greater than for monogamous males, and polygynous males fledged more young over the breeding season than did monogamous males. We interpret this difference as a simple function of the number of mates and/or nesting attempts, since average number of young per nest did not differ between monogamous and polygynous males. Mixed mating tactics also affect our ability to estimate population size of breeding adults. If polygyny occurs range wide, and at higher rates than previously suspected, simple use of male territorial song (assuming one female with every male) to estimate the number of birds at a site will underestimate population size.

Key Words: *Empidonax traillii extimus;* fledging success; mating systems; polygyny; reproduction; Southwestern Willow Flycatcher.

There is continuing development and elaboration of models to describe the evolution and maintenance of both monogamy and polygyny within single populations of birds (Verner and Willson 1966, Orians 1969, Emlen and Oring 1977, Searcy and Yasukawa 1989, Petit 1991, Soukup and Thompson 1997a, Johnson and Burley 1998). These models are built on the theory that mating systems are structured by male-male and female-female competition for resources and mates (Kempenaers 1995). The relative importance of intra-sexual competition depends on environmental features such as resource availability, quality, and distribution (Verner and Willson 1966), and on adult sex ratio (Smith et al. 1982). The mating system of a particular species is comprised of tactics that birds use under different situations (Johnson and Burley 1998). Here, we refer to polygynous and monogamous nesting as separate tactics.

Polygyny is generally assumed to be advantageous to males because polygynous males have the potential to produce more fledglings each breeding season (Wheelwright et al. 1992, Soukup and Thompson 1997b, Parish and Coulson 1998, Lubjuhn et al. 2000) and more recruits to future breeding populations (Carey and Nolan 1975, Soukup and Thompson 1997b). However, fitness consequences or trade-offs for females can be more difficult to assess (Smith et al. 1982, Bart and Tornes 1989, Petit 1991, Wheelright et al. 1992, Bensch 1996, Soukup and Thompson 1997a). Females may pair with an already mated male if male parental care contributes relatively little toward fledging success (Bart and Tornes 1989, Webster 1991, Parish and Coulson 1998), if territories of polygynous males contain higher quality habitat (Verner and Willson 1966, Orians 1969), if females are unable to discern pair status (Searcy and Yasukawa 1989), and/or if the genetic quality of the male is greater than that of unpaired males (Verner and Willson 1966, Soukup and Thompson 1997b, Slagsvold and Drevon 1999).

The Willow Flycatcher (*Empidonax traillii*) is considered a typically monogamous species (Sedgwick 2000), although polygyny has been reported in Canada (Prescott 1986), north-central Colorado and southeastern Oregon (Sedgwick and Knopf 1989, Sedgwick 2000), southern California (Whitfield et al. 1998), and on the lower Colorado River in Arizona and California (McKernan and Braden 2001). Within these populations, polygyny rates have been documented as high as 15% in Oregon, 50% in southern California (Sedgwick 2000), and 10% on the lower Colorado River (McKernan and Braden 2001).

To describe breeding status and reproductive consequences for monogamous and polygynous Southwestern Willow Flycatchers (*E. t. extimus*) in central Arizona, we compared their fledging

TABLE 1. ANNUAL MATING TACTIC INFORMATION FOR SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA

	1998			1999		
	San Pedro	Roosevelt	Combined	San Pedro	Roosevelt	Combined
Females						
Total	35	31	66	52	43	95
Monogamous	13 (37%)	19 (61%)	32 (48%)	15 (29%)	24 (56%)	43 (41%)
Polygynous	22 (63%)	12 (39%)	34 (52%)	37 (71%)	19 (44%)	56 (59%)
Males						
Total	26	28	54	35	34	69
Monogamous	13 (50%)	19 (68%)	32 (59%)	15 (43%)	23 (68%)	38 (55%)
Polygynous	10 (38%)	6 (21%)	16 (30%)	17 (48%)	9 (26%)	26 (38%)
Unmated	3 (12%)	3 (11%)	6 (11%)	3 (9%)	2 (6%)	5 (7%)
Active nests produced						
Total	63	43	106	79	58	137
By monogamous females	28 (24%)	29 (67%)	57 (54%)	27 (33%)	35 (60%)	62 (47%)
By polygynous females	35 (76%)	14 (33%)	49 (46%)	52 (66%)	23 (40%)	75 (53%)
Fledglings produced						
Total	92	70	162	93	76	169
By monogamous females	38 (41%)	40 (53%)	78 (48%)	33 (35%)	46 (61%)	79 (47%)
By polygynous females	54 (59%)	30 (43%)	84 (52%)	60 (65%)	30 (39%)	90 (53%)

success (probability of fledging one or more young), and the number of fledglings per nest and per breeding season. We also examined whether these measures of reproductive success differed between two breeding areas during the two years of the study.

METHODS

Data were collected during the breeding seasons of 1998 and 1999 as part of ongoing studies conducted at Roosevelt Lake (at the Salt River and Tonto Creek inflows) and the San Pedro and Gila Rivers (near the town of Winkelman), two of the largest Southwestern Willow Flycatcher breeding areas in Arizona (Paradzick and Woodward *this volume*). Cowbird trapping has been conducted within our study sites since 1996, and brood parasitism was < 1% in 1998 and 1999 (Paradzick et al. 1999, 2000). Vegetation in the study areas was comprised of varying proportions of native and exotic flora including saltcedar (*Tamarix ramosissima*), Goodding willow (*Salix gooddingii*), Fremont cottonwood (*Populus fremontii*), seepwillow (*Baccharis salicifolia*), and mesquite (*Prosopis* spp.).

Territorial males arriving on the breeding grounds were first located in late-April to early-May. As females began arriving in early-May, we followed pairing activities closely and conducted nest searches from mid-May through August. We monitored nests every two to four days following Rourke et al. (1999) and a modification of Martin et al. (1997). All nests in which at least one egg was laid were considered active.

A nest was defined as successful when one of four conditions were met: (1) one or more young were visually confirmed fledging from the nest or were located near the nest; (2) color banded adult flycatchers were seen feeding fledglings; (3) parents behaved as if dependent young were nearby when the nest was empty; and (4) nestlings were observed in the nest within two

TABLE 2. NEST SUCCESS OF MONOGAMOUS AND POLYGYNOUS SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA, 1998–1999

	Total	Monogamous	Polygynous
Active nests monitored	243	119	124
Successful nests (fledged ≥1 young)	138 (57%)	66 (55%)	72 (58%)
Unsuccessful nests	105 (43%)	53 (45%)	52 (42%)
Females	161	71	90
Successful (fledged ≥1 young season)	118 (73%)	52 (73%)	66 (73%)
Proportion of nests successful	0.61 ± 0.4 SD	0.65 ± 0.4 SD	0.58 ± 0.4 SD
Males	112	70	42
Successful (fledged ≥1 young season)	91 (81%)	50 (71%)	41 (98%)
Proportion of nests successful	0.61 ± 0.4 SD	0.63 ± 0.4 SD	0.58 ± 0.3 SD

TABLE 3. ODDS RATIOS OF THE LOGISTIC REGRESSION MODEL DESCRIBING FACTORS ASSOCIATED WITH FLEDGING SUCCESS (THE PROBABILITY OF FLEDGING ONE OR MORE YOUNG PER SEASON) OF SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA IN 1998 AND 1999

			Males			Females		
Factor	Baseline category (1)	Comparison category (2)	N (1)/(2)	Odds ratio for (2) vs. (1)	95% CI	N (1)/(2)	Odds ratio for (2) vs. (1)	95% CI
Mating tactic	Monogamy	Polygyny	70/42	17.8	2.2–141.7	71/90	1.1	0.5–2.3
Area	Winkelman	Roosevelt	55/57	0.4	0.1–1.1	87/74	1.1	0.5–2.3
Year	1998	1999	48/64	0.8	0.3–2.4	66/95	0.5	0.2–0.98

Notes: Analyses considered all nests for each male or female that successfully hatched young, including re-nests. Odds ratios describe the proportional change in the odds for every unit change in the variable, so odds of success for polygynous males were 17.8 times higher than for monogamous males. Odds of success for females in 1998 were two times (= 1/0.5) greater than in 1999. If the confidence interval for an odds ratio estimate includes 1, that variable is not associated with annual success ($\alpha = 0.05$).

days of the estimated fledge date. Nests not meeting these criteria, or from which eggs or nestlings were missing before hatch/fledgling dates, were considered unsuccessful. Similar criteria have been used in other studies (Conner et al. 1986, Patnode and White 1992, Martin et al. 1997, Drobney et al. 1998, Clotfelter and Yasukawa 1999). For each successful nest, we determined the number of young fledged.

Adult flycatchers were captured (per Sogge et al. 2001) and uniquely color banded by the U.S. Geological Survey. Throughout the breeding season, we confirmed the color band combination of each bird through multiple field observations by multiple observers, enabling us to describe pairing and breeding activities in each territory.

DESCRIBING MATING TACTICS

We defined monogamy as a mating tactic in which both male and female were mated to a single individual at any one time during the breeding season (Ford 1983, Møller 1986). Males were polygynous if more than one female nested simultaneously in the male's territory; females that mated with a polygynous male were also classified as polygynous. We identified each bird's mating tactic based on pair interactions, feeding behaviors, and nest placement within territories. Unbanded males and males with unconfirmed color bands were excluded from analyses along with their mates, because their mating tactic could not be determined. We were, however, able to determine mating tactic for many unbanded or unconfirmed females. Provided that their mates were banded, female mating tactic could be determined through observation of male interactions with females (or associated nests), and the combination of two or more nests found active concurrently within the same male's territory.

STATISTICAL ANALYSES

The large number of failed nests (usually late in the nesting cycle) resulted in a non-normal distribution for the number of fledged young per nest and adult. Therefore, in addition to calculating average productivity per nest and per breeding season for each sex and mating tactic, we proceeded through a series of hypothesis tests based on only successful nests to describe different components of productivity and their association with mating tactic. Activities of the same female or male in different years were treated as independent. All statistical tests were performed using SPSS for Windows (2000). ANOVA and logistic regression models were built starting with main effects and all possible interaction terms. Interaction terms with the largest non-significant ($\alpha = 0.05$) P-values were removed from the model sequentially; all main effects were retained in the iterative and final models. Each time, the model was rebuilt before evaluating statistical significance of the remaining interaction terms.

We used logistic regression to test whether nesting area (Roosevelt vs. Winkelman) or mating tactic was associated with fledging success (having at least one fledgling in a season), generating separate models for females and males, and including year as a blocking factor to account for between-year variability. Overall model fit was evaluated using the biserial correlation (Pearson's R; Pampel 2000) between observed and predicted success. We used the resulting odds ratios to estimate effect sizes on nesting success (Hosmer and Lemeshow 1989). We also calculated the proportion of nesting attempts that were successful, and used Fisher's Exact Test to examine whether the proportion of successful nests was independent of mating tactic.

To examine possible differences in the way mating tactic affects the ability of adults to maximize young fledged from otherwise intact nests (e.g., through parental care), we included only successful nests in our hypothesis test of factors related to number of young fledged per nest. We applied Fisher's Exact Test to the contingency table of number of young fledged by each adult using the two mating tactics over all nesting attempts in the breeding season. In the case of a significant hypothesis test, we interpreted the standardized residuals to describe how the distributions differed.

RESULTS

Seventy-five percent (286 of 380) of birds found within the nest monitoring sites in both 1998 and 1999 were included in these analyses based on color band identification and pairing confirmations. There were 112 mated, territorial, banded males (16 were monitored in both years); 80 of their 161 mates were banded (11 of which were monitored in both years). In both years, more than half of monitored females were mated with a polygynous male, and roughly one-third of males were polygynous (Table 1). Each year, some monitored males remained unpaired

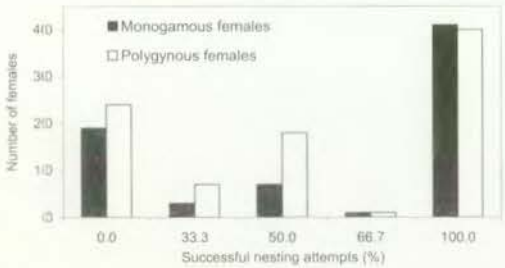

FIGURE 1. The number of monogamous and polygynous female Southwestern Willow Flycatchers experiencing different percentages of successful nesting attempts (i.e., nest fledged at least one young) in central Arizona, 1998–1999. Maximum number of nesting attempts = 3.

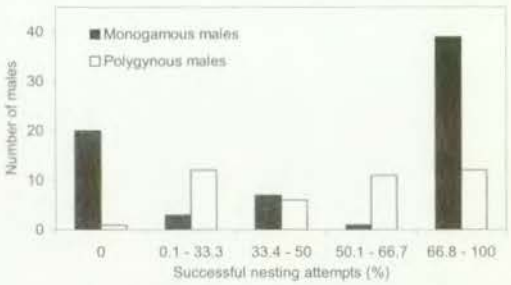

FIGURE 2. The number of monogamous and polygynous male Southwestern Willow Flycatchers experiencing different percentages of successful nesting attempts (i.e., nest fledged at least one young) in central Arizona, 1998–1999. Maximum number of nesting attempts = 7.

for the entire breeding season (Table 1). We located 243 active nests, of which 124 were built by polygynous females. At the San Pedro River, the majority of nests and fledglings were produced by polygynous females; at Roosevelt Lake, monogamous females built more of the nests and raised the majority of the fledglings (Table 1).

Fledging Success

Of the 243 active nests, 188 (77%) reached the nestling stage and 138 (57%) successfully fledged at least one bird. The majority of nests from both monogamous and polygynous matings were successful. Most (83 of 105) unsuccessful nests were attributed to predation.

Seventy-three percent of females fledged at least one young during the breeding season (Table 2). The logistic regression model did not indicate differences in fledging success between monogamous and polygynous females (χ^2 = 4.40, df = 3, P = 0.221; biserial correlation coefficient = 0.162; Table 3). Within each mating tactic, the proportion of successful nesting attempts did not differ by year or study area, so data were combined for testing differences by mating tactic. Monogamous females and polygynous females did not differ in expected nesting success (proportion of nesting attempts that were successful; Fisher's Exact Test, P = 0.266; Fig. 1; Table 2).

Eighty-one percent of males fledged at least one young during the breeding season (Table 2). The logistic regression model with main effects alone fit the data (χ^2 = 18.391, df = 3, P < 0.0005; biserial correlation coefficient = 0.371; Table 3) and no interaction effects were statistically significant. Polygynous males increased their odds of fledgling at least one young per season almost 18-fold over monogamous males (Table 3). Within each mating tactic, the proportion of successful nesting attempts did not differ by year or study area, so data were combined for testing differences by mating tactic. Despite the larger proportion of monogamous males that failed to fledge young, the proportion of successful nesting attempts was higher for monogamous than polygynous males (Fisher's Exact Test, P < 0.001; Table 2). Examination of standardized residuals indicated that polygynous males were much less likely to fail completely or to fledge young from all of their nests (Fig. 2).

Productivity

We confirmed the number of fledglings at 241 of the 243 monitored nests. Overall, 1.4 ± 0.09 SE (N = 241) young fledged per nest. Mating tactic was not significantly associated with per-nest productivity of successful females (Table 4), and successful monogamous and polygynous females had similar annual productivity (Table 5; Fig. 3). Productivity per nest was similar between monogamous and polygynous males. Although the pattern of differences depended on study year, annual productivity was consistently higher for polygynous males (Table 6). Among successful males, average number of fledglings at successful nests did not differ between mating tactics (Tables 4 and 6), but annual productivity was greater for polygynous males (Fisher's Exact Test, P <0.005 in 1998, P = 0.005 in 1999; Fig. 4).

DISCUSSION

The polygyny rates we documented were higher than reported for other Willow Flycatcher studies (Sedgwick 2000, McKernan and Braden 2001), but were comparable with those reported in southern California (Whitfield et al. 1998). Approximately half of our female population was associated with polygynous males each

TABLE 4. RESULTS OF ANOVA MODELS TESTING FOR DIFFERENCES IN AVERAGE NUMBER OF FLEDGLINGS PER SUCCESSFUL NEST FOR SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA IN 1998 AND 1999

	Males				Females			
Source	df	Mean square	F	P	df	Mean square	F	P
Mating tactic	1	0.020	0.039	0.847	1	0.002	0.004	0.953
Area	1	<0.0005	0.001	0.976	1	0.018	0.030	0.862
Year	1	0.070	0.137	0.712	1	0.898	1.53	0.218
Error	86	0.511			112	0.586		

year; therefore, the notion that Willow Flycatchers are largely monogamous should be reconsidered and better quantified in future studies. We found the likelihood of a female fledging at least one young over the season was independent of whether her mate was monogamous or polygynous. Instead, fledging success varied significantly from year to year ($P = 0.043$; Table 3), apparently as a function of causes other than mating system (e.g., nest predation, habitat quality, weather).

Because neither mating tactic affected female fledging success or productivity over the breeding season, there may be no strong selection for females to pursue a particular strategy at our study sites. Rather, females can apparently choose to be more flexible in their mating tactic, perhaps due to an inability to predict a male's paternal care (Wheelwright et al. 1992) and/or a poor correlation between a male's mating tactic and his assistance at the nest (Ettinger and King 1980, Slagsvold and Drevon 1999, Sedgwick 2000). If male parental care is minimal, and level of care is unpredictable (Sedgwick 2000), then males that occupy territories with better habitat, food supply, and nest sites may be more likely to attract multiple mates (Verner and Willson 1966, Soukup and Thompson 1997b, Slagsvold and Drevon 1999). The presence of unpaired territorial males during both breeding seasons suggests that females may choose among males and/or their territories (Bensch and Hasselquist 1992).

We found that fledging success (the probability of fledging one or more young) for males was improved for the breeding season by mating with more than one female, which is consistent with other studies (Smith et al. 1982, Wheelright et al. 1992, Kempenaers 1995, Soukup and Thompson 1997b, Lubjuhn et al. 2000). Polygynous males also fledged more young over the entire breeding season than did monogamous males. The pattern of differences was not the same across study years, however. In 1998, some polygynous males fledged up to nine young, compared to only four for monogamous males. In 1999, the maximum that were fledged was similar for the two mating tactics, but more monogamous males failed to fledge any young. Thus, the productivity of monogamous males appears to be more uncertain than that of polygynous males, for which multiple-mating decreases the odds of complete reproductive failure. Monogamous males had slightly higher per-nest success. In other avian species, monogamous and polygynous male tactics can include a trade-off, whereby polygynous males reduce parental care to acquire extra mates, even if it results in lower survival of nestlings per nest (Webster 1991, Soukup and Thompson 1997b). Unfortunately, comparative data are lacking on parental care by monogamous and polygynous male Willow Flycatchers. Ultimately, true reproductive success of both polygynous and monogamous males could be affected by factors that were not part of our study, such as extra-pair copulations and rates of offspring survival to breeding age.

Through analyses of only successful nests, we sought to determine if mating tactic influenced per-nest and/or annual productivity in nests that were not lost to predation or other factors. Such differences in productivity could arise through

TABLE 5. PRODUCTIVITY (PER NEST AND ANNUAL) OF FEMALE SOUTHWESTERN WILLOW FLYCATCHERS IN CENTRAL ARIZONA, 1998–1999

	Productivity per nest						Annual productivity	
	All nests of all females			Successful nests of successful females			All females	
Tactic	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI
Polygyny	1.5	1.2–1.7	90	2.5	2.3–2.7	66	2.2	1.8–2.5
Monogamy	1.6	1.3–1.9	71	2.5	2.3–2.7	52	2.1	1.7–2.5

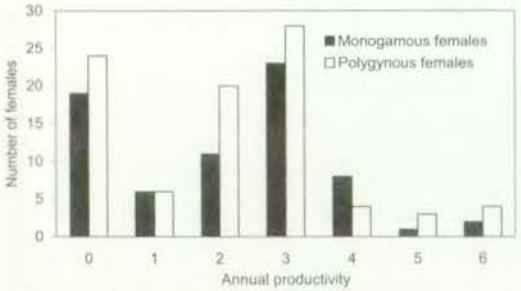

FIGURE 3. Annual productivity (total number of young fledged) for monogamous and polygynous female Southwestern Willow Flycatcher in central Arizona, 1998–1999.

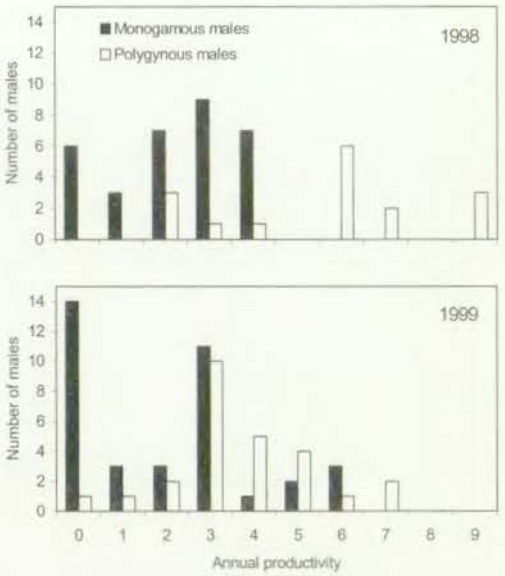

FIGURE 4. Annual productivity (total number of young fledged) for monogamous and polygynous male Southwestern Willow Flycatcher in central Arizona, 1998 and 1999.

differences in how monogamous and polygynous parents provide nestling care and/or protect against partial clutch losses (such as cowbird parasitism). However, neither male or female mating tactic significantly affected the number of fledglings per successful nest. Examining all nests (successful and unsuccessful), we also found that mating tactic did not influence the likelihood of a female failing to fledge young. Taken together, the lack of mating tactics effects suggest that male flycatchers may not play a major role in hatching or fledging of young. The same may not be true in other populations, especially where cowbird parasitism is more common and male nest defense therefore more important in deterring parasitism.

We found that the San Pedro River had higher rates of polygyny than Roosevelt Lake, and a sex ratio more strongly biased towards females. A more strongly biased sex ratio (Smith et al. 1982), as well as the distribution and quality of resources (Verner and Willson 1966, Emlen and Oring 1977), could influence an individual's mating tactic and therefore explain the differences in rates of polygyny between our study areas.

Management Implications

We do not know whether the high polygyny rates within our study areas are typical for the southwestern subspecies, or if they represent an adaptive strategy for members of a population in decline (Kunin and Gaston 1993). Polygyny may be advantageous for declining populations because within small populations of passerines, strictly monogamous species are more likely to suffer extirpation (Legendre et al. 1999). However, polygyny also results in lower effective population sizes (Nunney 1993), which may place endangered species in further genetic jeopardy. Small populations are also more likely to experienced unbalanced sex ratios, which could force some females to become polygynous despite any negative reproductive costs.

Considering the rates of polygyny that we documented, efforts to estimate the number of breeding flycatchers may be confounded by polygynous breeding and by fluctuating rates of polygyny from year to year. At our study sites, for example, surveyors assuming that each singing male represented only a breeding pair would have substantially underestimated the number of birds present. Underestimates would have been

TABLE 6. Productivity (per Nest and Annual) of Male Southwestern Willow Flycatchers in Central Arizona, 1998–1999

	Productivity per nest						Annual productivity					
	All males			Successful nests only			All males in 1998			All males in 1999		
Tactic	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N	$\bar{X}$	95% CI	N
Polygyny	1.5	1.3–1.8	42	2.5	2.3–2.7	41	5.6	4.3–6.9	16	3.7	3.0–4.3	26
Monogamy	1.6	1.3–1.9	70	2.5	2.2–2.7	49	2.2	1.7–2.8	32	2.0	1.3–2.7	38

more extreme at San Pedro (21% in 1998; 24% in 1999) than at Roosevelt (11% in 1998, 15% in 1999). Such site-specific differences in estimate errors are troubling, and demonstrate that estimates of the total number of flycatchers should not be based on singing males alone; accurate estimates require information on the number of nesting females as well. Between-site differences in levels of polygyny could exacerbate difficulties in comparing flycatcher counts among sites, if those counts are based only on singing males.

It is possible that longer-term studies may reveal more subtle effects of mating tactic on reproductive success of Southwestern Willow Flycatchers. As recovery efforts for this flycatcher continue, a better understanding of mating tactics and associated ramifications could prove important when evaluating the stability of populations into the future.

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