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Behavioral activities and breeding success of Willow Flycatchers in the Sierra Nevada

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BEHAVIORAL ACTIVITIES AND BREEDING SUCCESS OF WILLOW FLYCATCHERS IN THE SIERRA NEVADA

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ABSTRACT.—Observing survival and how individuals allocate time can provide insight into a species' ability to tolerate environmental constraints. We studied the Willow Flycatcher (*Empidonax traillii*) in the Sierra Nevada to determine if there were behavioral differences between pairs that successfully produced offspring and those that did not. This information will advance understanding of why these birds are declining in the Sierra Nevada and contribute to recommendations that may help to conserve them. We studied birds in 13 meadows in 2000 and 2001 using continuous focal-animal observations. Of the 43 territories we observed, 11 were occupied by males who never paired with a female, leaving 32 pairs for analysis. Of the 32 pairs, 13 were successful at breeding on their 1st attempt, and 9 pairs failed at their initial try but were successful on their 2nd breeding attempt. Throughout the breeding season, Willow Flycatchers spent 77%–78% of the day loafing during territory establishment and nest building, and loafing reached a low of 49% of the time budget during the nestling stage. Unsuccessful pairs spent on average 34% more time perching than their successful counterparts, while successful pairs spent on average 48% more of their time on the nest than unsuccessful pairs. Willow Flycatchers doubled the time spent foraging during the nestling phase because they had to meet the daily intake requirements for their young and themselves. Our results suggest that birds that spent more time on the nest and less time vocalizing had a significantly higher probability of successfully producing young because they were able to protect nests from predators, nest parasites, and inclement weather.

Key words: Willow Flycatcher, behavior, breeding success, foraging, Sierra Nevada.

The Willow Flycatcher (*Empidonax traillii*) was a common summer resident in California until the mid-1950s (Grinnell and Miller 1944) but has declined to a total state population of 300–400 individuals (Green et al. 2003). Loss of riparian vegetation has played a major role in reduction of the Willow Flycatcher population (Remsen 1978, Garrett and Dunn 1981). Over the last 150 years riparian ecosystems have been impacted by agricultural needs for fencing, lumber, fuel and irrigation, farming of natural levees, water diversions, grazing, and roads (Katibah 1984, Ratliff 1985, Kattelman and Embury 1996, Kondolf et al. 1996; see review by Green et al. 2003). Brown-headed Cowbird (*Molothrus ater*) nest parasitism may also negatively impact the Willow Flycatcher in California (Green et al. 2003).

Nest predation has been identified as the largest factor affecting Willow Flycatcher viability in the Sierra Nevada (Cain et al. 2003, Green et al. 2003). Weather influences the foraging behavior of insectivorous birds (Lederer 1972, Grubb 1979), disturbs the availability and distribution of their invertebrate diet (Digby 1958, Taylor 1963), and can physically destroy nests (Green et al. 2003). Thus, weather could potentially impede the availability of prey for this insectivorous bird and be a possible factor in reducing Willow Flycatcher nest success (Flett and Sanders 1987).

Observing behavior, reproductive success, and time allocation can provide insight into a species' ability to survive under particular constraints (such as habitat loss and nest predation) and can allow for an evaluation of its tolerance to such constraints (Menon and Poirier 1996). The survival and reproductive success of an organism are dependent upon the partitioning of time into activities (e.g., foraging and perching; Cody 1966, King 1974, Lunberg 1985, Zicus and Hennes 1993). Lunberg (1985) stated that constraints on diurnal birds are due not only to seasonal variation but also to the number of daylight hours available for necessary daily activities like foraging. If time is allocated

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poorly, or if inclement weather or other abiotic factors prevent optimal time allocation, necessary activities cannot occur and fitness can be lowered.

Ettinger and King (1980) conducted a study of a stable population of *Empidonax traillii brewsteri* in Washington. The population they studied was free of any serious environmental pressures such as heavy cattle grazing or an influx of Brown-headed Cowbirds. They found that throughout the breeding season, male Willow Flycatchers spent most of their time perching. Much less of the males' time was spent singing and even less was allocated to flying. Both the males and females spent a large amount of time "loafing" throughout the breeding season. Ettinger and King (1980) argued that this uncommitted time would allow the birds to cope with poor weather or food shortages.

Our goal was to determine if there were behavioral differences between pairs that successfully produced offspring and those that did not. We did this by (1) locating pairs and monitoring nest success, (2) collecting information on environmental conditions, and (3) measuring time budgets of adult Willow Flycatchers. The analysis of this information will aid in understanding why these birds are declining in the Sierra Nevada and will contribute to recommendations that may help to conserve them.

STUDY AREA

In 1999 we surveyed 20 sites in the Sierra Nevada for the presence of Willow Flycatcher pairs, with only 13 containing the species (Fig. 1). During our study we analyzed these 13 sites, which were located within meadows at Perazzo Meadows, Lacey Valley (Sierra County), Carpenter Valley (Nevada County), Grass Lake (El Dorado County), and Red Lake (Alpine County). These meadows are dispersed across approximately 1.2 million ha in the north central Sierra Nevada and contain approximately one-third of the Sierra Nevada's Willow Flycatchers (Bombay et al. 2003, Green et al. 2003).

Throughout this region temperatures are known to range between 0°C (especially at night) and 33°C (Western Regional Climate Center, Reno, Nevada [online http://www.wrcc.dri.edu/index.html]) in July and August. Yearly precipitation varies between 36 cm on the eastern slope and 205 cm on the western slope (Bombay 1999). Most of this precipitation falls as snow between November and May, with an occasional heavy snowstorm or rainstorm through the end of June. Meadow vegetation is composed of sedges (*Carex* spp.), rushes (*Juncus* spp.), and grasses. The riparian shrub community is predominated by willow (*Salix* spp.), while the tree community is mainly lodgepole pine (*Pinus contorta*).

METHODS

Territory and Nest Location and Monitoring

We determined territory boundaries using tape playback of male calls. When a Willow Flycatcher was detected, we recorded distance, direction, type of detection, and sex. Using that information, we then mapped the territory. The outermost observed song perches were assumed to be the outermost portion of the territory (Flett and Sanders 1987).

We chose territories for the time budget observations of Willow Flycatchers. On the larger sites, territories were chosen to represent different areas of the meadow (i.e., they were not clumped next to each other). Nests were monitored every 5–7 days and the number of eggs or chicks and any physical disturbances were recorded. A territory was considered reproductively successful if it fledged 1 or more young. Individuals were considered unsuccessful if the nest did not generate offspring.

Time Budgets of Adults

We observed birds in 43 different territories between 1 June and 24 August 2000 and 2001, 23 in 2000 and 20 in 2001. Due to high site fidelity of both male and female Willow Flycatchers (Walkinshaw 1966, Stafford and Valentine 1985), territories that we observed during the 1st year of study had a high probability of containing the same individuals the following year and therefore were not observed during the 2nd field season. Eleven of these 43 territories contained males that never shared the territory with a female, leaving 32 viable pairs for analysis.

The breeding season was divided into the 5 phases of the reproductive cycle as detailed in Ettinger and King (1980). Previous studies of the Willow Flycatcher set in the central Sierra

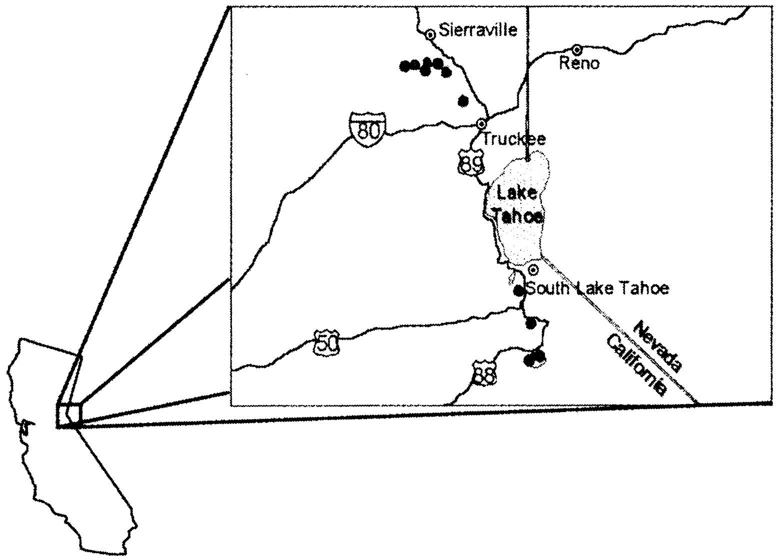

Fig. 1. Location of meadows with Willow Flycatcher pairs observed during 2000–2001, Sierra Nevada, California.

Nevada have established an estimated time for each phase (Flett and Sanders 1987, Harris et al. 1987, Sanders and Flett 1989, Bombay 1999). Phase 1: Arrival of males and establishment of territories occurs between late May and mid-June. Phase 2: Nest-construction period occurs in mid-June. Phase 3: Egg laying occurs between mid-June and mid-July. Phase 4: Incubation occurs between mid-June and mid-July. Phase 5: Nestling period occurs between mid-July and late August.

All Willow Flycatcher pairs do not concurrently pass through the different phases of the reproductive cycle because nests may fail mid-cycle, and re-nesting attempts put them back near the beginning of the cycle. Due to this overlap of phases between pairs, the current phase of each observed individual was assessed on a case-by-case basis.

Each territory selected was observed 3 times during each of the phases of the breeding season, and sessions were divided between early morning, midday, and evening. The result was that all parts of the day and season were equally represented in the final analysis (Harcourt and Stewart 1984).

We used continuous focal-animal observations (Altmann 1974, Martin and Bateson 1993) to record behaviors. Since this is a sexually monochromatic species (Verner and Wilson 1969) and the birds were not color banded, we attempted to identify individuals as male or female on the basis of behavior (Prescott and Middleton 1988). If differentiation between male and female was not possible, then the individual monitored in the selected territory was classified as unknown. If possible, adults were categorized into males establishing territories, females building nests, males paired to females building nests, females laying eggs, males paired to females laying eggs, incubating females, males paired to incubating females, females and males feeding nestlings, and males and females feeding fledglings (Sullivan 1990).

We maintained a distance of approximately 30 m from the bird, which allowed the focal bird to move both toward and away from the observer (Sullivan 1990, Mock 1991). Activity was monitored continuously until we had recorded a total of 15 minutes of bird activity. If the focal individual moved out of sight, recording ceased until the individual returned into view, at which time recording began again. Using a stopwatch, we recorded start and stop times for the following 10 activities for adults: (1) aerial chases—chasing intruders; (2) interactions—courtship flights, copulation, displays, interactions between males and females; (3) flying (>2 seconds)—flights longer than 2 seconds; (4) short flights (<2 seconds)—flights shorter than 2 seconds; (5) perching—perched and alert, also called loafing; (6) foraging—

includes hawking and the consumption of prey; (7) preening—grooming; (8) incubating eggs (on nest)—sitting on eggs, nestlings, or both; (9) feeding nestlings—the actual feeding of the young in the nest; (10) feeding fledglings—the feeding of young who have fledged.

We used a Dwyer hand-held wind meter for wind speed and a thermometer for temperature during each observation session (Bakken 1976, Mock 1991, Hinsley and Ferns 1994). We estimated cloud cover as a percentage, and precipitation was visually estimated in terms of percent of time it rained at the time of each observation.

Statistical Analyses

We pooled data from the 2 breeding seasons, combined sexes, and combined morning, midday, and evening observations for each territory within each phase to equally depict all parts of the Willow Flycatchers' daily activities. We then converted those data to fractions of time spent in each activity and tabulated data within each of the phases for successful and unsuccessful pairs to determine the mean percent of time spent in each activity. Parametric statistics were used because our data met the relevant assumptions (Zar 1999). We compared the means of the fractions of time spent in each activity in each phase between successful and unsuccessful pairs using a t test (Zar 1999), which was used to determine if there was a statistically significant difference between the behavior of birds within successful and those within unsuccessful pairs across phases. We performed simple linear regression (Zar 1999) to determine if there was a relationship between the rates of activities (dependent variable) and the environmental factors of wind speed, ambient temperature, cloud cover, and precipitation (independent variables). We considered correlations low if $r \leq 0.25$, moderate when $0.25 < r < 0.50$, and highly correlated if $r \geq 0.50$. We set α at 0.11 (Zar 1999:82). We did not conduct factorial ANOVA or multiple regression because of variable and relatively small sample sizes in many categories.

RESULTS

Of the 43 territories we observed, 11 consisted of males who never paired with a female, leaving 32 pairs for analysis. Ten territories contained pairs that were unsuccessful at breeding. Of the 32 pairs, 13 were successful at breeding on their 1st attempt. Nine pairs failed at their 1st try but were successful on their 2nd breeding attempt. In 2001 there were 5 more unpaired males in our sample than the previous year. Failures occurred during the nest-building, incubation, and nestling phases. Reasons for failure in the nest-building phase are unknown. Predation and brood parasitism contributed to failure in the incubation and nestling phases.

Throughout the breeding season, Willow Flycatchers spent the majority of time perching (Table 1). An average of 78% and 77%, respectively, of the day was spent loafing during territory establishment and nest building, which dropped to a low of 49% during the nestling phase.

The average amount of time singing varied throughout the season, with a high of 22% of the time budget during egg laying and a low of 5% during the nestling phase. Foraging comprised on average approximately 2% of the day across the breeding season until the nestling phase, when the average jumped to 4.9%, more than twice the average for the other breeding phases. Less than 1% of the time was spent in aerial chases, preening, or interactions (Table 1).

There were no statistically significant differences in behavior between successful and unsuccessful pairs during the nest-building stage (Table 2). During the incubation stage, however, there was a significant difference between time spent singing, perching, and on the nest. Unsuccessful pairs spent on average 14% more time each day singing than did successful pairs ($t = 2.51$, $P = 0.016$). Unsuccessful pairs spent on average 34% more of the entire time budget perching than their successful counterparts ($t = 3.0$, $P = 0.005$). Successful pairs spent on average 48% more of their time on the nest than unsuccessful pairs ($t = 3.1$, $P = 0.004$).

During the nestling phase there was only a moderate and nearly significant difference between successful and unsuccessful pairs and their average time perching. Unsuccessful pairs spent approximately 11% more time during the day perching during this phase ($t = 2.03$, $P = 0.055$).

In analyzing the observed activities for correlations with environmental conditions, we found that during territory establishment there was a high positive correlation between wind

TABLE 1. Average percent time spent by Willow Flycatchers in activities during the breeding season (2000–2001) for all territories. *N* is the number of territories observed.

	N	Aerial chases		Flying		Short flights		Singing		Preening	
		% time	*s*	% time	*s*	% time	*s*	% time	*s*	% time	*s*
Territory establishment	9	0.0	0.0	4.6	2.7	2.7	1.7	13.1	6.1	0.5	1.0
Nest building	28	0.03	0.1	6.9	3.7	2.3	4.8	10.2	18	1.0	1.8
Egg laying	12	0.1	0.3	7.9	10.1	0.5	0.6	21.8	30.3	0.5	0.9
Incubation	39	0.02	0.09	2.9	1.9	0.7	0.7	8.4	9.3	1.1	3.7
Nestling	25	0.1	0.4	5.8	3.5	1.4	1.4	4.9	8.8	0.1	0.4

	N	Perching		Foraging		Interactions		Incubation		Feeding nestlings	
		% time	*s*	% time	*s*	% time	*s*	% time	*s*	% time	*s*
Territory establishment	9	77.9	7.7	2.1	1.7	0.1	0.3	na[a]	na	na	na
Nest building	28	76.8	16.7	2.1	1.7	0.6	0.9	0.7	2.5	0.01	0.1
Egg laying	12	61.1	31.1	0.6	1.4	0.7	1.4	7.0	16.3	na	na
Incubation	39	51.0	30.9	2.1	3.8	0.3	0.6	33.5	37.8	na	na
Nestling	25	48.5	22.8	4.9	4.7	0.1	0.3	15.6	23.3	14.1	19.2

[a]na = not applicable

speed and short flights (r = 0.69, P < 0.001) and between temperature and perching (r = 0.64, P < 0.001; Table 3). There were moderate positive correlations between wind speed and perching (r = 0.35, P = 0.09) and between cloud cover and perching (r = 0.37, P = 0.08). There was a high negative correlation between temperature and singing (r = –0.76, P < 0.001) and a moderate negative correlation between wind speed and flying (r = –0.33, P = 0.10) and singing (r = –0.41, P = 0.06).

During the nest-building phase there was a positive correlation between temperature and foraging (r = 0.28, P = 0.03). High positive correlations between preening and wind speed (r = 0.72, P = 0.00) and cloud cover (r = 0.49, P = 0.04) were observed during the egg-laying phase, as well as a moderate correlation between interactions and temperature (r = 0.36, P = 0.10).

Throughout the incubation phase there were positive correlations between temperature and foraging (r = 0.23, P = 0.02), interactions (r = 0.19, P = 0.04), and time on the nest (r = 0.26, P = 0.01); between wind speed and aerial chases (r = 0.34, P = 0.00); and between cloud cover and flying (r = 0.21, P = 0.03). There were low positive correlations between wind speed and singing, cloud cover and preening (r = 0.15, P = 0.08), and temperature and preening (r = 0.13, P = 0.10). There were negative correlations between temperature and short flights (r = –0.19, P = 0.04), singing (r = –0.24, P = 0.01), and perching (r = –0.26, P = 0.01), and there was a low negative correlation between wind speed and singing (r = –0.17, P = 0.05).

For the duration of the nestling phase, there were positive correlations between wind speed and time on the nest (r = 0.17, P = 0.11) and between temperature and foraging (r = 0.19, P = 0.09). There were moderate negative correlations between temperature and aerial chases (r = –0.27, P = 0.03) and preening (r = –0.25, P = 0.04) and low negative correlations between wind speed and aerial chases (r = –0.18, P = 0.10) and short flights (r = –0.23, P = 0.05).

DISCUSSION

Throughout the breeding season the Willow Flycatcher spends most of its day perching.

TABLE 2. Differences in behavior for successful and unsuccessful Willow Flycatcher territories during the 2000 and 2001 breeding seasons. Only nesting phases in which birds failed are presented.

		Successful		Unsuccessful			
Activity	df	% time	*s*	% time	*s*	*t*	*P*
NEST BUILDING	32						
Aerial chases		0.1	0.174	0	0.071	0.184	0.854
Flying		8.6	3.72	6.5	2.56	0.145	0.887
Short flights		1.1	4.78	1.1	0.72	0.46	0.649
Singing		10.4	17.9	7.3	9.51	0.089	0.931
Preening		0.7	1.73	0.3	0.295	0.903	0.373
Perching		78.7	17.9	82.4	7.87	0.45	0.655
Foraging		2.1	1.71	2.1	2.01	0.65	0.52
Interactions		0.5	0.77	0.5	0.417	0.06	0.948
Incubation/On nest		0	9.49	0	0	0.474	0.638
INCUBATION	38						
Aerial chases		0	0.116	0	0.012	1.03	0.306
Flying		2.8	1.88	4	2.14	0.084	0.934
Short flights		0.6	0.547	0.4	0.875	0.421	0.676
Singing		4.8	10.1	19	6.57	2.51	0.016**
Preening		0.6	4.64	0.1	0.91	1.06	0.29
Perching		34.4	29.9	68.3	21.3	3	0.005**
Foraging		2.1	1.51	1.6	5.41	0.82	0.416
Interactions		0.2	0.478	0.1	0.685	0.83	0.411
Incubation/On nest		54.6	36.7	6.3	25.8	3.1	0.004**
NESTLING	22						
Aerial chases		0	0.408	0	0	0.405	0.69
Flying		5.6	3.73	3.8	2.46	0.43	0.672
Short flights		1.1	1.49	1.2	0.784	0.709	0.485
Singing		4.2	9.43	2.5	3.41	0.494	0.626
Preening		0.1	0.443	0.1	0.258	0.032	0.982
Perching		40.8	20.6	51.8	29.4	2.03	0.055*
Foraging		5.5	4.98	3.7	1.94	0.769	0.45
Interactions		0.1	0.28	0	0	1.02	0.317
Incubation/On nest		17.6	23.3	31	21.4	0.148	0.884
Feed nestlings		22	20.6	8.5	5.78	0.823	0.41

** $P < 0.05$
* $0.05 < P < 0.11$

This observation concurs with those of Ettinger and King (1980) and Prescott and Middleton (1988). Schoener (1971) first defined the concept of "time minimizers" as organisms that minimize foraging time (and therefore increase loafing time) and consequently maximize their fitness. As with Willow Flycatchers, time minimizers do not gain in terms of reproduction by increasing their foraging time since they have a fixed reproductive output (Schoener 1971). Prescott and Middleton (1988) showed that increasing food availability in Willow Flycatcher territories did not increase reproductive output. They believe that breeding insectivorous passerines, like the Willow Flycatcher, maintain a large portion of uncommitted time (i.e., perching or loafing) and that this allocation is thought to lessen the impact brought about by short-term variations in food supply and competitive pressures. This evolved behavior has helped the Willow Flycatcher survive under unpredictable adverse situations.

Willow Flycatchers doubled the time spent foraging during the nestling phase over the other 4 phases because during this time they had to meet the daily intake requirements of not only themselves but their young as well. In their time budget studies on breeding birds, both Sullivan (1990) and Mock (1991) found a doubling of foraging time during the feeding of nestlings. This shift in daily time budgets is necessary for survival of the parents and their rapidly growing young. Since Willow Flycatchers spent such a large proportion of their time budget perching, they had ample available time to make this adjustment to their time allocation during the nestling phase.

TABLE 3. Correlations between environmental conditions and time Willow Flycatchers spent in different activities. Results are divided into the 5 different breeding phases.

	Wind speed	Cloud cover	Temperature	Precipitation
TERRITORY ESTABLISHMENT				
Aerial chases	na[a]	na	na	na
Flying	–0.33*	–0.11	–0.32	na
Short flights	0.69**	–0.20	0.20	na
Singing	–0.41*	–0.26	–0.76**	na
Preening	–0.13	–0.08	0.26	na
Perching	0.35*	0.37*	0.64**	na
Foraging	–0.14	–0.30	–0.04	na
Interactions	–0.13	–0.07	0.27	na
On nest	na	na	na	na
Feeding nestlings	na	na	na	na
NEST BUILDING				
Aerial chases	–0.20	–0.14	–0.16	–0.03
Flying	0.19	–0.01	0.05	0.06
Short flights	–0.13	–0.12	–0.09	–0.01
Singing	0.07	0.08	–0.01	0.07
Preening	–0.03	–0.14	–0.19	–0.05
Perching	–0.12	–0.07	0.004	–0.07
Foraging	–0.01	0.05	0.28**	–0.12
Interactions	0.09	–0.05	0.01	–0.05
On nest	–0.09	0.06	0.02	–0.24
Feeding nestlings	na	na	na	na
EGG LAYING				
Aerial chases	–0.15	0.12	0.13	na
Flying	0.12	–0.16	0.19	na
Short flights	–0.09	0.04	0.26	na
Singing	–0.05	–0.31	–0.20	na
Preening	0.72**	0.49**	–0.13	na
Perching	0.25	0.08	–0.05	na
Foraging	–0.18	0.09	0.19	na
Interactions	0.20	–0.28	0.36*	na
On nest	–0.32	0.27	0.17	na
Feeding nestlings	na	na	na	na
INCUBATION				
Aerial chases	0.34**	0.09	0.04	–0.02
Flying	0.09	0.21**	–0.06	0.02
Short flights	–0.00	–0.04	–0.19**	0.00
Singing	–0.17*	–0.06	–0.24**	0.02
Preening	0.13	0.15*	0.13*	–0.02
Perching	–0.12	0.08	–0.26**	0.10
Foraging	–0.02	–0.04	0.23**	–0.04
Interactions	0.10	0.08	0.19**	–0.02
On nest	0.11	–0.12	0.26**	–0.09
Feeding nestlings	na	na	na	na
NESTLING				
Aerial chases	–0.18*	0.01	–0.27**	na
Flying	–0.08	0.21	–0.02	na
Short flights	–0.23*	–0.06	–0.15	na
Singing	0.07	–0.01	–0.02	na
Preening	–0.09	–0.10	–0.25**	na
Perching	0.03	0.13	–0.01	na
Foraging	–0.15	–0.12	0.19*	na
Interactions	–0.13	–0.04	0.06	na
On nest	0.17*	–0.02	–0.08	na
Feeding nestlings	–0.15	–0.11	0.10	na

[a]na = not applicable
** $P < 0.05$
* $0.05 < P < 0.11$

The average amount of time spent singing varied throughout the breeding season, reaching a peak during the egg-laying phase and then dropping substantially during the incubation and nestling phases. Our results are probably biased to some degree toward males because they were easier to observe prior to the nestling stage. In her study of Yellow-eyed Juncos (*Junco phaeonotus*), Sullivan (1990) also found that the time spent singing significantly decreased when birds began feeding nestlings. During the nestling phase, time allocation is modified to accommodate the pressures of feeding dependent young, and therefore less time can be allocated to activities such as singing and self-maintenance (Martin 1987).

Pairs that successfully made it through the incubation stage contained individuals that spent on average less time singing and perching and more time on the nest than pairs that were unsuccessful during that stage. Successful counterparts were more inconspicuous, spending 48% more time on the nest and out of site. Breeding birds can reduce the probability of predation by perching near or on the nest to guard and defend it (Ricklefs 1969, Nilsson 1986, Martin and Li 1992). These studies found that breeding birds that spend more time near or on the nest significantly decrease the probability of nest predation and therefore increase nesting success.

Uyehara and Narins (1995) found that the median vocalization rate of Willow Flycatchers at cowbird-parasitized nests was significantly higher than at unparasitized nests. They found that the presence of cowbirds in flycatchers' territories did not account for the difference in parasitism. Rather, nests were more likely to be parasitized if the birds were "noisy" and calling out at a greater frequency. In our study population, birds that were unsuccessful in the incubation phase spent 14% more of the total time budget singing than successful pairs. Between the predators and the brood parasites, the more time parents spent out in the open, calling attention to themselves and the nest area, the likelier they were to be unsuccessful at their breeding attempt.

During the nestling phase there was a continuation of the trend of unsuccessful individuals spending more time perching. Although unsuccessful birds spent on average 11% more total time perching, it was enough to differentiate them from their successful counterparts. Komdeur and Kats (1999) determined that the rate of egg loss from unattended warbler nests was 7 times as high as attended nests. The more nest attendance that occurred, the lower the rate of egg loss and hence the higher the nest success.

Our results suggest that Willow Flycatchers should allocate as much time as possible to be at or near the nest and should reduce vocalizations and flights to defend the nests and the young from predators or brood parasites. We also demonstrated that birds that spent more time on the nest and less time vocalizing had a significantly higher probability of successfully producing young.

During 3 of the 5 phases of the breeding season, temperature increase was correlated with increased foraging. This was likely due to the insectivorous diet of the Willow Flycatcher. Because they are exothermic individuals, insects exhibit a slowdown of their physiological processes at lower temperatures (Borror et al. 1989). Consequently, insect supply in a meadow is dependent upon time of day and weather. As the temperature increases, more insects are able to maintain activity and move about, providing Willow Flycatchers with foraging opportunities. Additionally, as environmental conditions became extreme (i.e., hot, cold, windy), males did not allocate much energy and time to activities such as singing and longer flights. As temperature increased during the nestling phase, adults decreased aerial chases and preening and increased foraging. This was likely because Willow Flycatchers had nestlings that needed to be tended. Because of the need to forage and feed young, and the fact that insect availability is related to temperature, adult Willow Flycatchers allocated more of their time to foraging as temperature increased and did not have available time or energy to chase off other birds or participate in self-maintenance activities such as preening. It is also likely that by this phase in the breeding season, defending their whole territory was less critical, hence the reduction in aerial chases.

Thus, our study showed that time allocations varied between successful and unsuccessful nesting attempts, at least in part because adults were able to protect nests from predators, nest parasites, and inclement weather. In degraded habitats birds are likely to allocate time and energy to activities that take away from foraging and territory (nest) defense. Our study lends insight into the mechanisms driving reproductive success and identifies several factors that can be manipulated by resource managers to potentially enhance populations of Willow Flycatchers. For example, managing populations of nest parasites and enhancing meadows through restoration to improve food abundance could alter flycatcher activity budgets.

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